GENETIC AND FUNCTIONAL CHARACTERIZATION OF THE 'CANARIAN CAMEL' BREED

CARACTERIZACIÓN GENÉTICA Y FUNCIONAL DE LA RAZA 'CAMELLO CANARIO'

DOCTORAL THESIS

Carlos Iglesias Pastrana

Doctoral Programme in *Natural Resources and Sustainable Management*

Supervisors: Juan Vicente Delgado Bermejo, Francisco Javier Navas González and Elena Ciani

Córdoba, 2023

TITULO: *Genetic and functional characterization of the ?Canarian Camel? breed*

AUTOR: *Carlos Iglesias Pastrana*

© Edita: UCOPress. 2023
Campus de Rabanales
Ctra. Nacional IV, Km. 396 A
14071 Córdoba

https://www.uco.es/ucopress/index.php/es/
ucopress@uco.es

«Distrust any project that does not start from an emotion»

REASONED REPORT OF THE THESIS ADVISORS

Ph.D. student
Carlos Iglesias Pastrana

Thesis title
Genetic and functional characterization of the 'Canarian Camel' breed

Reasoned report of the thesis advisors

All the directors participating in the present Ph.D. thesis have extensive experience in doctoral training, and we must emphasize here that the work carried out by the doctoral candidate, Carlos Iglesias Pastrana, has notably exceeded the results achieved in our career as doctoral thesis advisors.

The thesis posed a challenge due to its dedication to a species with currently unknown and poorly defined functional interest, with limited presence in the national sector and little general scientific interest to date. Thanks to the dedication, hard work, and passion of the candidate, it grew to surprising proportions, becoming the most spectacular thesis we have supervised in our careers.

To support these words, it is sufficient to provide a brief quantitative overview. The thesis has generated seventeen articles indexed in JCR, seven of which have already been published in top-quartile journals (one in the top decile), and ten submitted to journals of the same category. In addition, external collaboration on the thesis content resulted in three chapters of the book '*Dromedary camel behaviour and welfare: camel-friendly management practices*'.

Furthermore, the thesis has led to four articles in international journals indexed in databases other than Web Of Science JCR, but highly prestigious in the field.

Advances from these results have been presented at various international events in the form of twenty-nine communications. Five of them as posters and twenty-four as oral presentations, of which three were invited talks at events in Saudi Arabia, Algeria, and Spain, with funding from the university covering all candidate expenses.

Likewise, the doctoral candidate has not forgotten to transfer the results to the industry, accomplishing this with the publication of two popular science articles and the development of five interviews or informative videos.

With all that has been presented, we can only express our pride in having supervised this outstanding doctoral thesis and our gratitude to the candidate. Before confirming our unanimous agreement on the maturity of the thesis and the candidate's readiness for the defense.

In light of all this, the presentation of the doctoral thesis is authorized.

Cordoba, 14th September 2023

The Doctoral Thesis Advisors

Juan Vicente Delgado Bermejo   Francisco Javier Navas González   Elena Ciani

The present doctoral thesis has been developed under the joint supervision of the University of Cordoba (Cordoba, Spain) and the University of Bari 'Aldo Moro' (Bari, Italy):

Dr. Juan Vicente Delgado Bermejo

Dr. Francisco Javier Navas González

Department of Genetics, Faculty of Veterinary Sciences, University of Cordoba, Cordoba, Spain

Dr. Elena Ciani

Department of Biosciences, Biotechnologies and Environment, University of Bari 'Aldo Moro', Bari, Italy

FUNDING

The experimental studies and short-term mobilities carried out during the development of the present doctoral thesis have been funded by:

- FPU-PhD Fellowship (FPU19/00103) – Spanish Ministry of Universities.
- Pre-doctoral Contracts UCO 2019 – University of Cordoba (Cordoba, Spain).
- Erasmus+ KA107 Program.
- Fellowships for International Research Stays, Academic Course 2020/2021 – University of Cordoba (Cordoba, Spain).
- European Union-funded project 'CARAVAN' (Toward a Camel Transnational Value Chain).
- European Union-funded project 'CAMEL-SHIELD' (Camel breeding systems: actors in the sustainable economic development of the northern Sahara territories through innovative strategies for natural resource management and marketing).

ACKNOWLEDGEMENTS

I extend my profound gratitude and heartfelt appreciation to the numerous individuals, public and private institutions, and sources that have enriched my path to completing the present doctoral thesis. Their support, guidance, and encouragement have been instrumental in shaping this research work.

Foremost, I express my deepest appreciation to my esteemed advisors, whose unwavering commitment, expert guidance, and scholarly insights have been invaluable throughout this research endeavor. Your patient mentorship and dedication have not only refined my academic acumen and acted as a constant source of inspiration but have also set a high standard for intellectual rigor.

My gratitude extends to the staff of the AGR-218 Research Group from the University of Cordoba (Spain), ‘Animal Breeding and Genetics’ Research Group from the University of Bari ‘Aldo Moro’ (Italy), and the ‘Animal Breeding and Genetics’ Research Group from the University of the Republic (Uruguay), whose dedication to fostering a vibrant academic community has provided an intellectually stimulating environment for my growth as a scholar.

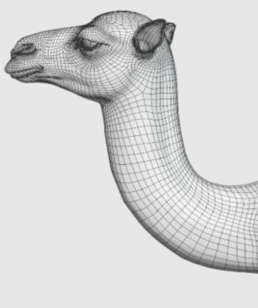
I wish to acknowledge the Spanish Ministry of Universities, the University of Cordoba, the University of Bari ‘Aldo Moro’, and the European Union for their financial support, which enabled the execution of this research with the necessary resources and facilities.

I am equally indebted to the camel farms, technical support personnel, and veterinary students that have generously contributed to the empirical foundation, progression, and completion of the present research work. Their integral involvement has led to intellectual discussions and innovative breakthroughs that have broadened my perspectives and elevated the quality of the doctoral thesis.

To my dearest family and friends, your support, enduring patience and understanding, and collaborative spirit have sustained me through the challenges of this academic pursuit. You all have provided me with the best emotional foundation for my aspirations.

Last, I want to highlight the most important lesson learned from the animal species that is the object of this work: you have to invest the necessary energy in what is truly necessary, with the best resource optimization. What is the same, only the precious deserves the consideration of essential.

With gratitude,
Carlos



GENERAL INDEX

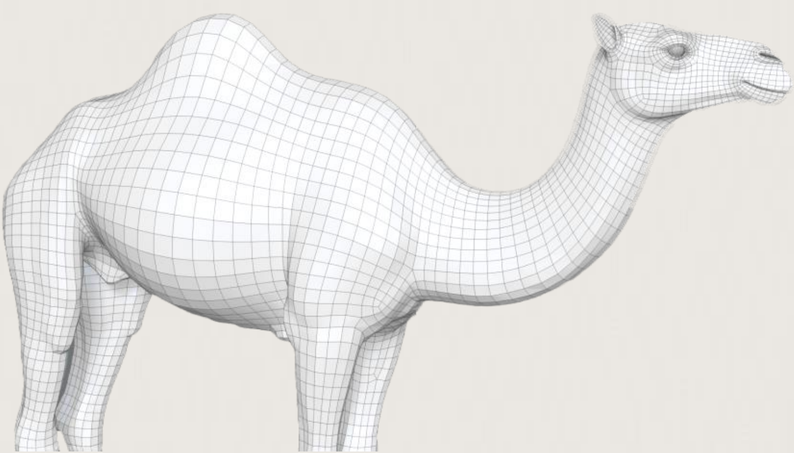
The present doctoral thesis aimed at the phenotypic/functional and genetic characterization of 'Canarian Camel' breed arises from the need to define new selection criteria for the genetic improvement and conservation of the only camel breed in Europe, officially declared at risk of extinction. Its main habitat distribution is the Canary Islands (Spain), with whose socio-economic development and cultural heritage the camel has been associated since the beginning of the 15th century. Despite its conservation status, this unique genetic resource lacks a systematic evaluation of phenotypic/functional characters and standardization of genealogical registries.

This doctoral thesis contains original research works for the standardized characterization of those phenotypic traits (zoometrics, biomechanics, and behaviour) that greatly shape the main current functional destination of the camel breed studied: camelback leisure riding tours. Since this functionality involves direct interaction with the customer in a specific environment, an investigation has also been carried out on the socio-cultural dimensions that largely influence the buying behavior, general satisfaction, and loyalty of users within this tourism segment. In addition, to further diversify the opportunities for sustainable exploitation of Canarian dromedary camels, proposals for functional valorization of new potential niches are presented (e.g., camel-assisted therapy, production of textile fibers, and applied biomedicine).

As a whole, the methodologies implemented, optimized, and validated in the present doctoral thesis are contactless methods that allow the accurate, repeatable, and reliable evaluation of camel phenotypic/functional traits, and the disentangling of the molecular basis of such traits. These methodologies are feasible for the extrapolation of other camel populations and breeds. Thus, they constitute a significant innovation within the list of available methodologies for the characterization of the global biodiversity of minor livestock species such as camels, with the greatest possible resources optimization.

Under the prism of institutional projection/intervention, the results derived from the current research works are intended to provide the public and private management institutions involved in the breeding and production of 'Canarian Camel' breed with the methodological tools for the implementation of systematics phenotypic evaluations of the animals and urge the annexation of this information with genealogical records. The combination of genealogy and phenotype-related information will allow to estimate, among other parameters, the inheritance of the different phenotypic traits evaluated, which will determine the intensity of selection to be applied according to the desired functional objectives. Furthermore, the identification of genomic regions which are controlling the most economically relevant traits will help to the design of marker-assisted selection (MAS) schemes, which will enhance the targeted genetic progress.

Overall, the proposed integrative phenotypic/functional and genetic characterization will promote the conservation of local endangered resources at a biological ('Canarian Camel' breed), socio-economic and cultural (small and medium-sized enterprises, and local heritage, whose economic base and icon, respectively, is the dromedary camel), and ecological (ecological niche and ecosystem balance) level.



SUMMARY/RESUMEN

Originally domesticated in South-East Arabia and Central Asia around the transition between the 4th and 1st millennia before the Common Era (B.C.E.), camels (*Camelus* spp.) were later introduced in Africa and Europe for different utilitarian reasons (pack, draught, and ride activities). Dromedaries or one-humped camels (*Camelus dromedarius*) started to be introduced into the African continent during the commercial incursions from the Arabian Peninsula through Egypt in the 3rd century B.C.E. Given their supreme functionality under extreme environmental conditions, dromedaries rapidly became a key element of household economies throughout the extension of the Sahara desert and such role has been conserved until the present day.

Since the Low Roman Empire period (284–476 C.E.), both dromedaries and Bactrian or two-humped camels (*Camelus bactrianus*) were also introduced in Europe. Although originally incorporated into the Roman army after campaigns in the Near East, camels in Europe participated additionally in leisure and draught activities, and were marginally used as food providers. Furthermore, direct imports of North African dromedaries into the Iberian Peninsula were prevalent during the Roman Empire period and these animals were predominantly linked to civilian sites (Roman villas and cities). At this last geographical emplacement, dromedary camels continued to be present, in relatively size-constant herds, during the Middle Ages (476–1492 C.E.).

In the late Middle Ages, the dromedary camel first arrived in the Canary Islands (Spain) from the nearby African coast (around 1405 C.E.), accompanying the expeditions during the colonization of the archipelago by Franco-Norman troops. Its rapid adaptation to the climatic and orographic conditions of the islands favored its expansion throughout the archipelago and its conversion into a fundamental tool for the development and consolidation of the local socio-economic and cultural heritage. Dromedaries in the Canary Islands participated in multiple agricultural tasks, transport of goods over short and long distances, and ride activities.

Mainly due to the limited suitable habitats, changing cultural roles, and reduced effective herd censuses, the presence of camels started to be almost anecdotal in practically all over Europe since the end of the 15th century, except for the Canary Islands. Indeed, 'Canarian Camel' (*Camelus dromedarius*) is, since 2012 (Order AAA/251/2012, Spanish Ministry of Agriculture, Food and Environment), the unique officially recognized camel breed in Europe. Nonetheless, the progressive mechanization of agricultural works and the adaptation of the road network to the rolling traffic from the last third of the 20th century on, relegated this local breed functionally to leisure tourism, which is still its main functional destination. A notable demographic recession of the

local camel census has also occurred, being the 'Canarian Camel' additionally cataloged as an endangered autochthonous breed.

Despite its conservation status, neither exhaustive phenotypic/functional characterization nor standardized selective breeding for leisure tourism-related traits with genetic improvement and conservation purposes have ever been carried out in an empirically-based manner for this camel breed. In fact, at a global level, although a relatively contemporaneous increase in the socio-economic interests in camel breeding and production is patent and considering the international basic and applied science results on the *Camelus* genus, the genetic and functional characterization of these livestock species, and the parallel evolution of specific welfare remains widely scarce. Hence, the design of programs for the phenotypic/functional characterization, and sustainable conservation and genetic improvement of the global camel biodiversity continues to be limited.

In the present doctoral thesis, which focuses on the 'Canarian Camel' breed and its main functionality (camelback leisure riding), several methodologies for the phenotypic/functional (zoometrics, biomechanics, and behaviour) characterization of dromedary camels have been implemented, optimized, and validated. In addition, the genomic regions that are responsible for the variation at such phenotypic traits and that can be integrated into the development of marker-assisted selection schemes have been identified. Moreover, given the fact that camelback leisure riding implies a close interaction between humans and camels within a specific environment, an investigation was also carried out on the socio-cultural dimensions that largely influence the buying behaviour, general satisfaction, and loyalty of users within this tourism segment. In order to further diversify the opportunities for sustainable exploitation of Canarian dromedary camels, other possible economic niches (textile fibers production, and the identification and isolation of bioactive molecules in the camel livestock by-products) have been also explored.

Although a slight genetic introgression between subpopulations is detected, a high degree of phenotypic variability for zoometric traits does exist between and within subpopulations of the 'Canarian Camel' breed, which predicts the success of the implementation of genetic improvement and conservation schemes for such functional characters. Sex, physiological status, and coat colour significantly impact zoometric traits in Canarian dromedary camels. Contactless methodologies for extracting accurate, repeatable, and reliable zoometric measurements based on bi-dimensional images and visual scoring are also optimized, aiding in efficient camel zoometric characterization.

Concerning biomechanics-related traits, angular measurements at the distal fore and rear extremity areas, the inclination of the pelvis, the relative volume of the hump, impact forces of the front limbs, post-neutering effects, and the kinematic behaviour of the scapula, shoulder, carpus, hip, and foot, have a pivotal role in athletic performance in dromedary camels. As a complementary tool in this field, post-exercise evaluation using infrared thermography helps at identifying individual tolerance to physical exercise-induced stress in dromedaries. Concretely, the local variability for the surface temperature at the cornea, withers, shoulder, pectoral muscles, semimembranosus-semitendinosus muscles, rump, and hind fetlock, and animal-dependent factors such as sex, neutering status, age, and iris pigmentation, serve to predict individual tolerance to physical exercise-induced stress in this animal species. Both biomechanical performance and thermophysiological response in dromedaries are feasible to be evaluated with non-invasive technologies (video and image analyses).

The study of physiological and behavioural-type coping strategies, the interindividual variability in cognition-related processes, the determinants of leadership behavior in dromedary camels, and camel behavioural performance during leisure riding activities provides significant results for the tailoring of improved management and selective breeding practices, and effective dromedary camel training methods. First, species-specific social ecology and body-fluid balance features to maximize parent fitness and offspring survival can explain the potential of the lunar cycle and ambient air to predict the onset of spontaneous parturition depending on the sex of offspring in Canarian dromedary camels. Second, at the time of training dromedary camels, methods utilizing negative reinforcement and visual-auditory stimuli are identified as the most effective. Furthermore, sex and interspecific communication signals (ear position) significantly determine the likelihood of the presentation of proactive and/or reactive responses in this animal species. Strongly related, several cognitive traits underlying intelligence and general cognition processes, and whose phenotypic variability is mostly mediated by factors such as animal sex, phaneroptics, owner, and training regime, can be reliably assessed in dromedaries by using a human-analogous, validated IQ scoring method. Third, body morphology and weight, neutering status, age, coat colour and particularities, and iris colour significantly determine the probability of an individual camel emerging as a leader of group movements, which can be used for refining camel handling routine procedures. Lastly, camel behaviour has also been identified as one of the main dimensions influencing the buying behaviour, general satisfaction, and loyalty of users within camelback leisure riding tours. Specifically, animals indifference towards humans and increased environmental curiosity, mediated by animal sex and age-attributed differences, are linked to user dissatisfaction. The other socio-cultural dimensions affecting customer satisfaction and loyalty within this tourism segment are staff performance, cultural geography, diverse and animal-friendly interaction with camels, socio-temporal context, and positive previous experiences in camelback leisure riding.

Annexed to the purely phenotypic characterization and existing variability for zoometric, biomechanical and behavioral characters in dromedaries, a genome-wide association study has allowed to identify seventy different candidate genes. Ten (*PVRIG*, *STAG3*, *GAL3ST4*, *TRAPPC14*, *LAMTOR4*, *U6*, *MIR187*, *FBXO8*, *TTC28*, and *CACNA1E*) out of these seventy genes are associated with various traits, which suggests that the interindividual variability that exists for zoometrical, biomechanical, and behavioural phenotypes in dromedary camels is regulated by determinants of polygenic nature. The majority of these genes are also known to be involved in the control of several neurodevelopmental processes and sensory systems' function, which agrees with the 'domestication syndrome' hypothesis in mammals. Besides, these results can be used in the design and implementation of marker-assisted selection schemes for dromedary camels.

Additional functional niches such as textile fiber production and biomedical applications of camel by-products have a non-negligible potential to be converted into sustainable economic revenues for the long-term conservation of the 'Canarian Camel' breed. Commercial possibilities for camel hair fibers can be reinforced on account of their valuable spinning performance, light reflection capacity, and heat-insulating properties. On the one hand, the high variability existing for coat colour in this camel breed also arises as a prominent source of variation contributing to differential quality attributes in camel hair-made textile products. On the other hand, bioactive molecules isolated from camel urine following standardized methodologies show promise in ethnomedicine and applied biomedicine research and applications.

Overall, the results derived from the present doctoral thesis will provide aid to the design and the implementation of effective strategies for the sustainable genetic improvement and conservation of a unique, endangered genetic resource in Europe. Apart from the protection of camel global biodiversity, the conservation of the 'Canarian Camel' breed implies the maintenance of the local socio-cultural heritage of more than 600 years, and small and medium-sized enterprises whose economic base is the dromedary camel. Moreover, the preservation of local animal genetic resources helps to maintain landscape and ecosystem balance. Under the prism of international research and projection, the methodologies implemented, optimized, and validated in the present research work are translatable to other dromedary camel populations and breeds, which supposes a significant innovation within the list of available methodologies for the characterization of the global biodiversity of minor livestock species such as camels.

Originariamente domesticados en el sudeste de la Península Arábiga y Asia Central en la transición entre el cuarto y primer milenio antes de la Era Común (A.E.C.), los camellos (*Camelus* spp.) fueron posteriormente introducidos en África y Europa por diferentes motivos utilitarios (actividades de carga, tiro y monta). En concreto, la primera introducción de dromedarios o camellos de una joroba (*Camelus dromedarius*) en el continente africano data alrededor del siglo III A.E.C., durante las incursiones comerciales realizadas con relativa frecuencia desde la Península Arábiga hasta Egipto. Dado su destacado potencial funcional aún en condiciones ambientales extremas, los dromedarios pronto se convirtieron en un elemento fundamental dentro de la economía familiar o doméstica a lo largo de la extensión del desierto del Sáhara, conservando esencialmente dicho rol hasta la actualidad.

Desde el período del Bajo Imperio Romano (284-476 de la Era Común o E.C.), tanto dromedarios como camellos de dos jorobas o camellos bactrianos (*Camelus bactrianus*) comienzan a ser introducidos también en Europa. Aunque inicialmente estos animales eran incorporados a las tropas tras las campañas militares de ejércitos romanos en Oriente Próximo, los camellos introducidos en Europa también participaron en actividades de ocio y tiro, y fueron usados de forma marginal como proveedores de alimentos. No obstante, durante este periodo histórico, se llevaron a cabo, asimismo, importaciones directas de dromedarios desde el norte de África hasta la Península Ibérica. Según registros históricos, la presencia de dromedarios en Iberia estaba vinculada, predominantemente, a entornos civiles (villas y ciudades romanas). En este último emplazamiento geográfico, los dromedarios continuaron estando presentes, en rebaños de tamaño relativamente constante, hasta finales de la Edad Media (476–1492 C.E.).

Durante el último periodo de la Edad Media o Baja Edad Media, el dromedario arriba también a Islas Canarias (España) desde la cercana costa africana (alrededor de 1405 C.E.), acompañando a las primeras expediciones durante el proceso de colonización europea del archipiélago por tropas franco-normandas. Su rápida adaptación a las condiciones climáticas y orográficas de las islas favoreció su expansión por todo el archipiélago y su conversión en una herramienta fundamental para el desarrollo y consolidación del tejido socio-económico y cultural local. Los dromedarios en Islas Canarias participaron en diversas tareas agrícolas, transporte de mercancías a corta y larga distancia, y actividades de monta.

Como consecuencia de la existencia limitada de espacios naturales potencialmente habitables por los camellos, la pérdida de vigencia de roles socio-culturales y la

reducción de los censos efectivos de los rebaños, la presencia de estos animales adquirió carácter anecdótico en prácticamente toda Europa desde finales del siglo XV, excepto en Islas Canarias. En efecto, el Camello Canario (*Camelus dromedarius*) es, desde el año 2012 (Orden AAA/251/2012, Ministerio de Agricultura, Alimentación y Medio Ambiente, Gobierno de España), la única raza de camello oficialmente reconocida en Europa. Sin embargo, la progresiva mecanización de las labores agrícolas y la adaptación de la red vial para el tránsito rodado desde el último tercio del siglo XX, provocaron una notable recesión demográfica del censo de dromedarios en el medio rural local, lo que condicionó la catalogación adicional de esta raza como recurso genético autóctono en peligro de extinción. El grueso de cabaña ganadera actual de la raza se conserva en las islas de Lanzarote y Fuerteventura, y su explotación funcional queda reducida fundamentalmente al turismo de ocio.

A pesar de su estado de conservación, la raza 'Camello Canario' continúa relegada a un escenario de baja presión selectiva para su producción, mejora y conservación sostenible. En un contexto global, esta realidad circunstancial enfatiza el carácter limitado de los esfuerzos de diseño de programas para la caracterización fenotípica/funcional, y la conservación y mejora genética sostenibles de la biodiversidad global del género *Camelus*. A pesar de la patencia de un incremento relativamente contemporáneo en el interés socioeconómico por la cría y producción de camellos, traducida en un desarrollo paralelo de la ciencia internacional básica y aplicada para con el género *Camelus*, los resultados y metodologías disponibles para la caracterización genética y funcional de estas especies de interés productivo, así como la evolución equivalente de reglamentaciones específicas en materia de bienestar animal, son efectivamente insuficientes.

En la presente tesis doctoral, cuyo objeto y modelo de estudio es la raza 'Camello Canario' y su principal funcionalidad (ocio turístico), se han implementado, optimizado y validado diferentes metodologías para la caracterización fenotípica/funcional (zoometría, biomecánica y comportamiento) de dromedarios. Adicionalmente, se han identificado las regiones genómicas que son responsables de la variación fenotípica en tales caracteres y que pueden integrarse en el desarrollo de esquemas de selección asistida por marcadores. Considerando además que el turismo de ocio con dromedarios implica un contacto estrecho entre humanos y animales en un contexto específico, el estudio de las dimensiones socio-culturales que influyen de manera distinguida en el comportamiento de compra, satisfacción general y fidelidad de los usuarios clientes dentro de este segmento turístico, permitirá customizar rigurosamente estas experiencias de ocio. A propósito de diversificar las oportunidades para la explotación sostenible de la raza 'Camello Canario', se han explorado también otros caracteres (producción de fibras textiles, e identificación y aislamiento de moléculas bioactivas en los subproductos de la ganadería camellar) con potencialidad de conversión en nichos económicos.

Aunque puede detectarse una leve introgresión genética entre subpoblaciones, existe un alto grado de variabilidad fenotípica para los caracteres zoométricos entre y dentro de las subpoblaciones de la raza 'Camello Canario', lo que predice el éxito de la implementación futura de esquemas de mejora genética y conservación para tales características funcionales. Factores como el sexo, estado fisiológico y color de la capa influyen significativamente en la expresión de los rasgos zoométricos en la raza estudiada. Por ende, estos factores han de constituirse como criterios a considerar para la selección mejorada de los animales. Para optimizar, tanto en tiempo como en recursos humanos y técnicos empleados, las tareas de caracterización zoométrica de dromedarios, se han validado en el presente trabajo de investigación diferentes metodologías mínimamente invasivas y basadas en la extracción de medidas zoométricas precisas, repetibles y fiables a partir de imágenes bidimensionales y calificación morfológica lineal.

En referencia a los caracteres fenotípicos relacionados con funcionalidad biomecánica en dromedarios, la angulación existente en determinadas áreas articulares distales de las extremidades delanteras y traseras, la inclinación de la pelvis, el volumen relativo de la joroba, las fuerzas de impacto de los miembros delanteros, los efectos morfo-fisiológicos derivados de la castración y el comportamiento cinemático de la escápula, hombro, carpo, cadera y pie, desempeñan un papel decisivo en la regulación del rendimiento atlético en esta especie animal. Como herramienta analítica complementaria, la evaluación post-ejercicio mediante termografía infrarroja permite la evaluación de la tolerancia individual al estrés inducido por el ejercicio físico en dromedarios. Concretamente, la variabilidad en el rango de temperatura superficial en las áreas de la córnea, cruz, hombros, músculos pectorales, músculos semimembranoso y semitendinoso, grupa y menudillo posterior, así como factores dependientes del animal como el sexo, estado fisiológico, edad y pigmentación del iris, sirven para predecir la tolerancia individual al estrés inducido por el ejercicio físico en estos animales. Tanto la funcionalidad biomecánica como la respuesta termofisiológica al ejercicio en dromedarios pueden evaluarse, de manera efectiva y precisa, mediante tecnologías no invasivas (análisis informático de video e imágenes).

El estudio de las estrategias de afrontamiento de tipo fisiológico y comportamental, la variabilidad interindividual para procesos cognitivos, los determinantes del comportamiento de liderazgo, y el rendimiento comportamental de los animales durante las actividades de ocio turístico, proporciona resultados destacados para la adaptación efectiva de las prácticas de manejo, cría selectiva y entrenamiento de dromedarios. En primer lugar, la ecología social y el particular metabolismo del agua en esta especie animal, como mecanismos gobernadores de la maximización funcional de la aptitud parental para garantizar la supervivencia de la descendencia, pueden explicar el potencial del ciclo lunar y viento atmosférico para predecir el inicio del parto espontáneo, dependiendo del sexo de la descendencia, en la raza 'Camello Canario'. Con respecto a las estrategias de afrontamiento de tipo comportamental, los métodos que utilizan refuerzo negativo y estímulos auditivos y/o visuales son los más eficaces para el entrenamiento de dromedarios. En este último ámbito, el sexo del animal y señales de comunicación interespecíficas (posición de las orejas) han de considerarse minuciosamente en tanto que influyen notablemente en la probabilidad de presentación de respuestas proactivas y/o reactivas en esta especie animal. En estrecha relación, numerosos rasgos cognitivos subyacentes a procesos de inteligencia y cognición general, y cuya variabilidad fenotípica es especialmente mediada por factores como el sexo del animal, características fanerópticas, propietario y régimen de entrenamiento, pueden ser cuantificados en dromedarios utilizando un método de puntuación del cociente intelectual que es análogo al empleado en la especie humana. Concerniente al comportamiento de liderazgo en dromedarios, la morfología corporal, el peso, el estado fisiológico, la edad, el color y particularidades de la capa y, la pigmentación del iris, condicionan la probabilidad individual de un dromedario de actuar como líder de movimientos grupales. Como última aproximación etológica de la raza 'Camello Canario' en el presente trabajo de investigación, la actitud conductual de los dromedarios se erige como una de las principales dimensiones que influyen en el comportamiento de compra, satisfacción general y fidelidad de los usuarios clientes de experiencias turísticas que involucran dromedarios como sujetos activos. Específicamente, la indiferencia de los animales hacia los sujetos humanos y el aumento excesivo de la curiosidad por los elementos circundantes, que son conductas influenciadas por el sexo y edad del animal, se asocian a una mayor insatisfacción del usuario turístico. Además del comportamiento de los camellos, el rendimiento y aptitudes del personal encargado del manejo de los animales, la geografía cultural, el desarrollo de una experiencia interactiva diversa y respetuosa para con los camellos, el contexto socio-temporal y experiencias positivas previas en este segmento turístico específico, también condicionan la satisfacción y fidelidad del cliente dentro de este segmento turístico.

Vinculado a la caracterización puramente fenotípica y la variabilidad existente para caracteres zoométricos, biomecánicos y comportamentales en dromedarios, un estudio de asociación de genoma completo ha permitido identificar setenta genes candidatos diferentes. Diez (*PVRIG*, *STAG3*, *GAL3ST4*, *TRAPPC14*, *LAMTOR4*, *U6*, *MIR187*, *FBXO8*, *TTC28* y *CACNA1E*) de estos genes candidatos están asociados con más de uno de los caracteres fenotípicos evaluados, lo que sugiere que la variabilidad interindividual vigente para rasgos zoométricos, biomecánicos y comportamentales en dromedarios se encuentra regulada por determinantes de naturaleza poligénica. De acuerdo a la literatura de referencia, la mayor parte de los genes candidatos identificados en la presente tesis doctoral están involucrados en el control genético de numerosos procesos de desarrollo y maduración del sistema nervioso y función de los sistemas sensoriales en mamíferos. Por ende, nuestros resultados aportan nuevas evidencias moleculares de los cambios producidos en la estructura genética de los animales como consecuencia del proceso de domesticación ('síndrome de domesticación') y que pueden ser utilizadas en el diseño de implementación de esquemas de selección asistida por marcadores.

En último lugar, las oportunidades de explotación comercial de fibras textiles producidas en ganaderías camellares podrían reforzarse en virtud de la destacada resistencia al hilado, capacidad de reflexión de la luz y propiedades de aislamiento térmico del pelo de dromedario. La marcada variabilidad cualitativa que existe para el color del pelo en la raza 'Camello Canario' constituye, asimismo, una fuente prominente de variación que contribuye a los atributos de calidad diferenciales en los productos fabricados con fibras textiles procedentes de estos animales. Otro nicho funcional y económico adicional podría ser la identificación y aislamiento, mediante metodologías estandarizadas, de moléculas con potencial bioactivo en orina de camello y que podrían utilizarse en la formulación de drogas terapéuticas.

En conjunto, los resultados derivados de la presente tesis doctoral ayudarán al impulso y enriquecimiento de estrategias eficaces para la mejora genética y conservación sostenibles de un recurso genético único y en peligro de extinción en Europa. Además de la protección de la biodiversidad animal y camellar mundial, la conservación de la raza 'Camello Canario' comprende la preservación del patrimonio histórico socio-cultural de Islas Canarias, pequeñas y medianas empresas cuya base económica es el dromedario, y el equilibrio del paisaje y ecosistemas locales. Bajo el prisma de la investigación y proyección internacional, las metodologías implementadas, optimizadas y validadas en el presente trabajo de investigación son extrapolables a otras poblaciones y razas de dromedarios, lo que representa una innovación significativa dentro del elenco limitado de procedimientos metodológicos constatados para la caracterización de la biodiversidad global de especies de ganado menor como son los camellos.

INTRODUCTION AND OBJECTIVES

1. History and uses of the domestic camel in Europe.

Archeozoological records contextualize the domestication of the camel (*Camelus* spp.) in South-East Arabia and Central Asia around the transition between the fourth and first millennia before the Common Era (B.C.E.). Dromedaries or one-humped camels (*Camelus dromedarius*) were first domesticated in the said region, while Bactrian or two-humped camels (*Camelus bactrianus*) were on the latter. From their respective places of first domestication, both species of domestic camel were distributed for different utilitarian reasons (pack, draught, and ride activities) to other geographical regions (Bökönyi, 1974; Faye, 2022).

The first presence of the dromedary camel in the African continent dates back to the beginning of the seventh century B.C.E. when these animals were introduced through Egypt during commercial incursions for carrying goods from the Arabian Peninsula. Being increasingly recognized for its functional capacities for diverse works and its physiological resistance to extreme environmental conditions, dromedaries expanded their geographical distribution along the Sahara desert. At the end of the fifth century B.C.E., the number of dromedaries and their role in household economies in the north of Africa were prominent (Agut-Labordère & Redon, 2020). In contrast, the presence of Bactrian camels has been constated, apart from Central Asia, in Mongolia (since the 3rd century B.C.E.) and Western China (since the 1st century B.C.E.) (Khomeiri & Yam, 2015).

At the beginning of the Common Era, both dromedaries and Bactrian camels had already occupied most of the arid and semi-arid lands of Africa and Asia. However, the camel started to be also introduced into Europe during the Low Roman Empire period (284–476 C.E.) (Bulliet, 1975; Epstein, 1971; I. L. Mason, 1984; Muñiz, Riquelme, & von Lettow-Vorbeck, 1995; Zarins, 1978; Zeuner, 1963). According to Bökönyi (1974), two-humped camels were the domestic camel species that reached Europe first. Although incorporated into the Roman army after campaigns in the Near East because of their higher speed and endurance when compared to horses, camels not only had a strict use for military purposes. Additionally, camels participated in public games, official Imperial mail and draught activities. They became a richness and social status symbol, represented a form of payment of tribute, and were marginally used as food providers (Muñiz et al., 1995; Orlando, 2016; Ripinsky, 1975). Bone remains of camels have been identified at Roman sites thus far (mostly at *castrum* or military camps of the Roman Empire) in different countries of Central and Southeastern Europe (France, Belgium, Germany, Switzerland, Italy, Austria, Slovenia, Hungary, Serbia, Russia, Ukraine, Romania, and Bulgaria) (Bălăşescu, 2014; Berger, Thenius, & Neumann, 1951; Boessneck, 1964; Bökönyi, 1974; Daróczi-Szabo et al., 2014; De Grossi Mazzorin, 2006; Keller, 1910; Marković et al., 2021; Pigière & Henrotay, 2012; Schmidt-Pauly, 1980; Tomczyk, 2016; Vuković & Bogdanović, 2013). Additionally, the introduction of these animals in the Iberian Peninsula is dated relatively synchronous to the other European findings and are linked to civilian sites (villas and cities). However, camel bones that were retrieved mainly along the Iberian Peninsula are thought, by some authors, to be direct imports from North Africa (Muñiz et al., 1995; Riquelme, Liesau, & Morales, 1997). In fact, according to the taxonomic classification of the camel bone remains, Tomczyk (2016) highlighted the relatively higher proportion of dromedary and Bactrian camels in Western, and Central and Eastern European countries, respectively.

At the Iberian Peninsula, camels continued to be present in a relatively regular manner during the Middle Ages (476–1492 C.E.), as constated by numerous bone findings, Arabic and Christian written sources, and representations of these animals during the peninsular Islamic period on ceramics, metal, ivory, and wall paintings (Cantal, 2013). Archaeofaunal analyses demonstrate that the oldest skeletal remains of dromedaries or one-humped camels from the Islamic period in the Iberian Peninsula belong to the Caliphate period (632–1258 C.E.) and that dromedaries had a relatively continuous presence at this geographical region until the end of the Nasrid Kingdom of Granada (1492 C.E.) (Riquelme Cantal et al., 2022). During this epoch, historical chronicles highlight two periods during which the census of dromedaries in Iberia was probably the highest ever recorded. At the end of the Caliphate period (around 1002 C.E.), Al'Mansur imported a vast number of dromedaries from northern Africa into Spain during the campaigns against the Christians. These camels were able to freely roam in the steppes of southeastern Spain during times of peace (Lévi-Provençal, 1956). A second remarkable importation of dromedaries into the Iberian Peninsula came along with the invasions from African Almoravids and Almohads (between 1090-1046 C.E.) (Gómez, 1934), who had introduced the dromedaries into their household economy and transported these animals into the newly inhabited areas. The detection, in general terms, of long bones and fragments corresponding to the axial skeleton of dromedaries, both in closed archaeological deposits together with ceramic fragments and at midden caliphal cities, and with some cut marks or exposure to fire, would reveal more regular human consumption of camel meat and the use of its bone material as raw material for the manufacture of various objects during this historical period (Díaz García, 1983; García Sánchez, 1986; Riquelme Cantal et al., 2022).

Simultaneously to the final decades of the Nasrid Kingdom of Granada, accompanying the first expeditions during the colonization process of the Canary Islands (Spain) by Franco-Norman troops, the dromedary camel arrived at the archipelago from the nearby African coast (around 1405 C.E.). Its rapid adaptation to the climatic and orographic conditions of the islands favoured its expansion throughout the archipelago. The camel soon became a fundamental tool for the development and consolidation of the socio-economic and cultural heritage of the archipelago, carrying out diverse agricultural tasks, transporting goods over short and long distances, and as a riding animal (Schulz et al., 2010; Torriani, 1959).

However, once the Spanish Reconquest was over, camels already constituted an exotic rarity that only reached the Iberian Peninsula anecdotally as booty from the raids and horseback rides carried out by the Christian troops from the North African prisons (i Tasis, 1988; Muñiz et al., 1995). In the rest of Europe, its presence also became anecdotal and exotic (Bartosiewicz, 2014), and was primarily associated with the collecting of exotic animals by princes and potentates from all over Europe; less likely with eventual battles (Daróczi-Szabo et al., 2014; Galik et al., 2015) and the caravans linking the Orient with Europe (Bălăşescu, 2014). Although the origin of this prestigious collecting dates back to the medieval centuries, it acquired particular intensity from the Renaissance and became one of the great hobbies of the European aristocracy between the 16th and 18th centuries (Baratay & Hardouin-Fugier, 2004; Hoage & Deiss, 1996; Loisel, 1912). Apart from their participation in parties and entertainment for the pleasure of the Court, camels were seen as vigorous animals, easy to feed, and very suitable for transporting heavy loads within courtly properties (Gómez-Centurión, 2008).

According to Muñiz et al. (1995), the conjunction of criteria of an ecological, demographic, and sociocultural/functional nature would explain the ineffectiveness in the inclusion of camels in the domestic fauna at a local level leading to their extinction in practically all over Europe. The potential habitats suitable in Europe are limited in size and availability of mineral and vegetable resources for these animals' natural adaptation. Secondly, the likelihood of successful colonization by reduced census is typically low. Lastly, the disappearance of cultural roles and traditions in which the camel was involved, as well as the lack of knowledge in camel handling and health care, played a significant role in preventing the successful establishment of dromedaries as domesticates. These same reasons are, however, what made camels colonize and prosper in the Canary Islands so far. Indeed, 'Canarian Camel' is, currently, the unique officially recognized camel breed in Europe ('Orden AAA/251/2012', Ministerio de Agricultura, Alimentación y Medio Ambiente - Gobierno de España ['Order AAA/251/2012', Spanish Ministry of Agriculture, Food and Environment]) and is mainly relegated to tourism activities (Schulz, 2008).

2. The role of the domestic dromedary camel in the development of Canary Islands' socio-economic and cultural heritage: a chronological review of literary and official regulatory sources.

Only two centuries after their first introduction into the archipelago, thousands of camels could be censed, considering the effective population numbers at the different islands. However, the historical rooting of the camel in the tradition and culture of the Canary Islands is especially evident on the eastern islands (Lanzarote and Fuerteventura), because of its more arid climate is suitable for this animal species, which does not support high levels of ambient moisture. The local vegetation, as well, constituted an excellent source of food resources, containing, among other minerals, a large amount of sodium chloride, which is necessary to optimize the correct development of the vital functions of the camel. The absence of natural predators also constitutes an additional criterion on favouring the demographic explosion of camels in the Canary Islands (Schulz, 2008).

Taking advantage of their physical endurance characteristics, these animals were used for centuries for the performance of varied agricultural tasks, grain milling, and goods transportation. Moreover, the camel contributed significantly to the modelling of the local agricultural landscape (e.g., the construction of terraces on the slopes of the mountains, where cereals and legumes were cultivated), which continues to be a characteristic and tourist-attractive icon of this geographical region thus far. Within a purely social context, these animals constituted a recognized symbol of prosperity and socio-economic status among the inhabitants of the islands (Schulz, 2008).

In the first chronicles of the Europeans who arrived on the islands between the 15th and 16th centuries, the importance of camel livestock for the inhabitants of Lanzarote and Fuerteventura is remarked. At the end of the 16th century, Leonardo Torriani, an Italian military engineer at the service of the Spanish crown, quoted in his work '*Descrittione et Historia del Regno de Isole Canarie, già dette le Fortunate, con il parere delle loro fortification*' ['*Description and History of the Kingdom of the Canary Islands, formerly Fortunate, with the views of its fortifications*'] (1592), which is devoted to the description of Lanzarote and its fertility: 'Esta isla posee abundancia de cabras, ovejas, cerdos, bueyes y camellos' ['This island has an abundance of goats, sheep, pigs, oxes and camels']. Also, in the aforementioned work, it is indicated about the island of Fuerteventura:

> 'Tiene abundancia de cebada y de trigo y de ganados; y de una relación hecha por gente principal de la isla resulta que tiene 60.000 cabras y ovejas juntas, 4.000 camellos, 4.000 burros, 1.500 vacas y 150 caballos de monta, además de otros infinitos caballos que son casi tan buenos como los de Lanzarote; de modo que esta tiene más de 70.000 cabezas de

ganado salvaje' ['It has an abundance of barley and wheat and livestock; and from a ratio made by the main people of the island it results that it has 60,000 goats and sheep, 4,000 camels, 4,000 donkeys, 1,500 cows and 150 horses, in addition to other endless horses that are almost as good as those of Lanzarote; so that this has more than 70,000 heads of wild livestock'].

At the end of the 18th century, livestock censuses endorsed by the Marquesado of Tabalosos certified the presence of 2,052 camels in Fuerteventura and 1,723 camels in Lanzarote. During this period, José Ruiz Cermeño also testified in his various writings related to local livestock (de Armas, 1981): 'Antiguamente se criaban en la isla [de Lanzarote] caballos de muy buena casta, pero de poco tiempo a esta parte se han perdido enteramente' ['Aforetime, horses of very good caste were raised in the island [Lanzarote], but they have been lost entirely']; and also adds that:

> 'Las caballerías que más usan sus naturales son los camellos, animales de admirable utilidad, asi para el tráfico como para el arado y la trilla; fuera de que se alimentan de sus carnes, y del cebo hacen jabón y velas de buena calidad' ['The cavalry that most use the locals is camels, animals of admirable utility, as well as for traffic as for wrapping and trill; they also feed on their meats, and make soap and good-quality candles with their tallow'].

According to the '*Censo de la Ganadería de España*' ['*Spanish Livestock Census*'] (1865), a total number of 3,090 camels were counted in the Canary Islands, with very little presence in other six provinces around mainland Spain.

Later literature further corroborates the long-lasting role that the camel has had especially in the islands of Lanzarote and Fuerteventura. De Viera and Alvar, in their work '*Diccionario de historia natural de las Islas Canarias*' ['*Dictionary of Natural History of the Canary Islands*'] (1866-1869) referred to the camel that inhabits these islands as follows:

> 'Es originario de Arabia, y esclavo del hombre en donde quiera que existe, con imponderable utilidad de sus dueños. Traído del África a Fuerteventura y Lanzarote, luego que los primeros conquistadores y pobladores de ambas islas conocieron las ventajas que sacarían de sus servicios, hallaron allí los camellos un clima favorable para la multiplicación de su especie, y desde entonces hacen parte de las conveniencias de aquellos naturales, criándose a muy poco costo. El camello es extremadamente frugal y sobrio. Susténtase con los pastos más despreciables de los campos, y bebe de una sola vez para algunos

días. Es a propósito para nuestros arenales y terrenos pedregosos. Camina muchas millas sin fatigarse, y viene a ser como un carruaje viviente para transportar grandes cargas, pues lo menos que suele soportar son 600 libras, y algunos más de mil (...). El preñado de la hembra es de casi un año, y el *camellito* o *majalulo* mama otro tanto tiempo, siendo su carne sana, del mismo sabor de la ternera, y buena para hacer tasajos. La leche de camella es gruesa y de buen alimento, si se mezcla con mayor cantidad de agua, de ella se hacen quesos' ['It is native of Arabia, and a slave of man wherever he exists, with immense utility from its masters. Transported from Africa to Fuerteventura and Lanzarote, after the first conquerors and inhabitants of both islands knew the advantages they would get from their services, the camels found there a favorable climate for their multiplication, and since then are part of the conveniences of the locals, being bred at very low cost. The camel is extremely frugal and sober. Stick with the most despicable pastures of the fields, and drink only once for a few days. It is intended for our sandy and rocky lands. It walks many miles without getting tired, and comes to be like a living carriage to carry large loads, for the least it usually stands are 600 pounds, and some more than a thousand (...). The gestation of the female lasts almost a year, and the *camellito* or *majalulo* is milked for almost one year, being its meat healthy, of the same taste as beef, and good for making jerky. Camel milk is thick and healthy, and if mixed with more water, it can be transformed into cheese'].

Although comparatively scarce, contemporary literature also refers to the breeding of camels on the island of Tenerife. Juan López Soler, in his work '*La isla de Tenerife: su descripción general y geografía*' ['*The island of Tenerife: its general and geographical description*'] (1906), quoted in allusion to the southern end of this island:

'El camello sustituye, para toda clase de transporte, al ganado caballar y mular, por lo cual se ven con frecuencia parejas de ellos en todos los caminos que enlazan a los llamados puertos de Los Cristianos, Abrigos, Médano, Porís y otros, con los caseríos a ellos inmediatos' ['The camel replaces, for all types of transportation, the cattle and the mule, so they are often seen in pairs on all the roads that link to the so-called ports of Los Cristianos, Abrigos, Medano, Poris and others, with their nearby hamlets'].

Regarding the management of the effective number of camels, for the case of Fuerteventura, which continues to be the largest reserve for this camel breed up to date, the local Cabildo issued with relative frequency specific regulations concerning the administration of the camel population and the products derived from it. For example, during times of drought and famine, local authorities banned the shipment of cheese, grain, and livestock to other areas of the archipelago. One of the most frequently imposed punishments was the following (Roldán Verdejo & Delgado González, 1970): 'A los camelleros se les castigará con la pérdida de los camellos y 15 días de cárcel' ['Camelers will be punished with the loss of their camels and 15 days in prison'].

Apart from these chronicles, biological inventories, and official censuses and regulations, extensive archives of regional vocabulary that contain rich dialectal material related to the camel, its breeding environment, and the reefs used for its routine handling, highlight the impact that camel breeding had on the livestock heritage and society of the Canary Islands (Aguiar, 1999; Fajardo Hernández, 1994; Morera, 1986, 1991, 2002, 2021). Vocables related to the camel can be found both in the argot used among the breeders of these animals, as well as in the toponymy, popular phraseology, and nicknames of some locals. Most of these linguistic elements are vocables of Arabic origin, justified their introduction and conservation in the Canary Islands' vocabulary by the continued presence of Muslim inhabitants in the archipelago and who were essentially dedicated to the breeding and care of camels since the arrival of these animals at the islands (Morera, 1990).

The numerous presence of camels at the islands, as well as the fascination and popular impressions about the camel that inhabits the archipelago, are also gathered in the literary works of Miguel de Unamuno, Agustín Espinosa, Pedro Perdomo Acedo, and Leandro Perdomo Spinola (Espinosa, 1929; Schulz, 2008; Unamuno, 2021). In particular, the Canarian writer Antonio Puente, in his work '*El bestiario insular en la poesía canaria del siglo XX: del camello vanguardista a las aves del 50*' ['*The insular bestiary in the 20th century's Canary poetry: from the avant-garde camel to the birds of the 50s*'] (2004), summarizes the personification of the camel in the Canary Islands by the first three literates mentioned above:

> 'Pero antes de pormenorizar en esta tríada sucesiva, reparemos por un momento en la elocuencia del animal, casi para una inspiración común; con su imponente cuerpo orografiado y ondulante y de color terroso, y con nuestro propio paisaje boquiabierto, que incluyera al propio paisanaje en la representación. En estos tres autores mencionados, de tan diverso registro, se da esa voluntad de hacer coincidir la figura del camello con el fenómeno insular; como si ese preciso animal pudiera instituirse como la gran sinécdoque o metonimia del espacio geográfico – esto es, el camello-isla –, y representar, al mismo tiempo, al hombre isleño, – el camello-islo –, quién, a través de la saliva del animal, émula del mar espumoso, y su corcova de riscos y acantilados, llevara todo el paisaje

> incorporado en la metáfora (…). Así pues, el camello representa a la isla y al hombre insular. Y en este sentido, al modo de una dialéctica tríada hegeliana pueden ser leídos, pongo por casos, el camello aún metafísico y esencialista, pergeñado por Miguel de Unamuno, el camello lúdico y creacionista de Agustín Espinosa y, algo más rezagado, el camello telúrico, azul y nocturno de Pedro Perdomo Acedo' ['But before getting into deeper details in this successive triade, let's look for a moment at the eloquence of the animal, almost for a common inspiration; with its imposing body orographed and ondulating and of terrestrial color, and with our own landscape, which included the own paisanage in the representation. In these three authors mentioned, of such a diverse background, it is given the willingness to make the figure of the camel coincide with the insular phenomenon; as if that precise animal could be instituted as the great synecdoque or metonymy of the geographical space – that is, the camel-island –, and represent, at the same time, the island man, – the camel-local –, who, through the saliva of the animal, emula of the foamish sea, and its corcova of risks and cliffs, would carry all the landscape incorporated in the metaphor (...). Thus, the camel represents the island and the island man. This scenario, in the way of a Hegelian triad dialectic, Miguel de Unamuno defines the camel as a metaphysical and essentialist creature, Agustin Espinosa perceives the camel as ludique and creationist, and Pedro Perdomo Acedo conceives this animals as telurical, blue and nocturnal'].

Furthermore, a recent investigation aimed at studying the traditional games as cultural heritage in the Canary Islands from an ethnomotor perspective has highlighted the use of natural elements (shells and fossils) to make camel figures (Luchoro-Parrilla et al., 2021). Such finding adds extra evidence of the relevance of camels for the local human population.

3. Official declaration and conservation status of the 'Canarian Camel' breed: intervention strategies.

As a result of the active participation of camels in loading and traction activities in the rural areas of the Canary Islands for centuries, the osteomuscular system of these animals, especially at the level of the neck-chest junction, has become notably developed. Besides, stronger limbs and shorter bones confer this local population, from a morphological point of view, a relatively more compact aspect compared to its direct ancestors. In general terms, the North African camel is an animal of lighter shape and longer and thinner limbs, given its main use for long-distance travel (Schulz, 2008).

From the last third of the 20th century, the progressive mechanization of agricultural works and the adaptation of the road network for rolling traffic brought about, however, a remarkable regression of the camel census in the rural environment and, therefore, its displacement from self-consumption agriculture. Hence, local breeders experienced the need for new functional niches to be explored. In fact, the main functional destination of this camel breed and artisan of its survival up to now, gradually became tourist leisure. Nearly a century after the approval of the 'Ley de Puertos Francos' ['Law on Free Ports'] (1852), tourism turned into mass tourism and camels began to be used as a traditional means of transport during guided tourist visits to national parks and natural reserves avoiding the introduction in these protected areas of other modes of transport with greater environmental impact on the natural environment. Progressively, tourist transportation on camels spread to other regions of the islands (Wilson & Gutierrez, 2015). Despite this revalorization, no selective breeding for such a functional purpose has ever been carried out in an empirically-based manner.

Under such circumstances, it becomes imperative to certify the differentiation of the local camel population from other populations of the same nature and, therefore, to assess the possibilities of the constitution of a distinguished breed that would deserve specific actions for its promotion and conservation. In this regard, Rege (2003) defines 'livestock breed' as a group of animals belonging to the same species which has a distinctive sociocultural, ecological, and geographical identity, and has become genetically different from other populations of the same animal species as a result of genetic drift and differential selection pressures, both natural and artificial. This author effectively emphasizes that sociocultural, ecological, and geographical distinctive characteristics of animal populations have to be considered for the recognition of new breeds, even if these specific populations are relatively closely related based solely on measures of genetic distance.

Thus, after centuries of successful adaptation to the local environments, a contemporary decline in foreign genetic interchanges, and strict health-based importing restrictions from other geographically closed camel populations since the end of the last century, a morphological, molecular, and ethnographic study with phenotypically characteristic dromedaries and whose immediate origin was known in the islands of Lanzarote and Fuerteventura, was carried out. Both islands were and continue to be the main biological reserves of this animal population. The results allowed to certify that dromedaries in the Canary Islands could differentiate themselves as a distinct camel population (Schulz, Dunner, & Cañón, 2005; Schulz et al., 2010). Such findings, together with further census analyses, culminated in the final declaration of the local population of camels as an endangered autochthonous breed ('Camello Canario' ['Canarian camel']) in 2012 by the 'Order AAA/251/2012' of the Spanish Ministry of Agriculture, Food and

Environment. Three years later, the specific regulation of the herdbook for the 'Canarian Camel' breed was approved as an effective tool for the conservation, genetic improvement, and purity breeding of this breed ('Orden de 2 de octubre de 2015', Consejería de Agricultura, Ganadería, Pesca y Aguas – Gobierno de Islas Canarias ['Order 2nd October 2015', Ministry of Agriculture, Livestock, Fisheries and Water - Government of the Canary Islands]). Etymologically, although Canarian camels are dromedaries or one-humped camels, the generic term 'camel' is used to identify this local breed since it is the only livestock species of the order *Artiodactyla*, suborder *Tylopoda*, that is present in the Canary Islands and Europe.

Currently, the main population of this local camel breed is preserved on the islands of Lanzarote and Fuerteventura, and the genealogy control exerted is scarce (Schulz, 2008). In other regions of the Iberian Peninsula, some minoritarian herds of dromedaries imported from the islands in recent years can be found. Given the fact that this local breed's major functionality is leisure riding, not only the morphological characteristics are important for their selective breeding and should be studied with greater extension ('Resolución de 29 de noviembre de 2019 de la Dirección General de Ganadería', Consejería de Agricultura, Ganadería, Pesca y Aguas – Gobierno de Islas Canarias ['Resolution 29th November 2019', Ministry of Agriculture, Livestock, Fisheries and Water - Government of the Canary Islands]), but it is also necessary to evaluate the locomotor behaviour and performance of these animals (Iglesias et al., 2020a, 2020c). Furthermore, considering the existence of a close interaction between camels and humans during riding activities, these leisure experiences are greatly shaped by the behavioural patterns displayed by camels, which in turn are a direct result of both the cognitive traits and training performance for each individual. Consequently, Canarian camel behaviour constitutes an additional dimension to be characterized (Iglesias et al., 2020b).

Altogether, morphological, biomechanical, and behavioural characteristics may also be erected as a theoretical basis for the valorization of the use of this camel breed in activities such as animal-assisted therapy. In fact, the natural human pelvic movement during walking is demonstrated to be very similar to the pelvic motion of a person when riding a camel (Ni, 2020). Besides, apart from the mere leisure objectives, the interactive experiences in which Canarian dromedaries are involved sometimes include educational activities on the physiology, behaviour, and ecology of this animal species. Therefore, Canarian camels could be, in the short time, implicated in the entire range of animal-assisted interventions (AAI) (recreation, therapeutics, and education).

In order to further strengthen the list of functional criteria for the promotion and conservation of the unique camel breed in Europe, it is feasible to explore other possible economic niches that could increase the profitability of the farms, such as textile fibers, and the identification and isolation of bioactive molecules in the camel livestock by-products. In the first case, moulting occurs naturally in camels every year and textile fibers are discarded given the absence of efforts to valorize them. On the other hand, the presence of bioactive molecules in the urine of camels is associated with diverse therapeutical applications within a culture-based background and predominant tradition in Muslim countries. Demonstrated the non-risk of genotoxicity for the ethnomedical use of camel urine (Anwar et al., 2021), the evaluation of its bioactive potential, coupled with the characterization of the metabolic profile of the urine samples used, will not only provide further evidence to confirm or refute the effectiveness of this practice but also allow the identification and isolation of new molecules that could be used in the formulation of therapeutic drugs. In any case, these new potential functional niches will have special relevance for the functional and economic sustainability of those camels that cannot be actively involved in the tourist sector due to their morphological, biomechanical, and behavioural characteristics.

Overall, this integrative functional valorization will not only promote the conservation of the 'Canarian Camel' breed, but will also preserve local socio-cultural traditions of more than 600 years, and small and medium-sized enterprises whose economic base is the camel. No less important are the ecological-environmental reasons, as local animal genetic resources help to maintain landscape and ecosystem balance (Hoffmann & Scherf, 2006).

Although potential revenues could emerge from the production of camel milk, milk-derived products, and meat in a European market (Schulz, 2008), the objective study of the opportunities for sustainable, functional exploitation of 'Canarian Camel' breed as a food provider, would be feasible as soon as local, specific facilities (technified milking parlors and specialized slaughterhouses) and a considerable number of producing camels are available.

4. Animal-assisted interventions (AAI): multi-agent ethical responsibilities.

Contemporary tourism marketing strategies offer, with increasing frequency, unique opportunities for contemplation and enjoyment of nature. Whether they are direct interactions with animals in domestic environments or the observation of wild species from a proper and safe distance, nature-based tourism or ecotourism constitutes a core of sustainable exploitation of faunistic resources with tangible benefits for their conservation (Carr, 2009; Moorhouse, Dahlsjö, Baker, D'Cruze, & Macdonald, 2015). In the particular case of wild animal species, their closest interaction with humans occurs with greater frequency at those varied locations where these species are kept in captivity with a triple basic functionality: conservation, education, and research; in addition to the mere leisure objective (Catibog-Sinha, 2008; Fennell, 2013; Miranda et al., 2023).

Raising social concerns is extended, however, to those destinations and activities where these animal-human interactions are not developed under recognized standards of animal health and welfare safeguarding and promotion. Abusive or negligent acts which affect the biological, physical, emotional, and behavioural needs of the animals can seriously compromise their well-being and survival (Fennell, 2022; Küçükaltan & Dilek, 2019). In this context, it is paramount to distinguish between wild and domestic species to be able to discern the potential differential impact that recreational activities that use animals as a claim can have on their general well-being, and enquire into the moral acceptability of these practices (Hall & Brown, 2006; Sheppard & Fennell, 2019).

Essentially, the maintenance and breeding of wild animal species in captive settings are intended to assist the *in situ* conservation tasks for threatened species. The educational function and the implementation of research projects with those species held in captivity support actions to protect and conserve natural resources in exchange for bringing the diversity of the animal kingdom closer to society. Within that combination of efforts carried out by zoological centers and aquariums, animals are, however, exposed in varying proportions to stressful situations (Davey, 2007). In order to avoid and minimize the negative and disruptive impacts of such circumstances and to assist the success of the conservation practices implemented, the personnel in charge of the animals shall design, adapt and practice training sessions and environmental enrichment programs with relative frequency (Young, 2013). Nonetheless, the susceptibility of wild animals to stressful conditions when they are outside of their natural habitat, continues to be one of the biggest troubles for conservationist institutions and a relatively underestimated topic within scientific research (G. J. Mason, 2010).

On the other hand, in domestic settings, human-animal encounters and interaction under controlled conditions and professional supervision can translate into a positive reinforcement of the general health and well-being status of both parties, according to scientific literature in this regard (Friedmann, Son, & Saleem, 2015). Ultimately, if the interaction is developed appropriately and the welfare of the animal is continuously safeguarded, it becomes feasible to create economic opportunities for the sustainable conservation of local animal and cultural resources at risk of extinction based on tourist offers that are founded on animal-human encounters (Barna, Epure, & Vasilescu, 2011). Domestication protocols that need to be implemented for the safe involvement of animals in such interactive experiences should be concisely adapted to both the specific conditions of the activities to be developed and the cognitive capabilities and individual physiological status of the animals (Wolfle, 2000).

In any case, it is the responsibility of tourists to create awareness to the pertinent collectives (e.g., animal welfare associations, and ecotourism stakeholders, researchers, and practitioners), guided by empirical data, the prevalence of neglective practices towards the health and well-being of the animals, as well as to praise those emplacements in which safe practices are implemented in this regard. From a scientific-technical background, the imperative responsibilities are (1) the instruction of owners/handlers/trainers on the evaluation of animal behaviour and welfare before, during, and after participating in assisted interventions, (2) the provision of efficient criteria for the selection of the animals based on functional performance and the potential impact of these interactive activities on their general health and well-being status (e.g., behavioural and physiological traits of stress coping styles) (Williams, Mazzola, & Pastorino, 2017), and (3) the validation of reliable methodologies for the estimation of both minimum and maximum working age, and maximum working load. Under this scenario, the impacts that this industry have on animals and the anthropomorphism attitudes (e.g., misattribution of human traits and emotions to nonhuman entities) that are detrimental to optimal animal welfare (McLean & McGreevy, 2010) will be minimized, and the social reputation of these interactive experiences improved toward an ethics-focused oncoming in tourism planning.

References

Aguiar, M. I. G. (1999). *Análisis y descripción onomasiológica del léxico canario*. Tesis Doctoral: Universidad de La Laguna (Canary Islands, Spain).

Agut-Labordère, D., & Redon, B. (2020). *Les vaisseaux du désert et des steppes: Les camélidés dans l'Antiquité (Camelus dromedarius et Camelus bactrianus)*: MOM éditions.

Anwar, S., Ansari, S. A., Alamri, A., Alamri, A., Alqarni, A., Alghamdi, S., Wagih, M.E., Ahmad, A., & Rengasamy, K. R. (2021). Clastogenic, anti-clastogenic profile and safety assessment of Camel urine towards the development of new drug target. *Food and Chemical Toxicology*, 151, 112131.

Bălăşescu, A. (2014). Camels in Romania. *Anthropozoologica*, 49(2), 253-264.

Baratay, E., & Hardouin-Fugier, E. (2004). *Zoo: A history of zoological gardens in the West*: Reaktion books.

Barna, C., Epure, M., & Vasilescu, R. (2011). Ecotourism–conservation of the natural and cultural heritage. *Review of Applied Socio-Economic Research*, 1(1), 87-96.

Bartosiewicz, L. (2014). Camels in the front line. *Anthropozoologica*, 49(2), 297-302.

Berger, W., Thenius, E., & Neumann, A. (1951). Über römerzeitliche Kamelfunde im Stadtgebiet von Wien. *Ausgrabungen und Funde im Wiener Stadtgebiet 1948/49 (Veröffentliche Historische Museum Stadt Wien 17)*, 60-68.

Boessneck, J. (1964). Die Tierknochen aus den Grabungen 1954–1957 auf dem Lorenzberg bei Epfach. *Studien zu Abodiacum-Epfach. Münchner Beiträge zur Vor-und Frühgeschichte*, 7, 213-261.

Bökönyi, S. (1974). *History of domestic mammals in Central and Eastern Europe*: Akadémiai Kiadó.

Bulliet, R. W. (1975). *The Camel and the Wheel*: Cambridge, Mass Harvard University Press.

Cantal, J. A. R. (2013). Nuevas evidencias arqueológicas de la presencia de dromedario, Camelus dromedarius, L., en el sur de la Península Ibérica: Cortijo de Los Robles (Jaén) y Torrevieja, Villamartín (Cádiz). *Cuadernos de Prehistoria y Arqueología de la Universidad de Granada*, 23, 347-364.

Carr, N. (2009). Animals in the tourism and leisure experience. *Current Issues in Tourism*.

Catibog-Sinha, C. (2008). Zoo tourism: Biodiversity conservation through tourism. *Journal of ecotourism*, 7(2-3), 160-178.

Daróczi-Szabo, L., Daróczi-Szabó, M., KováCS, Z. E., Kőrösi, A., & Tugya, B. (2014). Recent camel finds from Hungary. *Anthropozoologica*, 49(2), 265-280.

Davey, G. (2007). Visitors' effects on the welfare of animals in the zoo: A review. *Journal of Applied Animal Welfare Science*, 10(2), 169-183.

de Armas, A. R. (1981). Estructura socioeconómica de Lanzarote y Fuerteventura en la segunda mitad del siglo XVIII. *Anuario de Estudios Atlánticos*, 1(27), 425-454.

De Grossi Mazzorin, J. (2006). Cammelli nell'antichità: le presenze in Italia. *Journal of Intercultural and Interdisciplinary Archaeology*.

Díaz García, A. (1983). Un tratado nazarí sobre alimentos: al-kalam alà l-Agdiya de al-Arbuli: edición, traducción y estudio, con glosarios (II). *Repositorio Institucional de la Universidad de Granada*.

Epstein, H. (1971). *The origin of the domestic animals of Afric*a: CGSpace - A Repository of Agricultural Research Outputs.

Espinosa, A. (1929). *Lancelot 28-7*: Ediciones Insoladas.

Fajardo Hernández, L. (1994). «El camello en Canarias», Tradiciones populares, 1. Palabras y cosas. *Instituto de Estudios Canarios y Consejo Superior de Investigaciones Científicas (La Laguna)*, 93-111.

Faye, B. (2022). Is the camel conquering the world? *Animal Frontiers: the Review Magazine of Animal Agriculture*, 12(4), 8-16.

Fennell, D. A. (2013). Contesting the zoo as a setting for ecotourism, and the design of a first principle. *Journal of Ecotourism*, 12(1), 1-14.

Fennell, D. A. (2022). An animal welfare literacy framework for tourism. *Annals of Tourism Research*, 96, 103461.

Friedmann, E., Son, H., & Saleem, M. (2015). The animal–human bond: Health and wellness. In *Handbook on animal-assisted therapy* (pp. 73-88): Elsevier.

Galik, A., Mohandesan, E., Forstenpointner, G., Scholz, U. M., Ruiz, E., Krenn, M., & Burger, P. (2015). A sunken ship of the desert at the river Danube in Tulln, Austria. *Plos one*, 10(4), e0121235.

García Sánchez, E. (1986). La alimentación en la Andalucía islámica. Estudio histórico y bromatológico. II: carne, pescado, huevos, leche y productos lácteos. In *Andalucía Islámica: Textos y estudios*: Universidad de Granada, España.

Gómez-Centurión, C. (2008). Exóticos pero útiles: los camellos reales de Aranjuez durante el siglo XVIII. In *Cuadernos dieciochistas* (pp. 155-180): Ediciones Universidad de Salamanca.

Gómez, E. G. (1934). Bagdad y los reinos de Taifas. *Revista de Occidente* (127), 1-22.

Hall, D. R., & Brown, F. (2006). *Tourism and welfare: Ethics, responsibility and sustained well-being*: CABI Books.

Hoage, R. J., & Deiss, W. A. (1996). *New worlds, new animals: from menagerie to zoological park in the nineteenth century*: JHU Press.

Hoffmann, I., & Scherf, B. (2006). Animal genetic resources-time to worry. *The livestock report*, 57-74.

i Tasis, A. M. A. (1988). Animals exòtics als palaus reials de Barcelona. *Medievalia*, 8, 9-22.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S., & Bermejo, J. V. (2020a). Biokinematics and applied thermography in the Canarian camel breed. *Archivos de zootecnia*, 69(265), 102-107.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S., & Bermejo, J. V. (2020b). Ethological characterization of the Canarian camel breed. *Archivos de zootecnia*, 69(265), 108-115.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S., & Bermejo, J. V. (2020c). Zoometric characterization and body condition score in Canarian camel breed. *Archivos de zootecnia*, 69(265), 14-21.

Keller, C. (1910). Ein Kamelknochen aus Vindonissa. *Jahresberichte der Schweizer Gesellschaft für Urgeschichte*, 2, 111-112.

Khomeiri, M., & Yam, B. A. Z. (2015). Introduction to Camel origin, history, raising, characteristics, and wool, hair, and skin: a review. *Research Journal of Agricultural and Environmental Management*, 4, 496-508.

Küçükaltan, E. G., & Dilek, S. E. (2019). A philosophical approach to animal rights and welfare in the tourism sector. *Journal of Tourism Leisure and Hospitality*, 1(1), 1-11.

Lévi-Provençal, É. (1956). Histoire de l'Espagne musulmane, Kitāb A 'māl al-a 'lām, Texte árabe publié avec introduction et index. In *Beirut: Dār al-Makšūf*.

Loisel, G. A. A. (1912). *Histoire des ménageries de l'antiquité à nos jours (Vol. 2)*: Octave Doin et Fils.

Luchoro-Parrilla, R., Lavega-Burgués, P., Damian-Silva, S., Prat, Q., Sáez de Ocáriz, U., Ormo-Ribes, E., & Pic, M. (2021). Traditional Games as Cultural Heritage: The Case of Canary Islands (Spain) From an Ethnomotor Perspective. *Frontiers in psychology*, 12, 586238.

Marković, N., Ivanišević, V., Baron, H., Lawless, C., & Buckley, M. (2021). The last caravans in antiquity: Camel remains from Caričin Grad (Justiniana Prima). *Journal of Archaeological Science: Reports*, 38, 103038.

Mason, G. J. (2010). Species differences in responses to captivity: stress, welfare and the comparative method. *Trends in ecology & evolution*, 25(12), 713-721.

Mason, I. L. (1984). *Evolution of domesticated animals*: Longman Group.

McLean, A. N., & McGreevy, P. D. (2010). Ethical equitation: Capping the price horses pay for human glory. *Journal of Veterinary Behavior*, 5(4), 203-209.

Miranda, R., Escribano, N., Casas, M., Pino-del-Carpio, A., & Villarroya, A. (2023). The role of zoos and aquariums in a changing world. *Annual Review of Animal Biosciences*, 11, 287-306.

Moorhouse, T. P., Dahlsjö, C. A., Baker, S. E., D'Cruze, N. C., & Macdonald, D. W. (2015). The customer isn't always right—conservation and animal welfare implications of the increasing demand for wildlife tourism. *PloS one*, 10(10), e0138939.

Morera, M. (1986). Los arabismos del español de Canarias. *La Gaceta de Canarias*, 11, 62-74.

Morera, M. (1990). El componente árabe en el Español de Canarias. *Jornadas de Historia de Lanzarote y Fuerteventura*, 2, 363-391.

Morera, M. (1991). La tradición del camello en Canarias. *Anuario de Estudios Atlánticos*, 1(37), 167-204.

Morera, M. (2002). *Diccionario histórico-etimológico del habla canaria*: Editora de Temas Canarios.

Morera, M. (2021). Saharianización lingüística de Canarias. Canarización lingüística del Sáhara/Linguistic saharianization of Canary Islands. Linguistic canarization of Sahara. *Anuario de Estudios Atlánticos* (67).

Muñiz, A. M., Riquelme, J. A., & von Lettow-Vorbeck, C. L. (1995). Dromedaries in antiquity: Iberia and beyond. *Antiquity*, 69(263), 368-375.

Ni, B. B. (2020). *Human kinematic responses to walking and riding camels and horses*. Doctoral Thesis: Baylor University (Waco, Texas, USA).

Orlando, L. (2016). Back to the roots and routes of dromedary domestication. *Proceedings of the National Academy of Sciences*, 113(24), 6588-6590.

Pigière, F., & Henrotay, D. (2012). Camels in the northern provinces of the Roman Empire. *Journal of Archaeological Science*, 39(5), 1531-1539.

Rege, J. (2003). Defining livestock breeds in the context of community-based management of farm animal genetic resources. *Community-based management of animal genetic resources*, 27-36.

Ripinsky, M. M. (1975). The camel in ancient Arabia. *Antiquity*, 49(196), 295-298.

Riquelme Cantal, J. A., Montilla Torres, I., Garrido Anguita, J. M., Ruiz Nieto, E., Martín de la Cruz, J. C., Aparicio Sánchez, L., Simón Vallejo, M.D., & Vallejo Triano, A. (2022). El dromedario en Al-Ándalus. El registro arqueológico en el sur de la península ibérica en época islámica (siglos X a XIV). *Revista de Prehistoria y Arqueología*, 31(2), 316-330.

Riquelme, J. A., Liesau, C., & Morales, A. (1997). Archäozoologische funde von dromedaren auf der Iberischen Halbinsel. *Anthropozoologica*, 25(26), 539-543.

Roldán Verdejo, R., & Delgado González, C. (1970). Acuerdos del Cabildo de Fuerteventura (1605-1659). *Instituto de Estudios Canarios y Consejo Superior de Investigaciones Científicas (La Laguna)*.

Schmidt-Pauly, I. (1980). *Römerzeitliche und mittelalterliche Tierknochenfunde aus Breisach im Breisgau*. Dissertation in Veterinary Medicine: University of Munich (Munich, Germany).

Schulz, U. (2008). *El camello en Lanzarote*: Aderlan.

Schulz, U., Dunner, S., & Cañón, J. (2005). The Majorero camel (*Camelus dromedarius*) breed. *Animal Genetic Resources/Resources génétiques animales/Recursos genéticos animales*, 36, 61-72.

Schulz, U., Tupac-Yupanqui, I., Martínez, A., Méndez, S., Delgado, J. V., Gómez, M., Dunner, S., & Cañón, J. (2010). The Canarian camel: a traditional dromedary population. *Diversity*, 2(4), 561-571.

Sheppard, V. A., & Fennell, D. A. (2019). Progress in tourism public sector policy: Toward an ethic for non-human animals. *Tourism Management*, 73, 134-142.

Tomczyk, W. (2016). Camels on the northeastern frontier of the Roman Empire. *Papers from the Institute of Archaeology*, 26(1).

Torriani, L. (1959). *Descripción de las Islas Canarias*: Goya Ediciones.

Unamuno, M. (2021). *De Fuerteventura a París*: Lindhardt og Ringhof.

Vuković, S., & Bogdanović, I. (2013). A camel skeleton from the Viminacium amphitheatre. *Starinar*(63), 251-267.

Williams, C., Mazzola, S. M., & Pastorino, G. (2017). Animal Welfare in Ecotourism. *Annual Research & Review in Biology*, 19(1), 1-5.

Wilson, R., & Gutierrez, C. (2015). The one-humped camel in the Canary Islands: History and present status. *Tropicultura*, 33(4).

Wolfle, T. (2000). Understanding the role of stress in animal welfare: practical considerations. In *The biology of animal stress: basic principles and implications for animal welfare* (pp. 355-368): CABI Books.

Young, R. J. (2013). *Environmental enrichment for captive animals*: John Wiley & Sons.

Zarins, J. (1978). The camel in ancient Arabia: a further note. *Antiquity*, 52(204), 44.

Zeuner, F. E. (1963). *A history of domesticated animals*: Hutchinson & Co. Ltd.

The main aim of the present doctoral thesis is the implementation, validation, and optimization of different methodological procedures for the characterization of phenotypic/functional traits and genomic regions associated with economically relevant traits in the unique camel breed along Europe ('Canarian Camel'). It is officially cataloged as an autochthonous, endangered livestock breed, and mainly relegated to leisure riding activities, which are greatly shaped by animal body morphometry, biomechanics and behaviour-related traits. The results derived from the current research work are intended to broaden the list of methodologies available for the phenotypic and genetic characterization of minor livestock species such as camels, and aid at the definition of criteria for camel selective breeding with genetic improvement and conservation purposes.

To achieve this general objective, the following specific objectives have been addressed:

1. Bibliometric analysis on the evolution of research advances and their scientific impact in regards to the handling, breeding, and functionality of camel species (*Camelus* spp.) to highlight which specific academic disciplines require further research development and that support the implementation of the present doctoral thesis. This specific objective has been addressed in Chapter 1, which includes:

   Study 1: Iglesias Pastrana, C., Navas González, F.J., Ciani, E., Barba Capote, C. J., & Delgado Bermejo, J.V. (2020). Effect of research impact on emerging camel husbandry, welfare and social-related awareness. *Animals*, 10(5), 780. DOI: 10.3390/ani10050780

2. Zoometric characterization of 'Canarian Camel' breed to explore breed standard conformation traits and its phenotypic variability, and to develop, optimize, and validate alternative contactless methodologies for extracting accurate, repeatable, and reliable zoometric measurements of live dromedary camels. The derived results will aid at speeding up the activities for camel zoometric characterization and support the definition of physical fitness-linked breeding criteria. These specific objectives have been addressed in Chapter 2, which includes:

   Study 2: Iglesias Pastrana, C., Navas González, F.J., Ciani, E., Camacho Vallejo, M.E., & Delgado Bermejo, J.V. (2022). Bayesian linear regression and natural logarithmic correction for digital image-based extraction of linear and tridimensional zoometrics in dromedary camels. *Mathematics*, 10(19), 3453. DOI: 10.3390/math10193453

Study 3: Iglesias Pastrana, C., Navas González, F.J., Ciani, E., González, Ariza, A., Nogales Baena, S., & Delgado Bermejo, J.V. (2023) Evidences of subpopulation diversification and traces of introgression within Canarian camel breed zoometric standard: scope and opportunities for selection. Submitted to *Italian Journal of Animal Science*.

Study 4: Iglesias Pastrana, C., Navas González, F.J., Ciani, E., León Jurado, J.M., & Delgado Bermejo, J.V. (2023). Optimization and validation of a linear appraisal scoring system for physical fitness-linked zoometric traits in dromedary camels. Submitted to *Research in Veterinary Science*.

3. Biomechanical characterization and post-exercise examination by infrared thermography (IRT) of 'Canarian Camel' breed to define breeding criteria for gait proficiency and tolerance to physical exercise-induced stress in leisure dromedary camels, respectively. These specific objectives have been addressed in Chapter 3, which includes:

Study 5: Iglesias Pastrana, C., Navas González, F.J., Ciani, E., Marín Navas, C., & Delgado Bermejo, J.V. (2023). Determination of breeding criteria for gait proficiency in dromedary camels: a stepwise multivariate analysis of factors predicting overall biomechanical performance. Submitted to *Frontiers in Veterinary Science*.

Study 6: Iglesias Pastrana, C., Navas González, F.J., Ciani, E., Marín Navas, C., & Delgado Bermejo, J.V. (2023). Thermographic ranges of dromedary camels undergoing physical exercise: applications for physical health/welfare monitoring and phenotypic selection. Submitted to *Frontiers in Veterinary Science*.

4. Ethological characterization of 'Canarian Camel' breed through the study of physiological and behavioural-type coping strategies, leadership behaviour, and cognitive processes, to inform the tailoring of effective camel training methods, improved management practices, selective breeding programs for superior behavioural performance, and exploration of new potential functional niches. These specific objectives have been addressed in Chapter 4, which includes:

Study 7: Iglesias Pastrana, C., Navas González, F.J., Delgado Bermejo, J.V., & Ciani, E. (2023). Lunar cycle, climate, and onset of parturition in domestic dromedary camels: implications of species-specific metabolic economy and social ecology. *Biology*, 12(4), 607. DOI: 10.3390/biology12040607

Study 8: Iglesias Pastrana, C., Navas González, F.J., Ciani, E., McLean, A.K., & Delgado Bermejo, J.V. (2023). Behavioural-type coping strategies in leisure dromedary camels: factors determining reactive vs. proactive responses. Submitted to *Applied Animal Behaviour Science*.

Study 9: Iglesias Pastrana, C., Navas González, F.J., Ciani, E., McLean, A.K., & Delgado Bermejo, J.V. (2023). Cognitive processes and environment- and animal-dependent factors modulating Intelligence Quotient (IQ) and behavioural performance in dromedary camels. Submitted to *Animal Behaviour*.

Study 10: Iglesias Pastrana, C., Navas González, F.J., Ciani, E., Arando Arbulu, A., & Delgado Bermejo, J.V. (2021). The youngest, the heaviest and/or the darkest? Selection potentialities and determinants of leadership in Canarian dromedary camels. *Animals*, 11(10), 2886. DOI: 10.3390/ani11102886

5. Genome-wide association study (GWAS) and characterization of the genomic regions associated with zoometrics, biomechanics and behaviour-related traits in leisure dromedary camels. This conglomerate of information enriches the knowledge on the genetic basis underlying such complex traits in dromedary camels and will aid in implementing marked-assisted selection strategies for this livestock species. This specific objective has been addressed in Chapter 5, which includes:

Study 11: Iglesias Pastrana, C., Navas González, F.J., Macri, M., Martínez Martínez, M.A., Ciani, E., & Delgado Bermejo, J.V. (2023). Genomic regions regulating the expression of neuro-sensory development determine body morphometrics, biomechanics and behaviour in dromedaries. Submitted to *Journal of Animal Breeding and Genetics*.

6. Study of the sociocultural dimensions of camelback leisure riding tours to customize saddlery offers based on the diverse patterns influencing the buying behavior, general satisfaction, and loyalty of users within this tourism segment. This specific objective has been addressed in Chapter 6, which includes:

Study 12: Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Nogales Baena, S., & Delgado Bermejo, J.V. (2020). Camel genetic resources conservation through tourism: a key sociocultural approach of camelback leisure riding. *Animals*, 10(9), 1703. DOI: 10.3390/ani10091703

Study 13: Pastrana, C.I., González, F.J.N., Ciani, E., Ariza, A.G., & Bermejo, J.V.D. (2021). A tool for functional selection of leisure camels: Behaviour breeding criteria may ensure long-term sustainability of a European unique breed. *Research in Veterinary Science*, 140, 142-152. DOI: 10.1016/j.rvsc.2021.08.007

7. Preliminary assessment of the potential of conversion of additional functional niches into further long-term, economic opportunities for the conservation of 'Canarian Camel' breed. This specific objective has been addressed in Chapter 7, which includes:

Study 14: Iglesias Pastrana, C., Navas González, F.J., Ciani, E., López de los Santos, B., & Delgado Bermejo, J.V. (2023). A comparison of physical properties between Merino wool and camel hair through discriminant analysis. Under review in *Journal of Natural Fibers*.

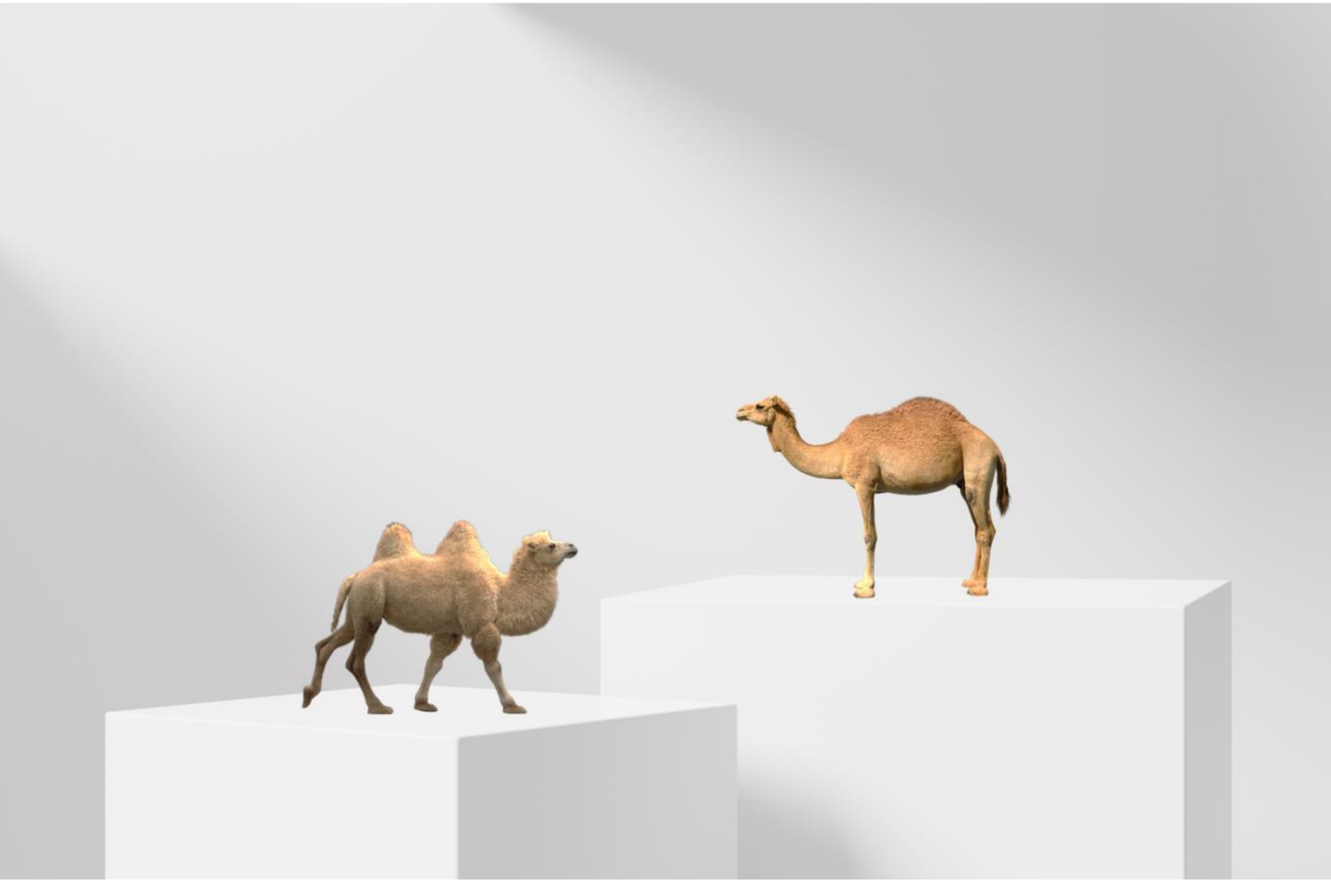
Study 15: Iglesias Pastrana, C., Navas González, F.J., Ciani, E., López de los Santos, B., & Delgado Bermejo, J.V. (2023). Body region sampling areas- and phaneroptics-associated hair fiber phenotypes in Canarian camel versus Merino sheep. Under review in *Journal of Natural Fibers*.

Study 16: Iglesias Pastrana, C., Delgado Bermejo, J. V., Sgobba, M.N., Navas González, F.J., Guerra, L., Pinto, D.C., Gil, A.M., Duarte, I.F., Lentini, G. & Ciani, E. (2022). Camel (*Camelus* spp.) Urine Bioactivity and Metabolome: A Systematic Review of Knowledge Gaps, Advances, and Directions for Future Research. *International Journal of Molecular Sciences*, 23(23), 15024. DOI: 10.3390/ijms232315024

Study 17: Iglesias Pastrana, C., Sgobba, M.N., Navas González, F.J., Delgado Bermejo, J.V., Pierri, C.L., Lentini, G., Musio, B., Osman, T.K.S., Gallo, V., Duarte, I.F., Guerra, L., and Ciani, E. (2023). Osmolarity-dependent modulation of cell viability by camel urine: implications for assessing bioactive properties. Submitted to *Journal of Cellular Biochemistry*.

CHAPTER 1

A STATE-OF-THE-ART REVIEW OF CAMEL (*Camelus* spp.) SCIENCE



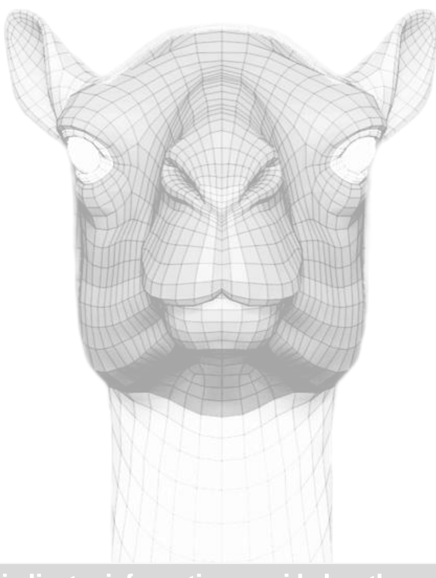
1.1 Effect of research impact on emerging camel husbandry, welfare and social-related awareness

Carlos Iglesias Pastrana[1], Francisco Javier Navas González[1], Elena Ciani[2], Cecilio José Barba Capote[3] and Juan Vicente Delgado Bermejo[1]

[1]Department of Genetics, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain

[2]Department of Biosciences, Biotechnologies and Biopharmaceutics, Faculty of Veterinary Sciences, University of Bari 'Aldo Moro', 70121 Bari, Italy

[3]Department of Animal Production, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain



Quality indicator information provided on the publication

Status of the manuscript: Published

Journal (year, volume, page(s)): *Animals* 2020, *10*, 780

International database in which it is indexed: Journal of Citation Reports (JCR)

Thematic area in the reference database: Veterinary Sciences

Impact index of the journal in the year of the article's publication: 2.752

Rank/number of thematic area journals: 19/146 (Q1)

Abstract

The lack of applied scientific research on camels, despite them being recognized as production animals, compels the reorganization of emerging camel breeding systems with the aim of achieving successful camel welfare management strategies all over the world. Relevant and properly-framed research widely impacts dissemination of scientific contents and drives public willingness to enhance ethically acceptable conditions for domestic animals. Consumer perception of this livestock industry will improve and high-quality products will be obtained. This paper draws on bibliometric indicators as promoting factors for camel-related research advances, tracing historical scientific publications indexed in ScienceDirect directory from 1880–2019. Camel as a species did not affect Journal Citation Reports (JCR) impact ($p > 0.05$) despite the journal, author number, corresponding author origin, discipline and publication year affecting it ($p < 0.001$). Countries with traditionally well-established camel farming are also responsible for the papers with the highest academic impact. However, camel research advances may have only locally and partially influenced welfare related laws, so intentional harming acts and basic needs neglect may persist in these species. A sustainable camel industry requires those involved in camel research to influence business stakeholders and animal welfare advocacies by highlighting the benefits of camel wellbeing promotion, co-innovation partnership establishment and urgent enhancement of policy reform.

Keywords

Animal welfare, bibliometrics, camels, emerging industry, international research, science–society dialogue, law enforcement

Introduction

Old World camels (*Camelus dromedarius* or one-humped camel, *Camelus bactrianus* or two-humped camel and the wild species *Camelus ferus*) are mainly found in the desert and semi-desert areas of the Middle East through northern India and arid regions in Africa (Yagil, 1982). Still, some feral populations of dromedary camels inhabit in some arid regions of central Australia, India and Kazakhstan (Nowak & Paradiso, 1991), and could also be found in the southwestern United States until the early 20th century (Baum, 2011). However, the critically endangered wild Bactrian (*C. ferus*) only survives in remote areas of northwest China and Mongolia (Burger, 2016).

The domestication process of these genus presumably started about 4000 years ago in southern Arabia (Khan, Arshad, & Riaz, 2003), and the main purposes for which these animals were utilized were its meat, milk, wool, hair and dung, or for draft purposes (Dahl & Hjort, 1979; Epstein, 1971). Domestic camels played an important role in Old World ancient nomadic civilizations' prosperity. A few low-income nomadic livelihoods in

Africa and Eastern Asia still depend on these pluripotential animals (Burger, 2016). Camels play a pivotal role as food providers, even under extreme environmental situations (severe drought periods or in rural livelihood areas where other domestic animals struggle to thrive) during which directly-dependent human nutrition is precarious (Yagil, 1982).

Nonetheless, the camel may have been one of the most ignored species compared with other domestic livestock from a productive, political or socioeconomic perspective. This inconsideration may have its basis on their usual relation with under-developed areas, which led to the misattribution of a low economic value and the underestimation and disregard by science of the potential of these animals as a multifunctional resource for humans with very low maintenance requirements (Acharya & Pathak, 2019).

Fortunately, the international relevance of camels has progressively increased due to their recognition as a sustainable livestock species worldwide. Such a distinctive position is strongly linked to the current concern and need to provide functional solutions to environmental emergencies like global warming or desertification (Khan et al., 2003; Naumann, 1999). Besides, as nomadic pastoralists progressively sedentarizate, nomad livestock-breeding simultaneously turns into intensive socialist livestock-breeding (Berque, 1959). Other deeply rooted traditional activities stemming from the Bedouin ancestral culture, such as camel racing, have also become a remarkable profitable interest in Middle East Arab countries (Nelson, Bwala, & Nuhu, 2015).

As a result, these growing social and economic interests in camel husbandry experienced during the past three decades (Khan et al., 2003) have parallelly promoted an increase in the scientific actions that are implemented and which deal with almost any discipline applied to the species. Regardless of the existence of widely applied scientific knowledge about anatomy, physiology and pathology in camels, planned research and codes of action on the best handling practices ensuring a sufficient welfare status in these animals are scarce and shallow (Fattah & Roushdy, 2016).

In this context, addressing the basic requirements and making efforts to seek niches of further development and reorientation of the camel industry becomes crucial. However, these objectives can only be achieved if they are understood and assimilated from people's perspectives on animal welfare and considering the social, political and economic causes that may support the new structures in the long term (Freire & Nicol, 2019). When attempting to assess quality of life, Fraser (2008) proposed three basic conceptual judgments of animal welfare: biological functioning, affective state and natural living. As domestic animals, camels share their natural living with humans. Intensive management could be affecting their natural behavioral repertoire, leading to the development of stereotypies (Padalino et al., 2014). Hence, owners and industry users need to be provided with the resources, skills and proficiency to handle them properly, to preserve their wellbeing and to improve their productivity in a sustainable manner.

This social awareness is grossly affected by science and vice versa, as the binomial science–society is immersed in a process of diachronic evolution with a sufficiently proven cultural base. Aiming to reach a consensus on camel wellbeing, science must revise the existing legislative rules and identify the changes needed to adapt them to the new challenges that this rather overlooked multipurpose species faces nowadays. Thus, research outputs may encourage lawmakers to develop official regulations and highlight the need for expanded awareness when aiming to meet new societal values and expectations (Reblando, 2018).

Under this theoretical framework, the present paper primarily aimed to evaluate the evolution of research advances and their scientific impact in regards to the camel species, considering potential conditioning factors such as the journal, number of authors per contribution, country of corresponding author, topic with which the different publications dealt, year of publication and camel species studied. We elaborated a map to depict the countries and disciplines reporting the highest level of expertise and research approaches in camel science, respectively. Bibliometric mapping enables visualization of scientific developments leading to an active involvement of stakeholders in the different subfields. Secondly, the demonstrable contribution that camel international research progress has made within the legal sphere was evaluated by tracing the number and academic content of the regulations implemented in terms of camel welfare promotion.

This conglomerate of information is intended to become a substantial reference source for academics studying these species, on the preliminary process of decision-making for which discipline may require further research development, identifying potential research collaborators and finding journals in which to publish the outcomes of such research. Additionally, legislative authorities could also appeal to and officially fund research projects in unexplored areas in camel science. The scientific outcomes may be translated into mandatory codes of practices, intending to achieve humane husbandry and care for and across all types of camel business.

Material and methods

Study premises: data obtention

The present methodology is based on a previous manuscript by McLean and Navas Gonzalez (2018). After typing the word 'camel' in the searching window of www.sciencedirect.com on 31 December 2019, we exported the results obtained into a .xlsx file. The reason why we chose to use www.sciencedirect.com is that the tool present in the website allows us to extract data for its analysis in a way that other platforms such as https://www.ncbi.nlm.nih.gov/pubmed/ do not. Therefore, the public filters that can be implemented are not exhaustive enough to perform the proper analysis required for this retrospective observational longitudinal study over the period of time between 1880 and 2019, both inclusive.

Data were filtered to discard those documents which did not focus on the *Camelus* genus or its species (*Camelus dromedarius*, *Camelus bactrianus*, *Camelus ferus* and other extinct species) by searching for the words 'camel/s', 'camelid/s', '*Camelus*', 'dromedary/ies', 'Bactrian' and 'feral' in each article. Papers containing unrelated homophone or analogous terms were discarded due to the lack of connection to the species with which this manuscript deals.

The documents selected were included in a database which comprised individual registries for each article. Each individual record consisted of the name of the journal in which the article was published, the Journal Citation Report (JCR) impact factor of the journal in the year in which the document was published, the mean JCR impact factor per journal in the whole period (1880–2019), the total number of citations of each paper, the mean number of citations per journal, the number of authors contributing to each publication, the country of the corresponding author, the topic or research area, the year of publication, the camel species being studied and the publication's doi in order to trace the documents back to the internet site in which they are available.

JCR impact factor was registered per journal and year by consulting the Journal Citation Reports on Web of Science. A value of zero was given in the database for all articles published in non-indexed journals in its year of publication (n = 254). The total number of citations per paper was assessed through the same scientific database. Table 1 reports a summary of the conditioning factors of paper impact related variables (Table 2) considered in the model used and the level within such factors.

Official regulations which specifically mention camels as production or companion animals and give advice and establish responsibility for persons or leaders in charge of them were traced back and evaluated in the online database of the Global Animal Law Association (https://www.globalanimallaw.org/database/index.html). It contains all the available and updated information until 1 January 2020 in the fields of law making, law enforcing, lobbying and scientific knowledge in animal protection from a local to universal level.

Preliminary statistics assumption testing

The Shapiro–Francia normality test of the test and distribution graphics package of the Stata Version 15.0 software was used to test the normality (Supplementary Table S1). The rest of the parametric assumptions (Levene's test to evaluate homoscedasticity, Mauchly's W test to evaluate sphericity and Tolerance and Variance Inflation Factor to

Table 1. Category description for conditioning factors considered to classify camel bibliography.

Factor	Type	Levels
Journal	Nominal	203 scientific journals
Number of authors	Ordinal	From 1 to 15, 20 and 24
Country of corresponding author	Nominal	56 countries
Topic	Nominal	Anatomy, Behaviour, Biomechanics, Biotechnology, Camel Hair, Clinical and Biomedical Research, Ecology, Food Science and Technology, Infectious diseases, Camel-related human injuries, Microbiology, Molecular genetics, Parasitic diseases, Phylogeny, Physiology, Production, Reproduction and General Review
Year of publication	Ordinal	1880 to 2019
Camel species or species cluster	Nominal	*Camelops* sp. (extinct)[1], *Camelops hesternus* (extinct)[1], *Camelus bactrianus*, *Camelus dromedarius*, *Camelus ferus*, *Camelus knoblochi* (extinct)[1], *Camelus* sp., *Camelus thomasi* (extinct)[1], *Megatylopus* sp. (extinct)1, *Paracamelus aguirrei* (extinct)[1], Species cluster 1 (*Paracamelus* sp. (extinct)[1], *C. hesternus* (extinct)[1], *C. bactrianus*, *C. dromedarius*) and Species cluster 2 (*C. bactrianus*, *C. dromedarius*)

[1] Study performed on fossils or stuffed collections.

Table 2. Mean, mode and interquartile range (IQR) for the variables of Journal Citation Report (JCR) impact factor per paper publication year, mean JCR impact factor per journal during the whole period, total citations of the paper, mean number of citations per journal and predictors in the model designed.

Variable	Median	Mode	IQR
JCR impact factor per paper publication year	1.50	0.00	2.30
Mean JCR impact factor per journal in the whole period	1.32	0.00	1.42
Total citations of the papers	12.00	0.00	25.00
Mean number of citations per journal	20.00	20.00	16.56
Journal	102	181	127
Number of authors	4	3	4
Country of corresponding author	30	41	30
Area/Topic	9	8	7
Year of publication	2010	2019	19
Camel species	4	4	4

test for multicollinearity, respectively) were performed using SPSS Statistics for Windows statistical software, Version 25.0, IBM Corp. (2016).

Statistical analysis

As preliminary tests and our study data had violated parametric assumptions, a nonparametric approach was suggested. A summary of the median and mode for the variables and predictors assessed in this study is reported in Table 2.

Initially, to determine the general evolution of camel research and its impact, a Kruskal–Wallis H test, Dunn test and Bonferroni correction were performed to identify differences in the distribution of the Journal Citation Report impact factor per paper publication year, the mean JCR impact factor per journal in the whole period, the total number of citations of papers and the mean number of citations per journal across levels of the variables name of the journal, number of authors, country of corresponding author, topic, year of publication and camel species studied while reducing the likelihood for an increased Type I error. Type I errors could potentially derive from redundancies resulting from the inclusion of an excessive number of factors (considering the relatively limited sample of our study) that are reducing the possibility to falsely detect an effect (noise), which indeed is not present, as a result of the inclusion of multiple variables (noise variables).

Afterwards, as a way to evaluate the second aim, an additional Kruskal–Wallis H test, Dunn test and Bonferroni correction were performed to identify and describe differences in camel research impact-related variables across the periods running from the publication of an international regulation and the following one. According to this criterion, the periods determined were 1880–2006, 2007–2011, 2012–2014, 2015 and 2016–2019.

These statistical analyses were aimed at evaluating the association between camel research progress and camel-related laws by opposing the specific topics and the critical points that these regulations approached to the scientific advances occurring during the period before each legislation was released. In the case that a previous legislation existed, advances considered were those comprised by the period between the previous legislation and the new one. Topics and critical points were quantitatively and qualitatively determined after empirical comprehensive examination of the content of regulation sources. In that connection, the mandatory or voluntary character and geographical scope of the application of such legislations are contemplated as the absence of derived legal responsibility and regional endowment policies can cause these guides to be overlooked.

Kruskal–Wallis H is based on a single independent factor accounting for the variance explained of a dependent variable with no additional factor contributing to the explanation of such variance at the same time. If a factor has reported a significant effect, then all levels in the same factor must be evaluated in pairs until all possible combinations have been tested.

Out of all possible comparison pairs, only statistically significant pairwise comparisons were considered by the Dunn test. Once pairs between which significant difference existed had been identified, a test of independence of the median was performed to detect differences in the median for the variable of 'Journal Impact Factor' across levels of the same factor.

Then, categorical regression (CATREG) with the Optimal Scaling Procedure from the Regression task in SPSS Statistics for Windows, Version 25.0, IBM Corp. (2016) was applied to issue specific regression equations to predict how research impact (scored through the dependent variables of JCR impact factor per paper publication year, mean JCR impact factor per journal and year, total citation number per paper and mean total citation number per journal, Table 2) linearly depended on the predictors which nonparametric tests determined to be significant ($p < 0.05$).

CATREG analysis can be used to summarize linear relationships between dependent variables that are simultaneously influenced by a set of independent variables. R squared was used to determine the ability of the model comprising the independent variables or factors reported in Table 1 to capture the variability in the continuous variables describing impact factor. R squared has also been defined as the coefficient of determination of a certain model. In these regards, higher R squared values may be a sign of smaller differences between observed data and fitted values derived from the application of the model.

Contextually, when factors lack a certain unit of measure (such as ordinal or categorical ones) or the units for the factor comprised within a certain model differ, β standardized coefficients should be used to interpret and compare their effects on our dependent variables. This way, models using standardized coefficients can be compared as a result of the intercept in each model being reduced to 0.00 after the standardization process. Following the common notation models, the regression equations for each predictor variable were $Y_n = \beta_n Z_n + \varepsilon$, where Y_n is the n variable predictor, β_n is the regression coefficient for the n variable obtained in the n main component, Z_n is the score obtained in the field for n variable and ε represents the estimation error. Specific regression equations are reported in the Regression Coefficients subsection of the Results section of the present manuscript.

During the process of evaluation of β standardized coefficients, 0.632 bootstrap cross-validation was used to estimate the prediction error of the CATREG model, provided our sample size was sufficient for the number of predictors comprised in the model in order for 0.632 bootstrap to be reliably computed as suggested by other authors (Mevik & Cederkvist, 2004).

As impact factor variables could somehow relate to the result of the methods used for them to be determined, to evaluate the correlation between the impact factor related variables compromised in our study, Spearman's rank-order correlation was performed using the Bivariate task of the Correlate Procedure in SPSS Statistics for Windows, Version 25.0, IBM Corp. (2016) (Supplementary Table S2).

Results

Database filtering process: study sample

The word 'camel' was included in 24,611 results on first search in ScienceDirect site. From 2000 until 2019, the number of results reported was 13,932, while the rest (10,679) were published between 1880 and 1999. For this 139-year period (1880–2019), the mean number of articles per year was 177. The study sample comprised publications until 2019 as this was the last complete year when the study was performed.

When sorted depending on their type, total publications including the word 'camel' comprised 1520 reviews, 14,122 research articles, 597 encyclopedia entries and 3060 book chapters. Approximately 5312 articles, conference abstracts, case reports, data articles or short communications had been published under an open access policy.

Those publications which did not focus on the *Camelus* genus or its species (rather allude to the term, not the animal itself) were discarded. In the end, the study sample comprised 1011 articles (135 were published in open access sources) which specifically dealt with camels and their products.

The number of different journals in which these articles were published was 203 (49 journals or book chapters non-indexed in JCR in the year of publication of their reviewed camel-related papers and 154 JCR indexed journals). Considering the country of the corresponding author for each article, camel research is present in 56 countries around the world.

Regarding specific protection-and-care laws, the World Organization for Animal Health (WOAH) 'Terrestrial Code' (2019) contemplates camels as livestock and thus has provided concrete welfare recommendations since its first edition in 1968 until the present. Simultaneously, national mandatory regulations that categorically include camels as goods-production livestock were solely endorsed in four countries through the following specific legislations; 'Decree on Animal Transport' (Tunisian Ministère de l'Agriculture et des Ressources Hydrauliques, 2007), 'Animal Welfare Regulations' (Government of South Australia, 2012), 'Regional Decree on Dromedary Transport Activities' (Government of Canary Islands, 2015) and 'Animal Welfare Act' (USA Department of Agriculture Animal and Plant Health Inspection Service, 2016). No further legislation was found at a national or international level.

Conditioning factors analysis

Publications dealing with camels have markedly increased since the beginning of the present century, as shown in Figure 1. The journals in which papers dealing with camels were more frequently represented are summarized in Figure 2.

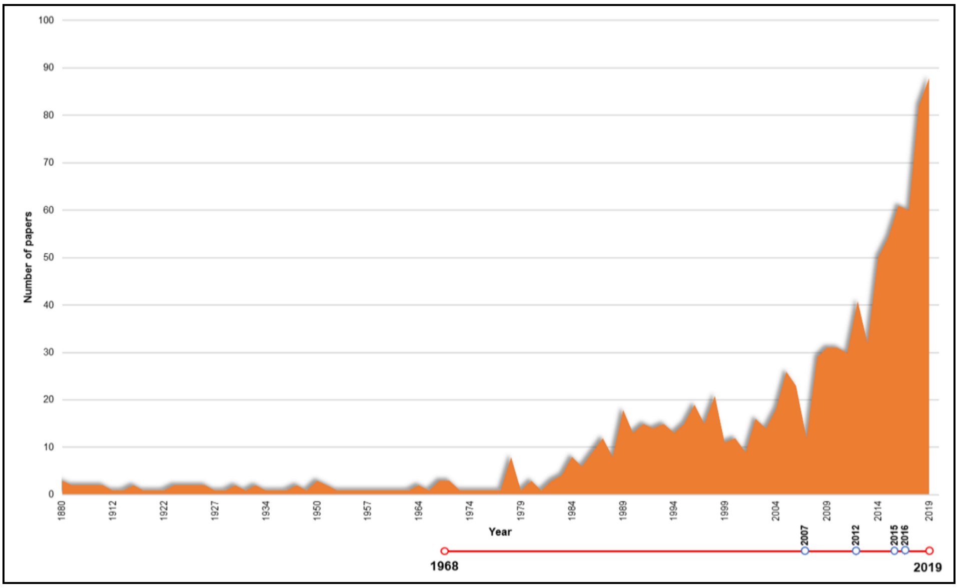


Figure 1. Number of camel research publications from 1880 to 2019. Timeline is represented below the graph in red, with blue-contoured spots marking the moment of release of a regulation document.

The highest JCR impact index (23.083) was reached by an article focused on functional heavy-chain antibodies in *Camelidae* and published in 'Advances in Immunology' in 2001 (https://doi.org/10.1016/S0065-2776(01)79006-2). On the other hand, the article with the lowest JCR impact index (0.128), which is about camel-related human injuries, was published in 'Injury' in 1994 (https://doi.org/10.1016/0020-1383(94)90152-X). Mean JCR impact index per year between 1992 and 2019 is shown in Figure 3.

The most cited publication (779 cites) focused on single domain camel antibodies and was published in 'Reviews in Molecular Biotechnology' in 2001 (https://doi.org/10.1016/S1389-0352(01)00021-6). Contrastingly, 83 scientific publications (with independence from the topic or the periods considered in this study) have received no citations until 31 December 2019. Mean number of citations per year is presented in Figure 3.

For JCR impact factor per paper publication year across journals, significant differences ($p < 0.05$, df = 202) were found between most of the pairwise comparisons.

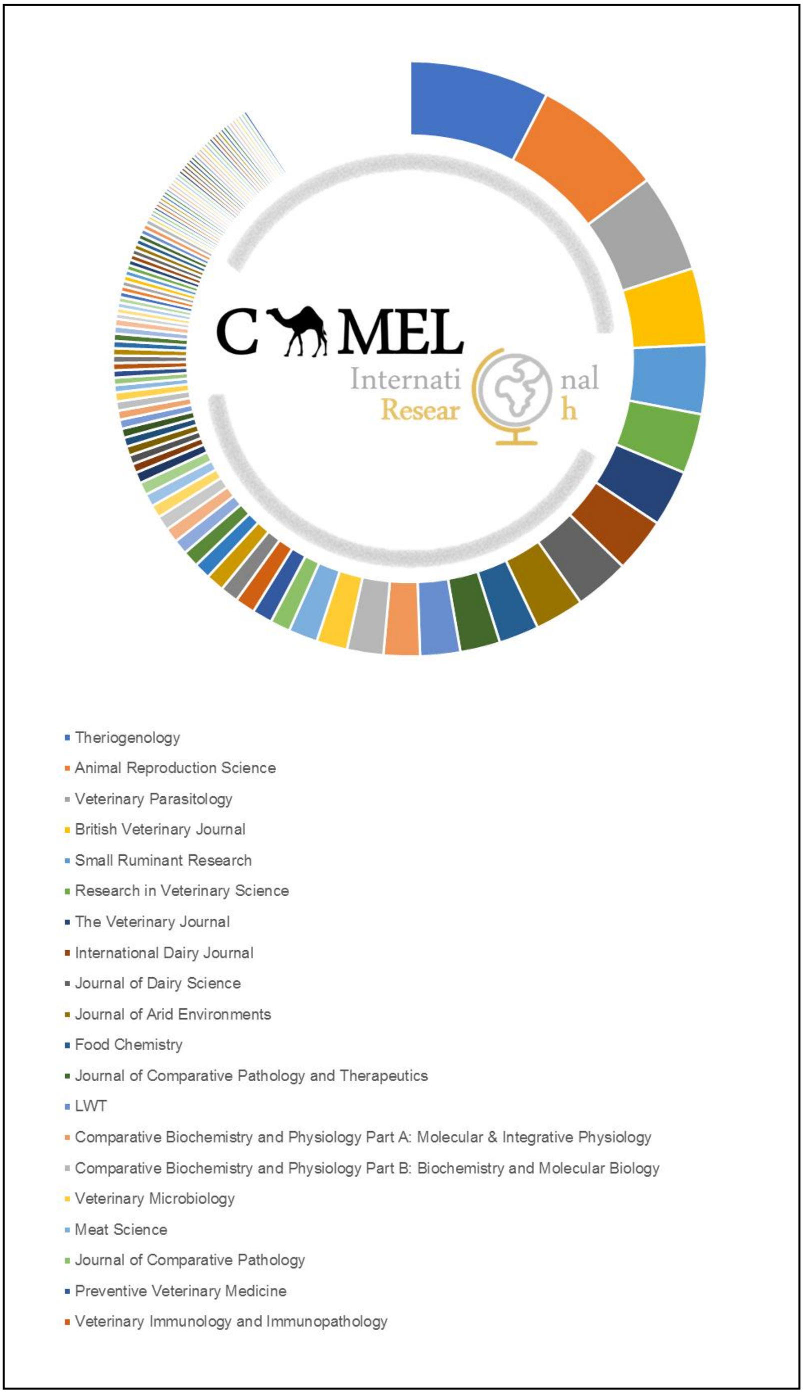


Figure 2. Number of historical publications on camels across journals.

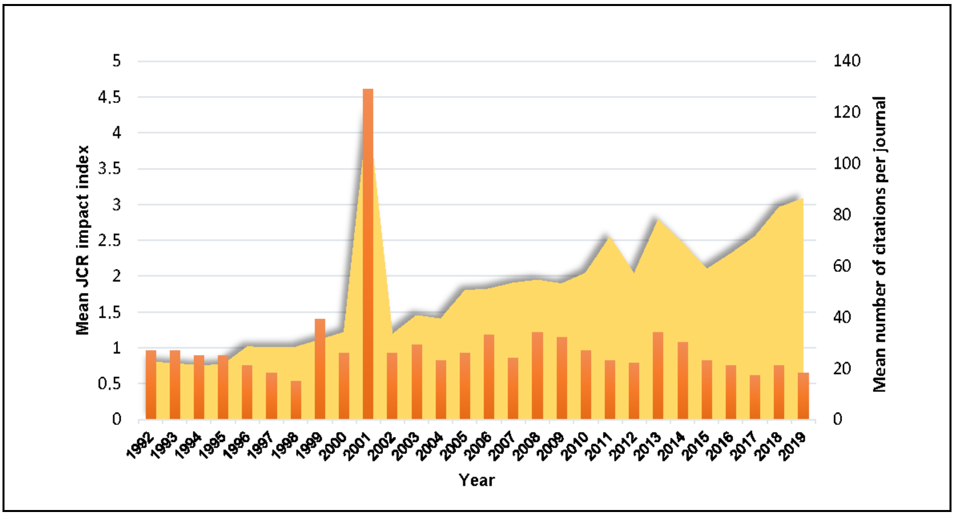


Figure 3. Mean JCR impact index and mean number of citations per year between 1992 and 2019.

For the other three variables (mean JCR impact factor per journal in the whole period, total number of citations of papers and mean number of citations per journal), there were significant differences ($p < 0.01$, df = 202) between the journals focused on Food Science and Technology, Camel Health and Camel Reproduction (median JCR > 1.5) and the remaining journals (median JCR > 1.5).

Similarly, when the number of authors participating per publication was considered, significant differences ($p < 0.05$, df = 16) were found for JCR impact factor per paper publication year, mean JCR impact factor per journal and the mean number of citations per journal between publications in which 7–12 or up to five authors had been involved; in the case of the latter, these were indeed the most frequent cases as well. No significant differences ($p > 0.001$, df = 16) were found for total number of citations per paper.

When evaluating scientific impact factor across country of corresponding author, significant differences ($p < 0.05$, df = 55) were found between central and north-east European and Asian and North African countries for the four variables considered. Within Asia, significant differences ($p < 0.001$) were found between Middle Eastern countries and other rather eastern countries of this area (China, Japan, Malaysia and Thailand) with scientific publications in camels. Figure 4 depicts a Quantum Geographical Information System (QGIS) map displaying the number of camel research papers per country to illustrate these results. The relative contribution of papers to camel science depending on the topic/s addressed by such papers is reported in Figure 5.

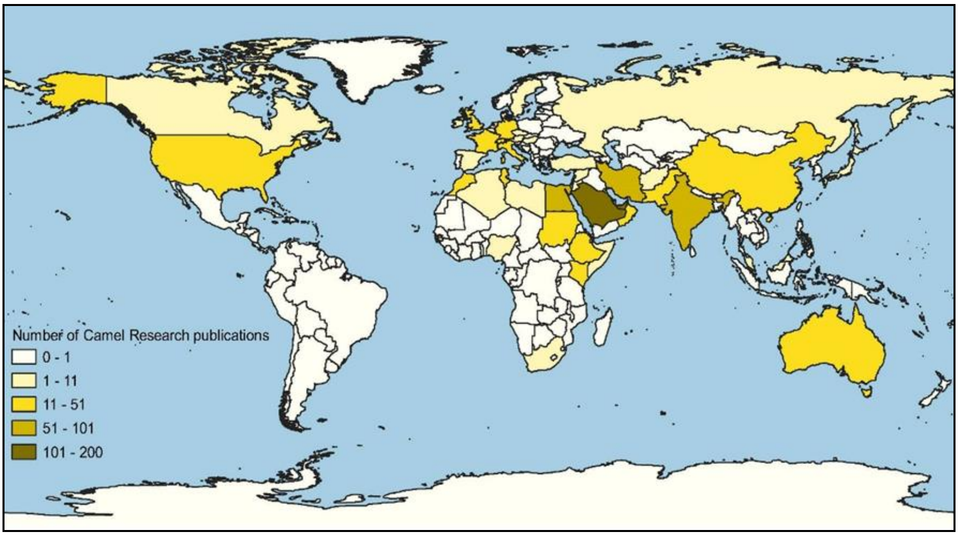


Figure 4. QGIS Map displaying number of camel research papers per country.

In relation with the different topics addressed by camel research, there were significant differences ($p < 0.05$, df = 17) for the four variables considered between Animal Health (Parasitic and Infectious Diseases), Food Science and Technology and Camel Reproduction in comparison with Livestock Management and Production, Physiology, Adaptative Ecology and Clinical and Biomedical Research. Figure 6 shows the frequency distribution of specific topics in international camel research. The most common topics (more than 90 publication at least), in increasing order of frequency, were Food Science and Technology, Reproduction, Clinical and Biomedical Research, Parasitic Diseases and Infectious Diseases. Figure 7 represents the evolution of the number of publications within the five most popular topics in camel research on a global scale.

The year of publication factor reported significant differences ($p < 0.005$, df = 85, as no impact factor had been registered for any of the journals before 1992) between the years in the early and mid-20th century and the articles published since 1990 (especially those from 2000 to 2019) for all variables considered.

When camel species conditioning effect was examined, no significant differences were reported ($p = 0.005$, df = 11) for any of the variables studied. However, when frequencies were compared, the number of publications for which *Camelus dromedarius* was the species studied was substantially higher than those for *Camelus bactrianus*.

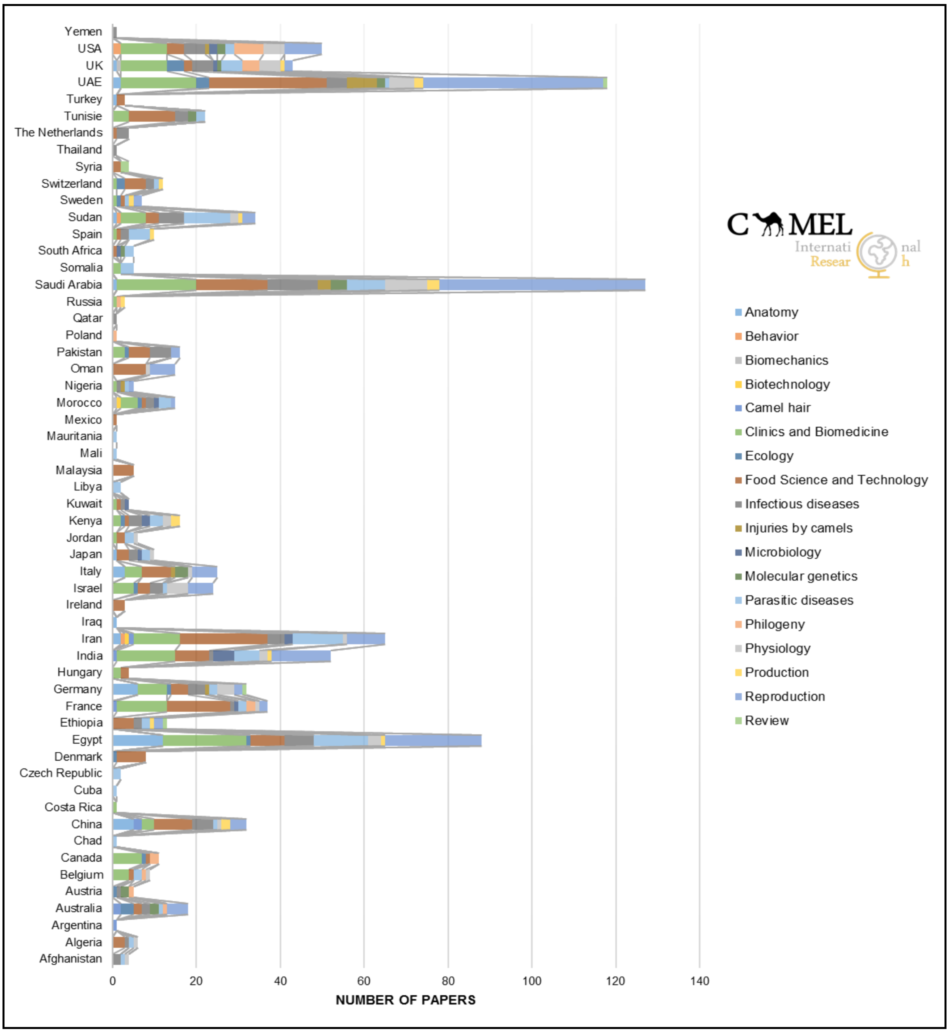


Figure 5. Number of scientific publications per country and research item within camel science.

Chronological evolution of specific legislation and research advances

Significant differences ($p < 0.05$, df = 4) were found between JCR impact factor per paper and publication year and mean JCR impact factor per journal in the whole period between scientific publications published between 1880–2006 and the remaining four periods considered in this study. When considering the total number of citations to papers and the mean number of citations per journal, there were significant differences ($p < 0.05$, df = 4) between the papers published between 2016–2019 and the papers published between 1880-2015. The parallel evolution of camel research advances and

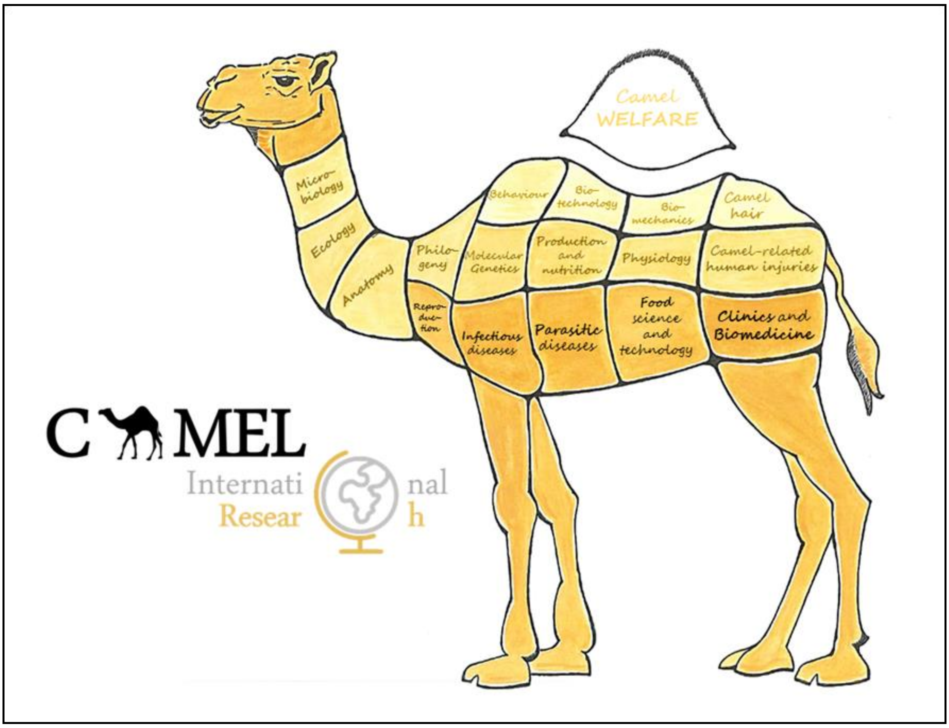


Figure 6. Specific topics in camel international research. Colour intensity is relative to the number of publications in each scientific area. The darker, the higher the number of publications dealing with that topic.

specific law enforcement are presented in Figures 1 and 7 (red chronological line).

The WOAH 'Terrestrial Code' describes and defines general protocols and directives that may be relevant to camel welfare such as standards for animal transport, their slaughtering process for human consumption and some specific facts and concerns applicable to specific diseases. This 'Terrestrial Code' is an annual-edition compendium that includes a user guide intended to help competent authorities and other interested parties worldwide to interpret its regulation content and encourages legislative councils to promote legislative adaptations both at a regional or wider international scale when necessary. In this context, national laws are reduced to a brief, technical-based approach for basic physiological needs satisfaction and handling practices during transportation and slaughtering, both with farmed and feral camels.

Regression coefficients

Table 3 reports standardized regression coefficients for each of the predictors for which a significant effect ($p < 0.05$) was detected using the Kruskal–Wallis H test. These

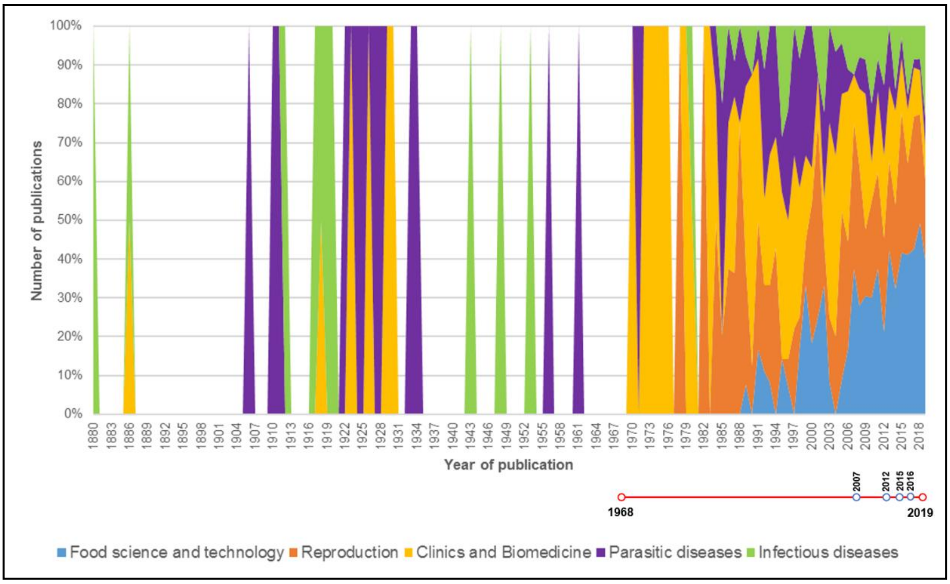


Figure 7. Numerical evolution of the five most popular items in camel international research from 1880 to 2019. Topics with publications number below 90 were omitted to improve the interpretability of the results. Timeline is represented below the graph in red, with blue-contoured spots marking the moment of release of a regulation document.

regression coefficients were used to issue the following equation describing the linear relationship between journal impact factor related variables and the predictors of journal, country of corresponding author, topic and year. Table 4 shows the regression equations that were used and a model summary for the regression equations issued for journal impact factor using standardized data.

Discussion

Potential conditioning factors in camel science progress

The progressive mechanization of agricultural labors relegated the camel to the background in tasks to which it had traditionally been used (to achieve an almost exclusive role as a source for food (meat and milk) or leisure (camel races and tourism)). However, camel cultural relevance has hardly been affected in countries where nomadic tribes still exist and whose survival depends on these animals, whose extended use is also frequently linked to an inefficient transport network (Wilson & Ababa, 1989).

Table 3. Standardized regression coefficients for each of the predictors reporting a significant value (P<0.05) at Kruskal-Wallis H test.

JCR impact factor per paper publication year	**β**	**0.632 Bootstrap Estimate of Std. Error**	**df**	**F**	**Significance**
Journal	0.732	0.028	202	660.910	0.001
Number of authors	0.089	0.032	3	7.785	0.001
Country of corresponding author	0.156	0.026	55	36.065	0.001
Area/Topic	0.266	0.064	17	17.260	0.001
Year of publication	0.575	0.030	17	359.966	0.001
$Y_{JCR/journal/year} = 0.732 \cdot X_{Journal} + 0.089 \cdot X_{Authornumber} + 0.156 \cdot X_{Country} + 0.266 \cdot X_{Topic} + 0.575 \cdot X_{Year}$, where X is the observation for each of significant predictors encoded as a number.					
Mean JCR Impact per journal in the whole period	**β**	**0.632 Bootstrap Estimate of Std. Error**	**df**	**F**	**Significance**
Journal	0.977	0.009	202	11022.598	0.001
Number of authors	0.001	0.055	16	0.001	1.000
Country of corresponding author	0.058	0.032	55	3.288	0.001
Area/Topic	0.100	0.036	17	7.457	0.001
Year of publication	0.155	0.033	82	21.577	0.001
$Y_{JCR/journal} = 0.977 \cdot X_{Journal} + 0.058 \cdot X_{Country} + 0.100 \cdot X_{Topic} + 0.155 \cdot X_{Year}$, where X is the observation for each of significant predictors encoded as a number.					
Total citations of the paper	**β**	**0.632 Bootstrap Estimate of Std. Error**	**df**	**F**	**Significance**
Journal	0.735	0.099	192	550.010	0.001
Number of authors	0.342	0.166	15	40.252	0.001
Country of corresponding author	0.290	0.073	53	150.724	0.001
Area/Topic	0.397	0.133	16	80.972	0.001
Year of publication	0.403	0.080	80	250.362	0.001
$Y_{totalcitations} = 0.735 \cdot X_{Journal} + 0.342 \cdot X_{Authornumber} + 0.290 \cdot X_{Country} + 0.397 \cdot X_{Topic} + 0.403 \cdot X_{Year}$, where X is the observation for each of significant predictors encoded as a number.					
Mean number of citations per journal	**β**	**0.632 Bootstrap Estimate of Std. Error**	**df**	**F**	**Significance**
Journal	0.987	0.007	202	19778.36	0.001
Number of authors	0.001	0.039	4	0	1.000
Country of corresponding author	0.065	0.031	55	4.465	0.001
Area/Topic	0.062	0.031	17	3.988	0.001
Year of publication	0.067	0.02	82	11.186	0.001
$Y_{meancitations/journal} = 0.987 \cdot X_{Journal} + 0.065 \cdot X_{Country} + 0.062 \cdot X_{Topic} + 0.067 \cdot X_{Year}$, where X is the observation for each of significant predictors encoded as a number.					

Table 4. Model summary for Categorical Regression of Journal Impact Factor using standardized data.

JCR impact factor per paper publication year			**Multiple R**	**R^2**	**Adjusted R^2**
			0.952	0.906	0.852
ANOVA	**Sum of squares**	**df**	**Mean square**	**F**	**Significance**
Regression	916.288	372	2.463	16.592	0.001
Residual	94.712	638	0.148		
Total	1011	1010			
Mean JCR Impact per journal in the whole period			**Multiple R**	**R^2**	**Adjusted R^2**
			0.999	0.999	0.999
ANOVA	**Sum of squares**	**df**	**Mean square**	**F**	**Significance**
Regression	1010.972	372	2.718	62822.211	0.001
Residual	0.028	638	0.000		
Total	1011	1010			
Total citations of the paper			**Multiple R**	**R^2**	**Adjusted R^2**
			0.901	0.812	0.695
ANOVA	**Sum of squares**	**df**	**Mean square**	**F**	**Significance**
Regression	753.584	356	2.117	6.930	0.001
Residual	174.416	571	0.305		
Total	928	927			
Mean number of citations per journal			**Multiple R**	**R^2**	**Adjusted R^2**
			0.999	0.999	0.999
ANOVA	**Sum of squares**	**df**	**Mean square**	**F**	**Significance**
Regression	1009.944	372	2.715	30624.972	0.001
Residual	0.056	637	0.000		
Total	1010	1009			

This relegation leads to the progressive social appreciation of these multipurpose animals because of their production performance even under extreme climatic conditions (Yagil, 1982), the biomedical applications of some of their derived products (Alebie, Yohannes, & Worku, 2017) and their potential for animal-assisted therapeutics (Parish-Plass, 2013). A notable and competitive increase in the interest provided to the functional potentialities of the species have appeared on the scene singularly in the last 30 years, reaching a mean annual growth of 11.02%, with their maximum value (141.67%)

reached in 2008. This academic upturn is simultaneous to an increase in worldwide camel census (Faye, 2014; Faye, Chaibou, & Vias, 2012) and ratified both by the largest peak in the mean impact factor achieved by the research documents dealing with camels occurring in 2001 (Figure 3) and the upward positive trends in camel science impact since then (Supplementary Table S2). In spite of these results, when compared to other domestic livestock, publications on camels are marginal from a quantitative point of view, which is largely due to world censuses on camels being smaller, the limited geographical distribution of these animals and to the fact that markets still continue investing little in products derived from camels given the misconception about them being unproductive animals. Therefore, scientific interventions may need to focus on exploring and implementing actions towards the achievement of new production niche opportunities, addressing challenges/constraints in marketing camel derived products and the efficiency and effectiveness of their commercial distribution chain (Gebremichael & Girmay, 2019; Gebreyohanes & Assen, 2017).

Fortunately, the relatively high number of open access publications have to be considered as it reflects the trends in camel research. Contrastingly, open access costs may be taken into account as these economic barriers could imply scientists may not be able to afford an effective wide communication. In this context, Freire and Nicol (2019) proposed self-archiving and open access policies should be promoted and subsidized as a way to encourage the role of developing countries in future scientific challenges.

The first countries to start paying attention to these animals in this regard were those in which a previous tradition forged in camel breeding and production existed, with the benefits derived from the species occurring at both an economic and socio-cultural level (Wilson & Bourzat, 1988). Our results address a relationship between the countries with the highest number of publications and the above-mentioned estimates of global growth of the dromedary and Bactrian camel populations; that is, a higher number of publications from those countries where there is a positive growth of these animal populations (Faye & Bonnet, 2012) and in which traditional camel breeding and production systems are well established (Figure 4). Therefore, given the economic and cultural role of camels in these geographical regions, the specialization of their research groups and desire to publish in journals of high impact factor would be higher. The demographics and institutional prestige of the corresponding author could also bias submitted manuscript outcomes (McGillivray & De Ranieri, 2018). As our results suggested and which could be somehow expected, eastern Africa and Middle Eastern countries reached the higher mean impact indexes, provided their tradition in the implementation of research advances and hence the scientific impact of the authors involved in the publications of papers.

Closely related to this and despite of the fact that the species studied appeared not to statistically significantly influence research impact in camel science, the number of publications dealing with *Camelus dromedarius* (n = 491) are substantially more numerous than those dealing with *Camelus bactrianus* (n = 40) and *Camelus ferus* (n = 3). This could be explained by the existence of a greater number of animals in the African continent according to published censuses (Faye, 2015) and because the animals in this continent are the fundamental subsistence base of human populations. In this context, development of research projects is necessary to investigate the different functional niches into which dromedaries can be functionally and potentially improved. On the other hand, Bactrian camels, which are mainly found in the Arabian Peninsula, are less numerous and are mostly confined to racing sports, which, compared to dromedaries, would be one of the main functional niches. Nonetheless, the average research impact index is higher for publications covering common aspects of the genus Camelus. Such a finding can be ascribed to the fact that those studies specially focused on one of the three camel extant species and are strongly dependent on the data derived from those focused on common issues in the genus *Camelus* and are thus cited at higher rates.

The progressive increase of the dromedary population in Africa is also linked to the sedentarization of previously nomadic populations in this continent and their initiation to camel breeding, the production for their subsistence and the development projects carried out in these countries since the end of the 20th century (Franck, Vall, Ibrahim, & Faye, 2004; Thébaud, 1988). The establishment of agropastoral systems due to the closure of important migratory routes derived from the privatization of sections of the drylands for large-scale agriculture forced pastoralists to diversify into agriculture and the market economy. For the scientific community, this would allow access to a greater number of dromedaries under human control, a fact that would facilitate its management and the planning of cooperative research studies.

In this context, when establishing international partnerships and preparing papers to be published, the number of authors involved affects the probability of publishing (Kalwij & Smit, 2013) in highly ranked journals (Al-Herz, Haider, Al-Bahhar, & Sadeq, 2014). If a study conjoins the efforts of multiple research centers, data is gathered by multiple persons, cross-sectional studies are carried out, statistical analysis are done by different people, and the complexity of the studies in higher, then it is justified to have an increased number of authors (Wren et al., 2007). Furthermore, these types of multi-center studies have higher sample sizes and are published in journals acknowledged with higher impact factors (Larivière, Gingras, Sugimoto, & Tsou, 2015). In particular, in consortium-derivative research, the creation of a solid network as specialized as possible is crucial to deal with the requirements of interdisciplinarity and thematic complexity required by certain research fields (Abramo & D'Angelo, 2015). Authors of a high professional background belonging to research institutions of recognized prestige or more advanced countries specialized in certain topics usually play important roles in the coordination and direction of international projects and networks. The magnitude of co-authorship and inter-institutional collaboration can be extrapolated to the quality and quantity of the work and collaboration networks established to carry out an investigation, which consequently implies a greater probability of the results obtained being transferred to society (Abramo & D'Angelo, 2015) and improves visibility in terms of journal importance (Bordons, Aparicio, & Costas, 2013). Contrastingly, some authors reject the existence of a positive association between the number of authors and the prestige of the journal when measured by its impact factor as this association is evaluated for a specific country or area, which may bias the results (Abramo & D'Angelo, 2015). These authors claim that if sample size is reduced, the study does not involve a multi-center background, and having a large number of authors may not be justified.

On the other hand, when evaluating research impact at a minor scale such as the total citations to each published paper, the number of authors does not necessarily condition it. Accordingly to this statement and our particular findings, the above-average visibility achieved by co-authored publications measured in terms of citations received is not an objective criteria when predicting research impact as self-citation can magnify it, especially when research is performed by more authors and from distinct institutions (Abramo & D'Angelo, 2015).

In summary, our results show the average impact is greater for the publications in which 7–12 authors are involved. Research groups from countries with traditional camel breeding and production systems (Africa and Middle Eastern countries), mainly involved in world-level cooperating projects for its specialty in the subject, reported the highest scientific outcomes. The greatest advances in camel international research were produced in the areas of Food Science and Technology, Camel Health (Infectious and Parasitic Diseases) and Camel Reproduction.

For the particular case of Clinical and Biomedical Research, although scientific papers in this applied field of research are one of the more numerous within camel science, their impact remains low. Although it can be considered as an emerging research topic due to its radical novelty and relatively fast growth, its novelty and the need for standardization of related methodologies may be conditioning its impact and dissemination in high-impact multidisciplinary journals that could favor a broader visibility of this promising research field among the scientific community (González-Alcaide, Llorente, & Ramos, 2016; Q. Wang, 2018). Such findings are also supported by the upturn of the topic 'Food Science and Technology' over the 'Clinical and Biomedical' discipline since the early 20th century (Figure 6), as prior to biomedical research for camel-derived products, it may have been useful and preferable to perform a characterization of these products, of which Food Science and Technology may be responsible.

Meanwhile, topics such as Management, Nutrition, Ecology, Genetic Management and Production are scarcely approached (Wardeh, 1994) and likewise, the results of these research topics are often inconclusive due to reduced sampling, scant observations or weak statistical treatment of data (Khan et al., 2003). This situation can be conditioning the current limited interest of the scientific community in camel welfare because of the close relationship between animal wellbeing and food-producing systems in the emerging scenario of this industry. Consequently, production-related topics must be urgently reoriented and assessed due to production–health–welfare complex interactions.

Camel research advances' impact on extended related legislation

Until the late 1990s, camel production was mainly based on a traditional husbandry system ascribed to rural livelihoods whose main purpose was the obtention of derived products such as meat and milk. Although the notorious impact of camel research, especially in the last two decades, clearly underlines the increase in the economic interests in camel breeding and the progressive technification of rearing systems for their productive potentialities (Faye et al., 2014), scarce scientific attention has been paid to such related topics (production and behavior physiology) (Figure 7). In the absence of quantitative information regarding the level of camel welfare in different housing systems, their basic needs may not be fully satisfied and their productive potential and profitability are devalued as their general health status might be affected by neglected practices. In this context, research impact factor related variables must be considered carefully when we aim to determine their potential conditioning effect on the evolution of regulations. Studies have shown that research documents need at least two to three years after publication to be cited enough for bibliometric indicators to be reliable and citations also continue accumulating over time (Abramo, Cicero, & D'Angelo, 2011; Wang, 2013). This means that older papers are more cited than younger ones just because they have had more time to accumulate citations, but not necessarily for their scientific impact or improvement they may entail.

As animal welfare could comprise and be conditioned by multiple factors such as different people's view or animal scientists' perspectives, it becomes crucial to present and identify common and opposing points of view to achieve the most comprehensive worldwide-accepted definition. Participative dialogues for extensive discussions involving industry, welfare research groups, experienced advisers and lawmakers have to be proposed so as to approach farmed camels' welfare and address the most appropriate ways to maximize their efficiency and productivity in a sustainable manner. For this purpose, advances in the understanding of animal physiology and behavior, technological changes in animal husbandry and their relationship to the welfare of animals must be taken into account (Vapnek & Chapman, 2010).

Since derived legislation in poultry, pigs, cattle, sheep, goats and fur animals' welfare is widely available, specific regulations and guidance concerning the welfare of reared camels are noticeably limited (Previti, Guercio, & Passantino, 2016). At an international level, the World Organisation for Animal Health (OIE) 'Terrestrial Code', an annual-edition compendium, describes and defines general, brief protocols and directives that may be relevant to camel welfare such as standards for animal transport, their slaughtering process for human consumption and some specific facts and concerns applicable to specific diseases. However, this 'Terrestrial Code' includes specific chapters containing detailed minimum requirements and recommendations for cattle, chicken, equid and pig welfare depending on production systems or regimes in which reared, from birth through to finishing; that is, specifically animal-based criteria or measurables that can be useful indicators of animal welfare and other outcome-based recommendations (i.e., biosecurity, environmental conditions and management practices). For camels, this information is lacking. Such a finding provides insight into the need for camel science to be reinforced in closely related topics, as the OIE standards are based on the most recent scientific articles in light of advances in veterinary science. Camels are only considered in this global code for transportation and slaughtering purposes.

When seeking both animal and human co-existence and prosperity, nationally competent authorities should promote alternatives and implement research and development projects for existing animals' sustainable exploitation. Only four countries in the world have enforced internal compulsory regulations on minimum, shallow requirements for the farming, transportation and slaughtering of camels. Both farmed and feral social awareness is presumably very low, which ratifies that certain camel science approaches remain little-known. In addition, global animal welfare councils are not encouraging national lawmakers to undertake specific mandatory regulations. Therefore, camel keepers may not be overcoming challenges provided by their emerging condition and the lack of specific legislation for these animals in terms of animal wellbeing.

Under this framework, while innovative legislation is being drawn up, well-organized camel industries are expected to demand high voluntary provisional welfare standards from their human resources and research needs to be compulsorily considered in the process. In this sense, the scientific community plays an additional role to prevent livestock producers from starting to think like business people for whom sustainable and good husbandry practices could be disregarded as a result of animals being considered mere economic products. By recognizing the positive effects of animal wellbeing on production rates, the public's perception of the livestock industry as a whole will improve, and the resultant regulations of collaborative conventions will be extended.

Countries where camel censuses are significantly higher and/or their outstanding research potential is widely recognized could be suitable for promoting large research consortia on a global scale. These consortia will be formed by solid entities to play advisory roles in camel welfare science using their direct empirical experience derived from the analysis of large samples, which may maximize the validity of their conclusive results. In turn, this may translate into the potential influence and interpretation of camel literature for policy purposes to promote the access to the financial resources for academics to carry out their research.

Conclusions

Despite animal welfare scientific interests having grown considerably due to consumers' concern worldwide, it remains overlooked in some minor species, such as farmed camels. Maintaining ethically acceptable conditions in these animals when reared requires the establishment of evidence-based guidelines measuring environmental and animal-based welfare indicators and scores. These implementations may lead to the prosperity of the species and its relationship with humans through the achievement of sufficient camel welfare outcomes. The present research highlights the current request for in-depth and constructive intercommunication between camel breeders, consumers, scientists and policymakers. This increase in communication must be implemented to seek the commitment for law enhancement to address specific emerging needs in these multipurpose animals. This situation may make camel production and functionality based on socially, economically sustainable production systems on a global scale. In this context, the relationship between science and authorities should become the leitmotif on which to rely to face and approach not only the productive opportunities, but also priority challenges and sustainable improvements to ensure the long-term future of camels. The world's highest-ranked research institutions in camel science are cardinal when establishing this pluridirectional communication interface due to the high research performance that they present, their innovation outputs and their impact in society.

Supplementary materials: The following are available online at http://www.mdpi.com/2076-2615/10/5/780/s1, Table S1. Results of Shapiro–Francia W' test with log transformation [51], Table S2. Spearman's rank-order correlations between impact factor related variables for camel research documents.

Author contributions: Conceptualization, C.I.P., F.J.N.G., E.C. and J.V.D.B.; Data curation, C.I.P. and F.J.N.G.; Formal analysis, C.I.P. and F.J.N.G.; Funding acquisition, C.J.B.C. and J.V.D.B.; Investigation, C.I.P., F.J.N.G. and J.V.D.B.; Methodology, C.I.P. and F.J.N.G.; Project administration, C.J.B.C. and J.V.D.B.; Software, C.I.P., F.J.N.G. and J.V.D.B.; Supervision, F.J.N.G., E.C. and J.V.D.B.; Validation, F.J.N.G.; Visualization, E.C., C.J.B.C. and J.V.D.B.; Writing—original draft, C.I.P.; Writing—review and editing, F.J.N.G., E.C., C.J.B.C. and J.V.D.B. All authors have read and agreed to the published version of the manuscript.

Funding: The present research was carried out in the financing framework of the international project CA.RA.VA.N—"Toward a Camel Transnational Value Chain" (Reference APCIN-2016-00011-00-00) and during the covering period of a predoctoral contract (Submodality 2.2 'Predoctoral research staff') funded by the University of Cordoba, Spain.

Acknowledgments: The authors would like to thank the contribution and support of the members of the AGR-218 research group of the University of Cordoba, Spain.

Conflicts of interest: The authors declare no conflict of interest. The founding sponsors had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, and in the decision to publish the results.

References

Abramo, G., Cicero, T., & D'Angelo, C. A. (2011). Assessing the varying level of impact measurement accuracy as a function of the citation window length. *Journal of Informetrics*, 5(4), 659-667.

Abramo, G., & D'Angelo, C. A. (2015). The relationship between the number of authors of a publication, its citations and the impact factor of the publishing journal: Evidence from Italy. *Journal of Informetrics*, 9(4), 746-761.

Acharya, K. P., & Pathak, S. (2019). Applied Research in Low Income Countries: Why and How? *Frontiers in Research Metrics and Analytics*, 4, 3.

Al-Herz, W., Haider, H., Al-Bahhar, M., & Sadeq, A. (2014). Honorary authorship in biomedical journals: how common is it and why does it exist? *Journal of medical ethics*, 40(5), 346-348.

Alebie, G., Yohannes, S., & Worku, A. (2017). Therapeutic applications of camel's milk and urine against cancer: current development efforts and future perspectives. *Journal of Cancer Sciences and Therapy*, 9, 468-478.

Baum, D. (2011). The status of the camel in the United States of America. Proceedings of the Camel Conference.

Berque, J. (1959). Nomads and Nomadism in the Arid Zone. *International Social Science Journal*, 11, 481-510.

Bordons, M., Aparicio, J., & Costas, R. (2013). Heterogeneity of collaboration and its relationship with research impact in a biomedical field. *Scientometrics*, 96(2), 443-466.

Burger, P. A. (2016). The history of Old World camelids in the light of molecular genetics. *Tropical animal health and production*, 48(5), 905-913.

Dahl, G., & Hjort, A. (1979). Dromedary pastoralism in Africa and Arabia pp. 144-160. The camelid all-purpose animal Volum I. Proceedings of the Khartum Workshop on Camels.

Epstein, H. (1971). *The origin of the domestic animals of Africa*: Africana publishing corporation.

Fattah, A. F. A., & Roushdy, E.-S. M. (2016). Productive performance and behaviour of calf camel (*Camelus dromedarius*) under semi-intensive and traditional rearing system. *Benha Veterinary Medical Journal*, 31, 1.

Faye, B. (2014). The camel today: assets and potentials. *Anthropozoologica*, 49(2), 167-176.

Faye, B. (2015). Role, distribution and perspective of camel breeding in the third millennium economies. *Emirates Journal of Food and Agriculture*, 318-327.

Faye, B., & Bonnet, P. (2012). Camel sciences and economy in the world: current situation and perspectives. Proceedings of the third ISOCARD conference.

Faye, B., Chaibou, M., & Vias, G. (2012). Integrated impact of climate change and socioeconomic development on the evolution of camel farming systems. *British Journal of Environment and Climate Change*, 2(3), 227-244.

Faye, B., Jaouad, M., Bhrawi, K., Senoussi, A., & Bengoumi, M. (2014). Elevage camelin en Afrique du Nord: état des lieux et perspectives. *Revue d'élevage et de médecine vétérinaire des pays tropicaux*, 67(4), 213-221.

Franck, S. V., Vall, E., Ibrahim, Y., & Faye, B. (2004). La traction cameline, un apport important dans l'évolution des pratiques de traction animale au Niger. *Revue d'élevage et de médecine vétérinaire des pays tropicaux*, 57(3-4), 177-179.

Fraser, D. (2008). Understanding animal welfare. *Acta Veterinaria Scandinavica*, 50(1), S1.

Freire, R., & Nicol, C. (2019). A bibliometric analysis of past and emergent trends in animal welfare science. *Animal Welfare*, 28(4), 465-485.

Gebremichael, B., & Girmay, S. (2019). Camel milk production and marketing: Pastoral areas of Afar, Ethiopia. *Pastoralism*, 9(1), 16.

Gebreyohanes, M., & Assen, A. (2017). Adaptation mechanisms of camels (Camelus dromedarius) for desert environment: a review. *Journal of Veterinary Science & Technology*, 8, 1-5.

González-Alcaide, G., Llorente, P., & Ramos, J. M. (2016). Bibliometric indicators to identify emerging research fields: publications on mass gatherings. *Scientometrics*, 109(2), 1283-1298.

Government of Canary Islands (2015). *Circular de 13 de Marzo de 2015, por la que se dictan Instrucciones para el Transporte de Animales de la Especie Camelidae (Dromedarios) en la Comunidad Autónoma de Canarias*; Dirección General de Ganadería: Canary Islands, Spain.

Government of South Australia (2012). *Animal Welfare Regulations*; Attorney-General's Department. Government of South Australia: Adelaide, Australia.

Kalwij, J. M., & Smit, C. (2013). How authors can maximise the chance of manuscript acceptance and article visibility. *Learned publishing*, 26(1), 28-31.

Khan, B. B., Arshad, I., & Riaz, M. (2003). *Production and management of camels*: University of Agriculture, Faisalabad, Department of Livestock Management.

Larivière, V., Gingras, Y., Sugimoto, C. R., & Tsou, A. (2015). Team size matters: Collaboration and scientific impact since 1900. *Journal of the Association for Information Science and Technology*, 66(7), 1323-1332.

McGillivray, B., & De Ranieri, E. (2018). Uptake and outcome of manuscripts in Nature journals by review model and author characteristics. *Research integrity and peer review*, 3(1), 5.

McLean, A. K., & Navas Gonzalez, F. J. (2018). Can Scientists Influence Donkey Welfare? Historical Perspective and a Contemporary View. *Journal of Equine Veterinary Science*, 65, 25-32.

Mevik, B. H., & Cederkvist, H. R. (2004). Mean squared error of prediction (MSEP) estimates for principal component regression (PCR) and partial least squares regression (PLSR). *Journal of Chemometrics*, 18(9), 422-429.

Naumann, R. (1999). *Camelus dromedarius*. *Animal Diversity Web*. Available online: https://animaldiversity.org/accounts/Camelus_dromedarius/ (accessed on 21 January 2020).

Nelson, K., Bwala, D., & Nuhu, E. (2015). The dromedary camel; a review on the aspects of history, physical description, adaptations, behavior/lifecycle, diet, reproduction, uses, genetics and diseases. *Nigerian Veterinary Journal*, 36(4), 1299-1317.

Nowak, R. M., & Paradiso, J. (1991). *Mammals of the World*: John Hopkins Press.

Padalino, B., Aubé, L., Fatnassi, M., Monaco, D., Khorchani, T., Hammadi, M., & Lacalandra, G. M. (2014). Could dromedary camels develop stereotypy? The first description of stereotypical behaviour in housed male dromedary camels and how it is affected by different management systems. *PloS one*, 9(2).

Parish-Plass, N. (2013). *Animal-assisted psychotherapy: Theory, issues, and practice*: Purdue University Press.

Previti, A., Guercio, B., & Passantino, A. (2016). Protection of farmed camels (*Camelus dromedarius*): welfare problems and legislative perspective. *Animal Science Journal*, 87(2), 183-189.

Reblando, J.R. (2018). Social changes' impact on the creation of new social and legislative rules and norms. *International Journal of Novel Research in Interdisciplinary Studies*, 5, 1–3

Royston, P. (1991). Estimating departure from normality. *Statistics in Medicine*, 10(8), 1283-1293.

Thébaud, B. (1988). *Élevage et développement au Niger - Quel avenir pour les éleveurs du Sahel?*: Editions du Bureau International du Traival.

Tunisian Ministere de l'Agriculture et des Ressources Hydrauliques (2007). *Conditions Techniques et Sanitaires pour le Transport des Animaux Concernés par l'Identification*; Ministère de l'Agriculture et des Ressources Hydrauliques: Tunis, Tunisia.

USA Department of Agriculture Animal and Plant Health Inspection Service. (2016). *Animal Welfare Act*; Department of Agriculture Animal and Plant Health Inspection Service: Riverdale, MD, USA.

Vapnek, J., & Chapman, M. S. (2010). *Legislative and regulatory options for animal welfare*: FAO legislative studies.

Wang, J. (2013). Citation time window choice for research impact evaluation. *Scientometrics*, 94(3), 851-872.

Wang, Q. (2018). A bibliometric model for identifying emerging research topics. *Journal of the Association for Information Science and Technology*, 69(2), 290-304.

Wardeh, M. F. (1994). The camel applied research and development network. *Journal of Arid Environments*, 26(1), 105-111.

Wilson, R., & Bourzat, D. (1988). Past, present and future research on the one-humped camel in Africa. *Journal of Arid Environments*, 14(1), 1-15.

Wilson, R. T., & Ababa, A. (1989). Camels and camel research in Ethiopia. Proceedings of Camel Pastoralism as a Food System in Ethiopia.

World Organisation for Animal Health (2019). *Terrestrial Animal Health Code* (28th edition); World Organisation for Animal Health: Paris, France.

Wren, J. D., Kozak, K. Z., Johnson, K. R., Deakyne, S. J., Schilling, L. M., & Dellavalle, R. P. (2007). The write position. *EMBO reports*, 8(11), 988-991.

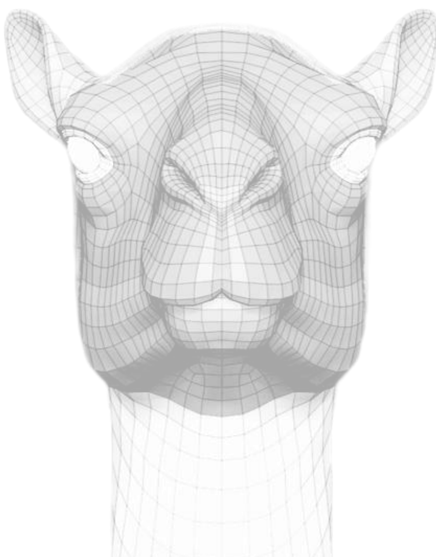
Yagil, R. (1982). *Camels and camel milk*: Food and Agriculture Organization of the United Nations (FAO) editions.

CHAPTER 2
ZOOMETRIC CHARACTERIZATION OF
'CANARIAN CAMEL' BREED

2.1 Bayesian linear regression and natural logarithmic correction for digital image-based extraction of linear and tridimensional zoometrics in dromedary camels

Carlos Iglesias Pastrana[1], Francisco Javier Navas González[1,2], Elena Ciani[3], María Esperanza Camacho Vallejo[2] and Juan Vicente Delgado Bermejo[1]

[1]Department of Genetics, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain
[2]Andalusian Institute of Agricultural and Fisheries Research and Training (IFAPA), Alameda del Obispo, 14004 Cordoba, Spain
[3]Department of Biosciences, Biotechnologies and Biopharmaceutics, Faculty of Veterinary Sciences, University of Bari 'Aldo Moro', 70121 Bari, Italy



Quality indicator information provided on the publication

Status of the manuscript: Published

Journal (year, volume, page(s)): *Mathematics* 2022, *10*, 3453

International database in which it is indexed: Journal of Citation Reports (JCR)

Thematic area in the reference database: Mathematics

Impact index of the journal in the year of the article's publication: 2.4

Rank/number of thematic area journals: 23/329 (D1)

Abstract

This study evaluates a method to accurately, repeatably, and reliably extract camel zoometric data (linear and tridimensional) from 2D digital images. Thirty zoometric measures, including linear and tridimensional (perimeters and girths) variables, were collected on-field with a non-elastic measuring tape. A scaled reference was used to extract measurement from images. For girths and perimeters, semimajor and semiminor axes were mathematically estimated with the function of the perimeter of an ellipse. On-field measurements' direct translation was determined when Cronbach's alpha (Cα) > 0.600 was met (first round). If not, Bayesian regression corrections were applied using live body weight and the particular digital zoometric measurement as regressors (except for foot perimeter) (second round). Last, if a certain zoometric trait still did not meet such a criterion, its natural logarithm was added (third round). Acceptable method translation consistency was reached for all the measurements after three correction rounds (Cα = 0.654 to 0.997, $p < 0.0001$). Afterwards, Bayesian regression corrected equations were issued. This research helps to evaluate individual conformation in a reliable contactless manner through the extraction of linear and tridimensional measures from images in dromedary camels. This is the first study to develop and correct the routinely ignored evaluation of tridimensional zoometrics from digital images in animals.

Keywords

Endangered breed, perimeters and circumferences, on-field measurements, mathematical modelling, software-assisted image analysis

Introduction

Zoometry, or the measurement and comparison of the sizes and proportions of animals or animal parts, has traditionally been considered a key element for breed characterization (Alhajeri, Alaqeely, & Alhaddad, 2019). Such a determinant role not only relies on the implication of body conformation and dimensions in the definition of breed standards, but also on the functional classification of individuals depending on their better suitability for the development of certain tasks (Dorantes-Coronado et al., 2015). In these regards, zoometric analysis may help to detect differences among live- stock populations or breeds which may be the source for niche specialization or exploration opportunities. As a direct consequence, zoometrics has been reported as one of the driving agents for the conservation (seeking a particular breed standard) and selection strategies (intraherd and interherd breeding criteria definition) that are eventually implemented (Alhajeri et al., 2021) in local breeds.

Animal body measurements have been traditionally obtained manually with the use of a diverse range of instruments (Parés & Sañudo, 2009). However, these tasks are not exempt of risks and inconveniences for both the animals and the workers, such as the increased stress induced in the animals or the errors in measurements due to the difficulty of maintaining the animals in a complete stationary position, among others. If sedation or the use of anesthetics is required for animal immobilization due to temperament issues, therefore becoming potentially hazardous to the operators, not only can the animal welfare be compromised, but this also makes the time and costs of the zoometric tasks increase (Gaudioso et al., 2014).

For these reasons, several methods aiming at automatizing zoometric measurements collection in non-invasive, contactless, cheaper, and faster ways have been attempted in different species over the past decade (Rahagiyanto & Adhyatma, 2021). Literature has reported the success of bidimensional and tridimensional image-based zoometric analysis methods in domestic and wild animal populations (Azzaro et al., 2011; Bell, Hindell, & Burton, 1997; Bewley et al., 2008; Cervantes et al., 2009; de Bruyn et al., 2009; de Kock et al., 2021; De Wet et al., 2003; Negretti et al., 2008; Negretti, Bianconi, & Finzi, 2007; O'Malley et al., 2021; Proffitt et al., 2008; Shrader, Ferreira, & Van Aarde, 2006; Waite et al., 2007; White et al., 2004). Among them, software-assisted digital imaging zoometrics offers a sound and solid alternative, which has not only solved the aforementioned issues, but also overcome the accuracy of traditional zoometric practices (Gaudioso et al., 2014; Rahagiyanto & Adhyatma, 2021). The evaluation of static images may reduce the biases derived from human data collection due to the animals' spontaneous movements. However, the use of high-resolution images may be needed, and inferring certain tridimensional measurements such as perimeters from bidimensional photographs is still critical. In this sense, mathematic modelling can help correct potential computational biases from both linear and tridimensional measures, while at the same time providing an economically affordable opportunity to perform zoometric comprehensive analyses, and the stress induced in animals at the time of being held and measured is substantially minimized (Gaudioso et al., 2014).

Some minor species such as camels, despite being increasingly prevalent at livestock scenarios for their contemporary recognition as a sustainable species (Iglesias Pastrana et al., 2020), have only anecdotally been attempted for zoometric evaluation and breed characterization (Alhajeri et al., 2021). Dromedaries or one-humped camels (*Camelus dromedarius*) are a typical element in the scene of developing economies and constitute the vast majority of the world's camel census. Due to the economical context in which they are normally evaluated and the lack of attention paid to them in the past (Iglesias Pastrana et al., 2020), the scarce initiatives towards morphometrics phenotypic variability collection have mainly been implemented via on-field sampling (Abdallah & Faye, 2012; Al-Atiyat et al., 2016; Alhajeri, Alaqeely, & Alhaddad, 2019; Bitaraf Sani et al., 2022; Meghelli et al., 2020). However, these practices are not free from challenges. Indeed, the combination of camels' large size and often strong temper may compromise the integrity of operators (Alhajeri et al., 2021) and turn zoometric analysis into a dangerous time and a demanding human resources practice (de Kock et al., 2021). As a consequence, certain measurements, or medial regions like udders (Ayadi et al., 2016) and genitals (Abdullahi, Musa, & Jibril, 2012), are routinely almost never registered due to the difficulty or danger that their access implies.

Contextually, for the safe accomplishment of on-field zoometric collection, camels need to be properly restrained for their secure handling (Parés & Sañudo, 2009), and the use of a wide diversity of measuring tools is compulsory. Hence, camels still lack contactless methods which may help to safely improve the efficiency and accuracy of zoometrics for camel breed characterization and the definition of adapted selection criteria for the maintenance of camel global genetic diversity (Köhler-Rollefson, 2022). This becomes even more crucial when the camel breed being considered is at risk of extinction and has a very defined applicability for tourism, work development, or therapeutic kinetics (Iglesias Pastrana et al., 2021), as occurs for the Canarian camel.

The early development of image-analysis methodologies for measuring zoometrics in dromedaries is evidenced by the first body zoometric digital reconstruction (Çağlı & Yılmaz, 2021). As a result, the 3D modeling method is confirmed to be used as a remote method to extract morphological features of camels in a reliable manner. However, the experimental nature of this initiative and the time and costs needed for it to be implemented at a large scale make it compulsory to explore other alternatives. In this sense, a recent investigation has approached the accuracy of image analysis for the extraction of some linear zoometric measurements in dromedaries (Gherissi et al., 2022). Nevertheless, the evaluation of tridimensional measurements (such as perimeters) is still misconsidered. Thus, the relatively scarce data that are obtained continue to be incomplete, given that relevant functionally important traits might not be recorded (Padalino, Monaco, & Lacalandra, 2015). In this framework, the present research aims to develop a standardized and validated method for the comprehensive collection of both linear and tridimensional zoometric measurements in live dromedary camels by using 2D images. The combination of bidimensional digital imaging and logarithmically adjusted Bayesian regression methods provides a timely response to the need for the accurate registration of linear and tridimensional zoometric measurements. The method proposed not only offers a time and money affordable precise alternative that can be used as the main source for breed characterization and functional evaluation at a large scale, but also in a comparative manner which may be translatable to other camel populations.

Material and methods

Zoometric parameter definition

The bibliography on the topic was reviewed to obtain a comprehensive database of zoometric measurements in camels during the whole month of September 2019. Bibliographic analysis was performed using Google Scholar search engine (https://scholar.google.com/) (accessed on 1 September 2019), as suggested by other papers in which document library data extraction has been performed, due to the possibilities this search engine offers in regards to data extraction (Iglesias Pastrana et al., 2020). After this document search, six papers dealing with camel zoometrics, regardless of the measuring method used, published from 1994 to 2019, were found (Iglesias et al., 2020a). The list of measurements included in the aforementioned documents was completed with other variables relevant for camel functional development (Alhajeri et al., 2021). After a variable list was completed, a total of 30 zoometric measures were determined to be collected on-field and later extracted from digital images. Table 1 presents a description of the aforementioned zoometric variables.

Table 1. Description of the zoometric measures in Canarian camels collected for the study.

Area	Measurements	Description
Head	Head length	Distance from the anterior edge of the nasal bones to the nuchal crest.
	Head width	Distance between the midpoint of both orbits.
	Ear length	Distance from the base to the tip of the ear.
	Ear width	Widest distance perpendicular to ear length.
Neck	Neck length: dorsal line	Distance from the base of the neck (cervicothoracic junction) to the base of the head (atlanto-occipital joint) following the upper line of the neck.
	Neck length: ventral line	Distance from the base of the neck (cervicothoracic junction) to the base of the head (jaw angle) following the lower line of the neck.
	Neck girth: cranial third	Circular perimeter of the neck measured at its insertion to the base of the head.
	Neck girth: middle third	Circular perimeter of the neck measured at its middle part.
	Neck girth: caudal third	Circular perimeter of the neck measured at its insertion to the chest.
Thorax and Dorsum	Chest width	Distance between the medial point of the front of the forelimbs, measured at the base of their insertion into the torso.
	Heart girth	Circular perimeter of the chest measured directly behind the sternal callosity and before the hump.
	Height at withers (stature)	Distance from the withers to the ground.

Table 1. *Cont.*

Area	Measurements	Description
Thorax and Dorsum	Body length	Distance between the shoulder to the point of the hip.
Hump	Hump-to-tail distance	Distance between the most caudal point of the base of the hump to the base of the tail
	Hump length	Distance between the front and the back of the hump passing through the top of it.
	Hump width	Distance between the front and the back of the hump passing through one of its laterals.
	Hump heigth	Distance between the middle points of the base of the hump at each lateral, passing through the top of the hump.
	Hump girth	Circular perimeter of the hump measured at its base
Rump and Tail	Rump length	Distance from the coxal to the ischial tuberosity.
	Rump width	Distance between the right and left coxal tuberosity.
	Tail length	Distance from the base to the tip of the tail, excluding the tail skirt.
	Width at the base of the tail	Distance between the most lateral points of the base of the tail.
Extremities	Thigh perimeter	Circular perimeter of the thigh measured at its middle part.
	Hock perimeter	Circular perimeter of the hock measured at its middle part.
	Fore cannon bone perimeter	Circular perimeter of the front cannon bone measured at its middle part.
	Rear cannon bone perimeter	Circular perimeter of the hind cannon bone measured at its middle part.
Feet	Sole length	Distance from the front to the back of the sole, measured at the planter surface.
	Length of toe dorsal line	Distance from the external reference of the fetlock to the upper edge of the hoof.
	Heel height	Distance from the caudal point of the fetlock to the ground.
	Foot perimeter	Circular perimeter of the foot measured at its plantar edge.

Animal sample

Zoometric record collection took place between September 2019 and August 2020 for 130 ‘Canarian Camel’ breed individuals (58 females and 72 males). Camels were located in three representative emplacements where Canary camels are bred (Doñana National Park) Huelva (36.972330,-6.427498), Almería (36.902180,-2.429520), and Fuerteventura (28.186777,-14.158361) in Spain. Animals were clinically examinated to ensure the proper condition of the animals, which enabled their participation in the study. Furthermore, to prevent bias issues derived from the sexual status of the animals at the moment of sampling, sexually immature individuals were discarded (below 3 years of age). Parallelly, only non-gravid she-camels were included in this study, since pregnancy may be a source of bias in zoometric measurements in the thoracoabdominal region (Yakubu, Ladokun, & Adua, 2011). Age or live weight did not normally distribute ($p < 0.05$). Live weight was calculated using the following formula (Equation (1)) by Boujenane (2019):

$$\text{Live Weight} = 6.46 \times 10^{-7}\,(HW + ChG + HG)^{3.17}$$

where HW is height at the withers, ChG is chest girth, and hg is hump girth, respectively. The sampling of each of the 30 zoometric measures taken from each animal was collected from its left side following the premises in Iglesias et al. (2020a) and Alhajeri et al. (2021). Females and males' age and live body weight descriptive statistics are represented in Figure 1.

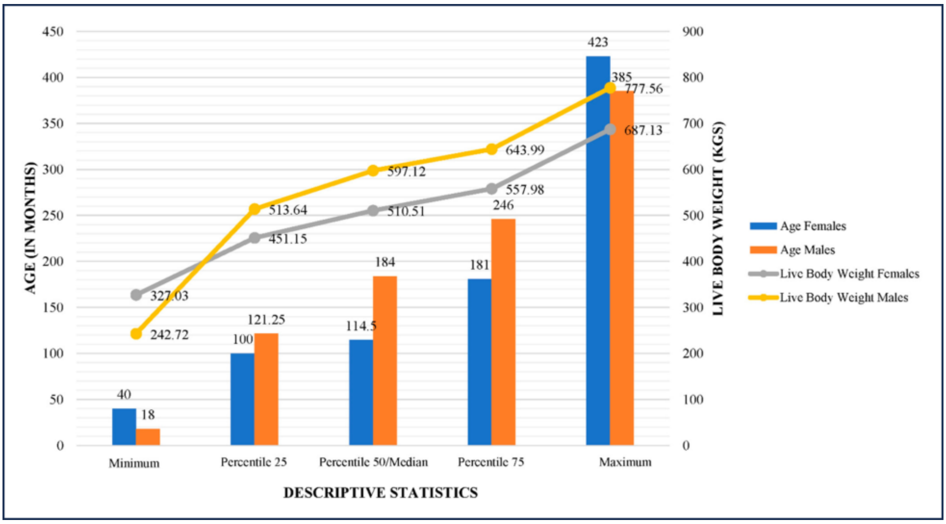


Figure 1. Descriptive statistics for age and live body weight in females and males, respectively.

Sampling

The end of the molting season, which is a six-to-eight-week period starting in late spring (Babu, 2015), was chosen as the sampling moment to prevent the bias which may potentially be ascribed to hair length and texture (Negretti et al., 2007). Figure 2 presents a flowchart summarizing the research methodology.

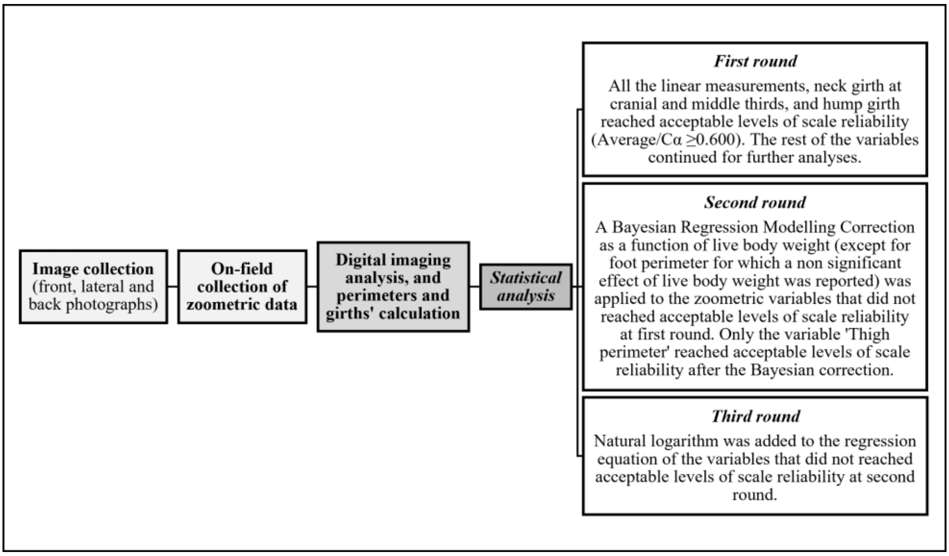


Figure 2. Flowchart summarizing the methodology proposed in the present study.

On-field zoometrics

Live animal-based measurements sampling took place with the animals holding a static upright position with their head naturally raised and in correct aplomb (parallel fore and hind legs perpendicular to the ground with lined toes). Animals were measured on a flat and hard ground surface. Measure collection was performed using a non-elastic measuring tape. All operators were trained. The first operator performed on-field measurement collection and digital image measurement extraction. The first operator was assisted by a second operator in zoometric measurements collection, while a third operator annotated the outputs of zoometric evaluation and held a one-meter measuring bar to be used as a reference for calibration on digital zoometrics extraction (Figure 3).

Digital imaging

Three photographs (front, lateral, and back perpendicular to the camera) were taken per animal right before on-field zoometric evaluation. The second operator took these three photographs for digital imaging analysis (front, lateral, and back views). The third operator was in charge of holding a one-meter measuring bar at the same midline of the body to be used for reference calibration of distances on the computer measurement software for digital imaging zoometrics while taking the aforementioned photographs. The obtained images were digitally processed using Kinovea 0.95 (Free Software Foundation, Inc., Boston, MA). Zoometric linear measurements were obtained

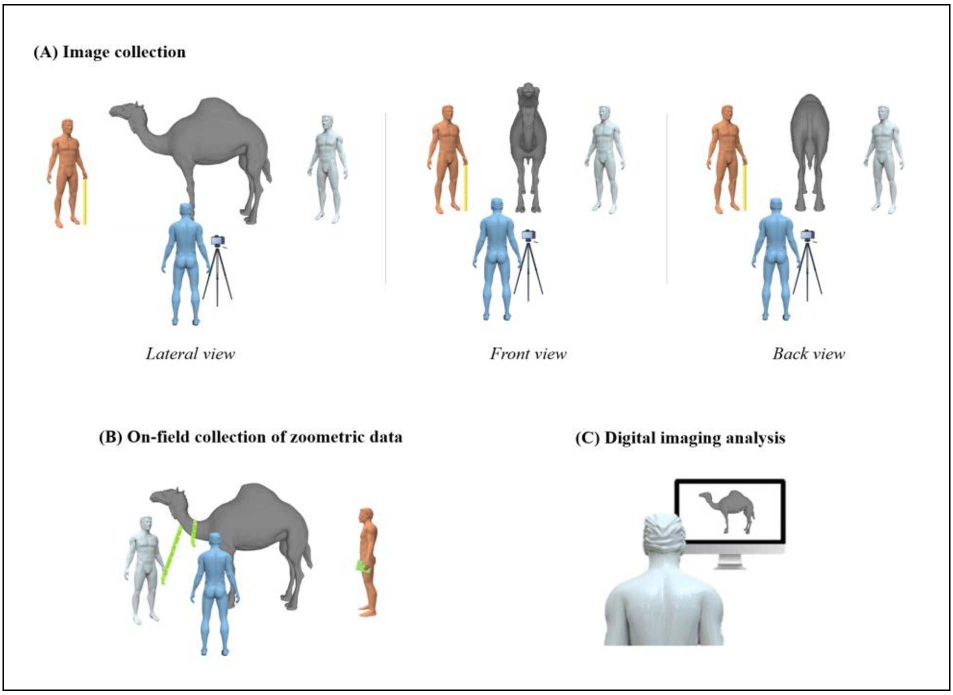


Figure 3. Graphic representation of the relative position of operators during across data collection phases. During (A) image collection, first operator (Grey) was responsible to hold camel on correct aplomb at a completely static position while keeping the photographic and camel midsagittal planes parallel; second operator was responsible to take photographs for digital imaging analysis; Second operator (Blue): responsible to take photographs for digital imaging analysis, and third operator (Orange): responsible to hold a one-meter measuring bar (yellow bar) near the animal body to be used as a reference for image calibration on digital zoometrics. During (B) on-field collection of zoometric data, first (Grey) and second (Blue) operators perform on-field measurement collection with a non-elastic tape (green tape) while third operator (Orange) annotates the outputs of zoometric evaluation. During (C) digital imaging analysis, first operator (Grey) performs digital image measurement extraction.

in pixels by drawing a straight line between two points in the picture and automatically converted into cm after calibration of the software using the measuring bar as a reference using the *Calibrate* option of the *Line* tool of the software (Iglesias et al., 2020b). Puig-Diví et al. (2019) reported Kinovea software to be a valid and reliable tool which is able to measure accurately at distances up to 5 m from the object and at an angle range of 90°–45°.

Image collection was performed on an open hard ground and flat area. Light conditions were chosen so as for the animal not to be placed in a shaded area or in one in which light exposure may distort image capture. The animal color was considered to ensure background color did not lead to any measure distortion or measure misregistration. The camera was positioned at a standardized height of 1 m on a camera stand 4 m away from the camel center of balance. The aforementioned distance and height permitted framing of the animals being evaluated on the whole. We followed the premises in Iglesias et al. (2020a) to determine the proper aplomb of the animals and tracing standard lines on the ground before photograph taking to ascertain the animal was in the right position. Image capture was performed using a digital camera (Sony DSC-RX100 SENSOR CMOS Exmor 1.0 of 20.1 MP, F1.8–4.9, Zoom 20–100, Optical Zoom 3.6x, 3″ LCD Screen Image stabilizer) in standard mode. Joint Photographic Experts Group (JPEG) compression format was used. One trained operator performed zoometric measurement digital extraction from photographs manually.

Statistical analysis

Method comparison/reproducibility and repeatability: Interobserver Correlation Coefficient (ICC)

Intraclass correlation coefficient (ICC), based on multiple paired Cohen's κ tests, was run to compare zoometric on-field analysis to digital imaging zoometric analysis. As suggested in Bunting et al. (2019), the intraclass correlation coefficient (ICC) is a reference method to determine the reproducibility and reliability of numeric measurements organized into groups beyond a simple pairing, for example, different operators measuring the same variable in different animals or the same operator using different methods on different animals. In this study, we issued the equations, and equations were solved. Then, we used ICC to compare the results from model solving and real measurements to test for the reproducibility and reliability of models.

Fleiss and Cohen (1973) established reproducibility/repeatability guidelines for ICC interpretation as less than 0.4 (low); between 0.4 and 0.59 (reasonable); 0.6 to 0.74 (good); and 0.75 to 1.0 (excellent) to determine whether reproducible, repeatable, and reliable enough levels were attained. A "Two-Way Random" model was chosen from the premises in Koo and Li (2016). Then, we computed 95% confidence intervals after the following expression 95% kappa Confidence Interval (95%CI) = κ±1.96 SEκ, where SEκ = ((po (1 - po)/n (1 - pe) 2) 0.5, with the reliability analysis routine of the scale procedure of SPSS Statistics for Windows, Version 25.0, IBM Corp. (Corp., 2017b).

Scale reliability and repeatability: Cronbach's alpha (Cα)

Instrument scale internal consistency was measured using Cα. Internal consistency, when applied to instrument comparison, is an estimate of 'reliability based on the average correlation among items within a test', with each of these items being each of the measuring methods, zoometric on-field evaluation, and zoometric digital imaging, in our case (Nunnally & Bernstein, 1994), and examines the degree to which such instruments measure the same characteristics or domains of knowledge (Beanland et al., 1999). Typically, internal consistency is measured by the calculation of a reliability coefficient (Beanland et al., 1999), such as Cα.

In this context, Cα represents the reliability level of the instrument being compared to a reference instrument (zoometric digital imaging to zoometric on-field analysis as a reference) (Creswell, 2010). As a general criterion, George and Mallery (2003) suggest the following recommendations for evaluating Cα coefficients: > 0.9 is excellent, > 0.8 is good, > 0.7 is acceptable, > 0.6 is questionable, > 0.5 is poor, and < 0.5 is unacceptable. However, when comparing internal consistency between instruments, Pallant (2020) reported that Cα value above 0.6 is considered a highly reliable and acceptable index (Nunnally & Bernstein, 1994). Furthermore, retaining variables with values over 0.5 has been suggested due to their ability to explain data variability (González Ariza et al., 2019).

As suggested by González Ariza et al. (2019), single measures of ICC determine how a single observation taken at random may correlate to another single observation, that is, in our case, how a zoometric measure from on-field evaluation may correlate with its paired counterpart from digital imaging. By contrast, average ICC and Cα determine how consistent the set of instruments being compared are on average. Consequently, in instrument comparison, average measures somehow prevent potential measuring errors affecting particular measurements, and as a result, report erroneously decreased instrument reliability and accuracy values for the instrument being tested (digital imaging zoometrics in our case).

Parametric assumptions testing and approach decision

The statistical approach was decided after parametric assumptions testing. The Shapiro–Francia W' test (for 50 < n < 2500 samples), Shapiro–Wilk test (for n < 50 samples), and Levene's test were used to determine whether normality and homoscedasticity parametric assumptions were met. The Shapiro–Francia W' test was run using the Shapiro– Francia normality routine of the test and distribution graphics package of the Stata Version 15.0 software (StataCorp, College Station, TX, USA) (StataCorp, 2017). Homoscedasticity was run using the explore procedure of the descriptive statistics package in SPSS Statistics (Version 25.0, IBM Corp., Armonk, NY, USA) (Corp., 2017b).

Perimeters and girths calculation

As suggested by Singaraju et al. (2020) in their study performing ellipsoid biometric computations, Ramanujan's equation of ellipse model for ellipsoid perimeter (P) was used to fit zoometric perimeters and girths (neck girth (cranial, middle, and caudal thirds), heart girth, hump girth, thigh perimeter, hock perimeter, fore cannon bone perimeter, rear cannon bone perimeter, and foot perimeter, respectively) as follows:

$$P \approx \pi(a+b)\left(1+\frac{3h}{10+\sqrt{4-3h}}\right)$$

where *a* is the semimajor axis, *b* is the semiminor axis, and *h* is computed as follows $h = (a - b)^2/(a + b)^2$. This approximation is within about 5% of the true value, as long as *a* is not more than three times longer than *b*. Figure 4 schematically represents semimajor and semiminor axis digital imaging collection references for perimeters and girths computation. Ramanujan's equation of the ellipse model was applied using Microsoft Office Excel 2016 as suggested in the literature (Alexander & Kusleika, 2016; Chandrupatla & Osler, 2010).

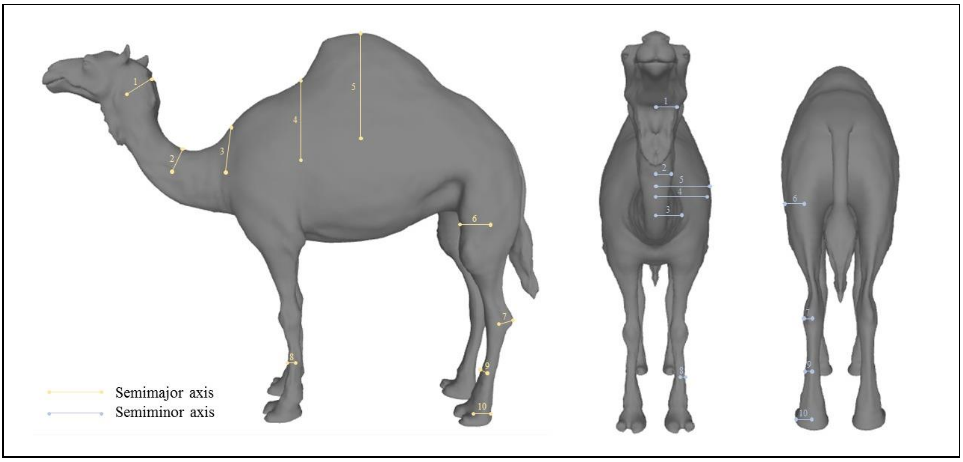


Figure 4. Schematic representation of semimajor and semiminor axis digital imaging collection references for perimeters and girths computation in Canarian camels. (1) Neck girth: cranial third; (2) Neck girth: middle third; (3) Neck girth: caudal third; (4) Heart girth; (5) Hump girth; (6) Thigh perimeter; (7) Hock perimeter; (8) Fore cannon bone perimeter; (9) Rear cannon bone perimeter and (10) Foot perimeter.

Bayesian linear regression modelling and natural logarithmic correction for perimeters and girths

Limited sample sizes derived from endangered populations may distort the distribution of variables that are presumably sampled from normally distributed populations, such as zoometrics. Such distortion may be ascribed to highly skewed data appearing as a result of valid outliers. A valid outlier would be an animal that is considerably smaller or larger than the rest, but which may still fit in the context of an endangered breed standard, even if it statistically distorts sample distribution properties.

If valid outliers are not present, skewness may not be forced towards one of the distribution ends, and applying the logarithmic bias correction may not be necessary. However, body score condition and live body weight have been reported to act as sources of bias when performing zoometric analyses in dromedary camels (Iglesias et al., 2020a). The bias effect of other factors, such as age or coat color, was also considered.

In such cases, regressing the variable measured in the field against the potentially originating factor of the bias during the collection of measurements from digital sources (live body weight, age, or coat color in our case) and the same variable measured with digital methods (given our aim is to perform a comparison between methods) may have to be performed to ensure the replicability between methods. This ensures that the accuracy of estimation of real measurements after digital measurements is maintained.

The effects derived from outlier distortion become stronger in perimeters, girths, or circumferences calculations given that these cannot be extracted from photographs straight away. The inability to account for such a bias while evaluating tridimensional zoometric parameters from bidimensional images makes it compulsory to apply correction methods. According to States (1989), to correct for skewness derived bias in estimations, a bias correction should be issued. To solve this issue, States (1989) suggests that sample size limitations could be buffered by regressing the log transformation of the variable to which regression models were initially aimed.

Once the variable measured in the field has been regressed against the potentially originating factors of the bias, and the same variable is measured with digital methods, bias correction may be obtained after summing the outcomes of this regression to the natural logarithm of the zoometric variable measured using digital methods.

In these contexts, the application of regression equations may be difficult due to the alteration of sample properties and ordinary least squares regression assumptions. However, these distribution distortions events may be saved using statistical alternative methods such as Bayesian linear regression, which are less sensitive to outliers and distribution alterations (Bao et al., 2010), and their estimations may be subject to wide confidence intervals.

Valid outliers' detection in our data sample was performed using the identify outliers procedure of the *Analyze/Built-in* analysis of the column analyses package of GraphPad Prism version 8.3.0. The ROUT method was applied to prevent the effects of outliers. The ROUT method combines robust regression and outlier removal and is based on the false discovery rate (FDR). A maximum desired FDR must be predefined (Q coefficient). ROUT method assumes all data except for outliers to be sampled from a Gaussian distribution. When data does not meet the aforementioned assumption, outliers may follow the same distribution as data.

The ROUT method strength to detect outliers was determined using the Q coefficient. Higher levels of Q are indicative of lower threshold strictness for outliers' detection, thus, the higher the outlier detection power, but also the higher the probability for a false outlier to be identified as a true one. Lower Q values set stricter thresholds for outlier definition, which consequently translates into lower power to detect real outliers, but also lower chances for false outlier consideration. A Q coefficient of 1% is the recommended threshold to be used as a default (Motulsky & Brown, 2006), given it implies a lower than 1% false discovery rate for outlier detection.

Consequently, after considering the presence of outliers, when evidence of a lack of acceptable fit ($C\alpha < 0.600$) between perimeter or girth on-field zoometric evaluation and digital imaging mathematical computation using Ramanujan's equation for ellipsoid perimeter was found, we used Bayesian linear regression modelling to correct measurement as a function of live body weight.

The presumably large dependence of zoometric parameters on age may have suggested the inclusion of age in the regression models, as according to Carlin (2019), Bayesian inferences are sensitive to the dependence of variables on time (conditional on θ and x). In our case, zoometric analyses were performed when animals had reached the adult stage to prevent age-derived biases from occurring, as suggested by the lack of pieces of evidence or a significant effect of age ($p > 0.05$). Contextually, the age variation coefficient (CV) was 0.598. As a rule of thumb, a $CV \geq 1$ indicates a relatively high variation, while a $CV < 1$ can be considered low, hence, the lack of a significant interindividual variability prevented age from being considered as a covariate.

Pieces of evidence for a non-significant bias effect of coat color effect were also re- ported ($p > 0.05$ and CV of 0.376). This lack of bias ascribed to coat color variability may derive from the fact that photographs were taken once the hair molting season had passed and an appropriate lighting scenario that remarked the topographic shadows of bone accidents (references for measurement) had been considered. Furthermore, animals were photographed and measured by the same people trained for this purpose, with the same technological equipment, and information regarding their coat color was registered to minimize the effects of the aforementioned potentially biasing factors.

Those zoometric perimeters and girths did not reach acceptable levels of scale reliability (Cα < 0.600), and hence were considered the dependent variables of Bayesian regression models to apply body live weight correction.

As suggested in Koehrsen (2018), Bayesian linear regression uses probability distributions rather than point estimates. This means response, y, is not estimated as a single value, but is assumed to be drawn from a probability distribution. The output, y, is generated from a normal (Gaussian) distribution characterized by a mean (the transpose of the weight matrix multiplied by the predictor matrix) and variance (the square of the standard deviation σ, multiplied by the identity matrix, given it is a multi-dimensional model formulation). Hyperparameters' means and variance were used to obtain the best values of the hyperparameters of the prior distribution, as suggested by Kundu (2008).

The objective of Bayesian linear regression is to determine the posterior distribution for the model parameters, rather than the best value for model parameters. Not only is the response generated from a probability distribution, but the model parameters presumably come from the same distribution. The posterior probability of the model parameters is conditional on the training inputs and outputs. In contrast to frequentist Ordinary Least Squares Regression (OLS), there is a posterior distribution for the model parameters proportional to the likelihood of the data multiplied by the prior probability of the parameters.

This implies two primary benefits of Bayesian linear regression: priors and posteriors. When there is knowledge, or a guess for what the model parameters should be, these priors can be included in the model (for example, the influence of live body weight on zoometrics). This approach contrasts the frequentist approach, which assumes everything there is to know about the parameters comes from the data. Indeed, in Bayesian regression, when there is no prior information known, non-informative priors for the parameters such as a normal distribution can be used.

Afterwards, posteriors, or the results of performing Bayesian linear regression, are a distribution of possible model parameters based on the data and the priors. Posteriors enable quantifying uncertainty about the model. Hence, the fewer data points, the greater the dispersion of posterior distribution will be. As the amount of data points increases, the likelihood washes out the prior, and in the case of infinite data, the outputs for the parameters converge to the values obtained from OLS.

To summarize, in Bayesian inference for linear regression, we use priors as initial estimates, and as we gather more evidence, testing our model against data (posteriors), the model supports or disproves our prior hypotheses. In practice, the evaluation of the posterior distribution for the model parameters is intractable for continuous variables when we implement Bayesian linear regression. Thus, sampling methods are used to draw random samples from the posterior distribution to approximate the posterior distribution to which it should be using Monte Carlo algorithms method and its variants.

The Metropolis–Hastings random walk algorithm, which uses Markov Chains to perform Monte Carlo estimate via the Gibbs Sampler algorithm, was used as aforementioned given a different prior to the default uniform prior specified in IBM SPSS Statistics Algorithms v. 25.0. by IBM Corp. (Corp., 2017a) was selected. The random walk Metropolis algorithm is the preferable option for data imputation from the collection of Markov Chain Mote Carlo (MCMC), as suggested in MacKay (2003), given that neither admissibility nor stability were selected.

The following general equation was used for each of the regression models defined in this study $y_i = X_1\beta_1 + \ldots X_i\beta_i + \varepsilon_i$, where i = 1, 2, . . . i is the ith number of factors; y_i is the vector of records for the aforementioned dependent variables with dimension n (a total of 910 records, one record per each of the seven circumferences/perimeters which did not reach acceptable reliability levels and each of the 130 dromedary camels measured); X_i is the appropriate incidence matrix for factors; β_i is the standardized regression coefficients for the ith number of factors and covariates considered, respectively. The general regression equation used for each perimeter or girth was Y = Intercept + $\beta_{\text{on field perimeter/girth (cm)}}$ x on-field perimeter/girth (cm) + $\beta_{\text{Live body weight (Kg)}}$ x body live weight (Kg).

As Brewer (2002) suggested, the intercept was necessary given that we used unstandardized coefficients. The magnitude of intercept confidence intervals was an empirical indicator of the need for its estimation. Residual effects (ε_i) normality was assumed as follows $\varepsilon_i \mid X_i N(0, \sigma^2_{\varepsilon i})$, where X_i is an identity matrix and $\sigma^2_{\varepsilon i}$ is the residual variance, respectively. Continuous predictor variable unstandardized coefficients were produced by the linear regression model using the independent variables measured in their original scales.

As suggested by Hayes et al. (2012), unstandardized coefficients (βi) can be defined as the average increase of βi units in Y associated with an increase of one unit in Xi maintaining the rest of the variables constant. Below, a detailed summary of the priors and posterior distributions used in this study is reported. The complete description of the algorithms used by SPSS to perform Bayesian inference on multiple linear regression models in this study can be found in IBM SPSS Statistics Algorithms v. 25.0. by IBM Corp. (Corp., 2017a).

Quadratic approximation was discarded (even if it has been reported to be computationally faster in terms of discretization and computing the likelihood over all possible parameter combinations). Instead, the Markov Chain Monte Carlo (MCMC) approximation was used, as it does not assume the fact that the posterior distribution follows a normal distribution.

Bayesian linear regression analyses were performed using the linear regression package from the Bayesian statistics task of SPSS Statistics, Version 25.0, IBM Corp. (Corp., 2017b). The Bayesian linear regression test routine of the linear regression and related package of the Stata Version 16.0 software process was used to compute posterior distribution statistics for the factors considered. Afterwards, we evaluated the estimated effect of the factors considered in the resulting predictive models, its confidence intervals, and posterior distribution statistics to build linear regression equations, calculate digital perimeter/girth extrapolation, and ICC was run again. When Cα had not significantly improved over acceptable levels, the natural logarithm of each particular perimeter or girth was added to each aforementioned equation, and ICC was calculated again to ensure that reliability levels had been attained.

Jeffrey–Zellner–Siow (JZS) mixture of g-priors

The Jeffrey–Zellner–Siow mixture of g-priors (Liang et al., 2008) was used given it successfully satisfies several theoretical requirements such as the equality constraint on the test-relevant parameters, for instance of β, which leads to the null hypothesis H0 = β = β0 [64], as suggested by Heck (2019). Rouder et al. (2012) and Liang et al. (2008) also acknowledged the benefits of JSZ prior distribution. Contextually, conditional on the residual variance ($\sigma^2_{\varepsilon i}$), the JZS prior defines a multivariate Cauchy distribution for the slope parameters of the full model, as follows:

$$(\beta_i | \sigma^2_{\varepsilon i}) \sim MVC(0_P, \gamma_i{}^2 \sigma^2_{\varepsilon i} C_i{}^{-1})$$

which is defined by a P-dimensional zero vector (location vector) and a scale matrix. The constant γ_i determines the amount of scaling, which is chosen by the user a priori, the residual variance $\sigma^2_{\varepsilon i}$, and the matrix $C_i = X'_i X_i / N_i$, which is the covariance matrix of the centred design matrix X_i.

JZS prior (Rouder et al., 2012) is especially appropriate in Bayesian linear regression analyses given that it is symmetric and centered at zero, as explained by Bayarri et al. (2012). This means that positive and negative values of the parameters of the slope are a priori equally likely to occur. Moreover, JZS prior does not depend on the scale of the variables, factors, or covariates considered. Hence, the Bayes factor is scale-invariant, and outputs remain the same when the variables expressed in different units are evaluated, which is likely to occur in multifactorial studies.

Scaling the multivariate Cauchy distribution by the residual variance $\sigma^2_{\varepsilon i}$ ensures the achievement of such independence from the measurements of model elements (*a priori*, a larger residual variance implies larger slopes) and by the inverse of the covariance matrix C_i (*a priori*, a covariate with a larger variance implies smaller slopes). In this context, the process of definition of scaled priors for unstandardized coefficients (β_i) equals the process of definition of priors for standardized coefficients (β^*_i) (Rouder et al., 2012).

Third, the scale parameter γ is fixed to a constant, hence prior beliefs are specified about the expected effect size remain constant as well. The IBM Corp. algorithm guide (Corp., 2017a), in its section for the algorithm of JZS prior for linear regression analyses, sets the default value of $\gamma = 2\sqrt{\pi} = 3.5$ to compute Bayes Factor. This reflects a belief of a priori medium effect size, which, for a single covariate x, implies a priori probability for the standardized regression slope $\beta^*_I = \beta_i \times SD(x_i)/\sigma_i$ of 53.2% of being in the range (-0.50, +0.50).

Rouder and Morey (2012) explained other benefits from the choice of the JZS prior, for instance, its model selection aimed at consistency (this is that Bayes factor, goes to infinity as the number of observations N increases without bound-favoring the data-generating model) or consistency in information (the Bayes factor for a certain effect goes to infinity as the proportion of explained variance or R Squared (R^2) increases to 1. Additionally, Bayes factors for JZS prior are highly precise and relatively easy to compute (Morey & Rouder, 2015), resulting in its wide applicability for the default *t*-test (Rouder et al., 2009), ANOVA (Rouder et al., 2012), and linear regression (Heck, 2019).

Bayesian modelling of factor and covariate effects (FCEBM)

Being y_i, any of the effects of any of the independent variables (covariates) considered in this study (live body weight, age, and coat color), the posterior distribution of y_i in the context of the data, D, is

$$p(y_i/D) = \sum_{i=20}^{i} p(y_i|M_i, D)\, p(M_i|D)$$

This means each model's average of posterior distributions is weighted by their posterior model probabilities. In the aforenoted equation, the posterior predictive distribution of y_i given a particular model M_i is,

$$p(y_i|M_i D) = \int p(y_i|\beta_i, M_i, D) p(\beta_i|M_i D)\, d\beta_i$$

and the posterior probability of the model M_i is given by

$$p(M_i|D) = \frac{p(D|M_i)p(M_i)}{\sum_{i=20}^{i} p\,(D|M_i)p(M_i)}$$

where,

$$p(M_i|D) = \int p(D|\beta_i, M_i)p(\beta_i|M_i)\, d\beta_i$$

is the integrated probability of the model M_i, β_i is the vector of parameters of the model M_i, $p(\beta_i \mid M_i)$ is the prior density of β_i under model M_i, $p(D \mid \beta_i \mid M_i)$ is the probability, and $p(M_i)$ is the prior likelihood that M_i is the true model.

The number of models (K) for a problem with P potential covariates can be enormous ($K = 2^P$ in the absence of other constraints). Only a small number of these K models will be sufficiently supported by the data, and hence selected by SPSS for each of the P covariates. Gibbs sampling algorithm was used to estimate marginal posterior distributions of all unknowns.

Factors and covariate effect Bayesian interpretation (CEBI)

The detection of issues before model estimation was evaluated using the checklist proposed by Depaoli and Van de Schoot (2017). Among the issues checked, we tested for those occurring after model estimation before interpreting results, in priors' influence comprehension, and after interpreting results for conclusion drawing. Interpreting the effect of each particular covariate (independent variables used in this study) was made as follows.

First, the posterior probability $p[\beta i^* = 0/D]$ expresses the probability that every single independent factor or covariate affects each particular dependent variable. Standard rules of thumb (Kass & Raftery, 1995) for posterior probability interpretation are as follows: <50% evidence against the effect; 50–75% weak evidence; 75–95% positive evidence; 95–99% strong evidence; >99% very strong evidence, which is comparable to commonly used thresholds that define the level of significance of evidence using Bayes factor (BF) (Supplementary Table S1).

Second, posterior distribution means determines the magnitude of the effect of every single factor and covariate. For metric covariates (continuous predictors) or the numeric variables used in this study, regression coefficients define the difference in the predicted value of the response variable for each one-unit change in the predictor variable, with all other predictors being constant. When dependent variables are metric, β regression coefficients are a measure of effect sizes by themselves.

Third, a 95% credibility interval suggests that a 95% likelihood for these regression coefficients (every single covariate and factor posterior distribution means) lies within the corresponding credibility intervals. A significant effect is reported when 0 is not contained within the credibility interval for each particular factor. In the present study, only live body weight significantly influenced zoometric measurements ($p < 0.05$).

Convergence criterion

Iteration rounds continued until a tolerance convergence criterion of 10^{-8} was reached (Arora, 2017). After this, initial parameters were defined, and model fitting properties were analyzed. The maximum number of iteration rounds was 2000 for each analysis as stated in IBM SPSS Statistics Algorithms version 25.0 by IBM Corp. (Corp., 2017a). Such a convergence criterion was defined given its wide application in Bayesian ANOVA and linear regression analyses in limited sample sizes research contexts (Pizarro Inostroza et al., 2020a).

Model validity and explanatory power of present data, and predictive power of future data

Validation and comparison of Bayesian models were described in Geweke (1996). Contextually, other authors (Analla, 1998) suggest model validation should base on models' mean square error (MSE). Although mean square residual or error (MSE) and minimum mean-square residual or error (MMSE) have been widely used to measure the closeness between a regression line and a set of points (model fit to explain data), mean square prediction error, or MSPE (=RSS/no. of observations), was used to measure error variation due to the MSE being influenced by the number of predictors (Doğan, 2018) in reduced sample sizes cases (Pizarro Inostroza et al., 2020a; Pizarro Inostroza et al., 2020b).

The residual sum of squares (RSS) quantifies the amount of variability in a data set not explained by a regression model. That is, the RSS measures the amount of error remaining between the regression function and the data set, thus it essentially defines the ability of a certain regression model to explain or represent the data. Smaller values of RSS are indicative of better suitability of the regression function to model for the data it intends to model.

Specific to Bayesian inference, Monte Carlo standard error (MCSE), which is defined as the standard deviation of the chains divided by their effective sample size, measures the accuracy of the chains. MCSE is the non-parametric or Bayesian counterpart of MSPE, and should be used as the validation criteria in Bayesian linear regression model comparison studies (Hall & Maiti, 2006).

Bayes factor (BF) is an indirect measure of models' explanatory power to describe observed data. Larger values of BFs evidence higher probabilities for the combinations of the factors modelled to explain dependent variables. Supplementary Table S1 reports common thresholds to define the significance of evidence as suggested by Jeffreys (1961) and Lee and Wagenmakers (2013). Bayesian R^2 is related to BF and can be considered as a data-based estimate of the fraction of variance explained for data. Parallelly, acceptance rate, efficiency, and Monte Carlo standard error (MCSE) were used to determine Bayesian methods' validity. Supplementary Table S2 presents the description and interpretation of model validity parameters. The predictive accuracy of the model's Bayesian statistics (Kaplan & Depaoli, 2012) can be estimated through posterior predictive checking (Gelman et al., 2013).

Afterward, the Bayesian information criterion (BIC) or Schwarz information criterion (also SIC, SBC, SBIC) was calculated to determine the model predictive ability of new data as follows:

$$BIC = N * N\ ln(MCSE) + K * ln(N)$$

where MCSE is the Monte Carlo standard error, N is the number of observations or records, and K is the number of independent parameters of the model.

BIC was used to compare predictive power across models as it considers the statistical goodness of fit and the number of parameters to be compulsorily estimated to reach such fitness degree, as it penalizes every time the number of parameters considered increases (Clyde et al., 2019; Drton & Plummer, 2017). As a result, BIC quantifies the balance between model fit and model complexity (Gelman et al., 2019). Lower BIC values mean that a particular model is a comparatively better predictive model than the rest. Contrastingly, Bayesian R^2 estimates the explanatory power of observed data.

In consequence, although the addition of "noise" variables to the fit, variables that explain small redundant fractions of variance, will slightly increase R^2 values, model predictive power will decrease (as denoted by its higher BICs). Indeed, as more variables are added to the model, its predictive accuracy decreases. This is, higher R^2 will also translate into higher—and therefore worse—BIC values.

Results

Parametric assumptions testing and approach decision

All variables did not grossly meet the normality assumption ($p < 0.01$), respectively. Homoscedasticity was violated as well ($p < 0.01$), hence, a parametric approach was discarded, and Bayesian methods resulted in being the most preferable option. No likely outlier was detected, and therefore we preserved all observations for further analyses.

Initial/first round of method comparison/repeatability and scale reliability

Among the zoometric perimeters and girths measured, neck girth at cranial and middle thirds and hump girth reached acceptable levels of scale reliability (Average/Cα 0.600, Table 2). Therefore, their direct extrapolation after the application of Ramanujan's equation of the ellipse model for ellipsoid perimeter calculation was feasible and no further analysis was performed. The rest of the variables, which did not reach acceptable reliability levels, continued for further analyses (Average/Cα < 0.600, Table 2).

Table 2. Intraclass correlation coefficient (ICC) for single and average measurements (Cronbach's alpha, Cα) comparison between on-field zoometrics and digital imaging zoometrics.

Area	Measurements	Parameters	Intraclass Correlation	95% Confidence Interval Lower Bound	95% Confidence Interval Higher Bound	F Test with True Value 1	df1	df2	Sig	Round [a]
Head	Head length	Single	0.975	0.965	0.982	78.434	129	129	0.001	1st
		Average/Cα	0.987	0.982	0.991	78.434	129	129	0.001	
	Head width	Single	0.738	0.649	0.808	6.64	129	129	0.001	1st
		Average/Cα	0.849	0.787	0.894	6.64	129	129	0.001	
	Ear length	Single	0.854	0.800	0.895	12.697	129	129	0.001	1st
		Average/Cα	0.921	0.889	0.944	12.697	129	129	0.001	
	Ear width	Single	0.875	0.827	0.910	14.973	129	129	0.001	1st
		Average/Cα	0.933	0.906	0.953	14.973	129	129	0.001	
Neck	Neck length: dorsal line	Single	0.847	0.791	0.890	12.108	129	129	0.001	1st
		Average/Cα	0.917	0.883	0.942	12.108	129	129	0.001	
	Neck length: ventral line	Single	0.992	0.989	0.994	247.029	129	129	0.001	1st
		Average/Cα	0.996	0.994	0.997	247.029	129	129	0.001	
	Neck girth: cranial third	Single	0.556	0.425	0.664	3.504	129	129	0.001	1st
		Average/Cα	0.715	0.596	0.798	3.504	129	129	0.001	
	Neck girth: middle third	Single	0.664	0.555	0.750	4.947	129	129	0.001	1st
		Average/Cα	0.798	0.714	0.857	4.947	129	129	0.001	
	Neck girth: caudal third	Single	0.541	0.407	0.652	3.357	129	129	0.001	3rd
		Average/Cα	0.702	0.579	0.789	3.357	129	129	0.001	

Table 2. *Cont.*

Area	Measurements	Parameters	Intraclass Correlation	95% Confidence Interval Lower Bound	95% Confidence Interval Higher Bound	F Test with True Value 1	df1	df2	Sig	Round [a]
Thorax and Dorsum	Chest width	Single	0.779	0.701	0.838	8.036	129	129	0.001	1st
		Average/Cα	0.876	0.824	0.912	8.036	129	129	0.001	
	Heart girth	Single	0.682	0.578	0.764	5.285	129	129	0.001	3rd
		Average/Cα	0.811	0.732	0.866	5.285	129	129	0.001	
	Height at withers (stature)	Single	0.986	0.979	0.990	152.735	129	129	0.001	1st
		Average/Cα	0.993	0.989	0.995	152.735	129	129	0.001	
	Body length	Single	0.865	0.814	0.902	13.78	129	129	0.001	1st
		Average/Cα	0.927	0.897	0.949	13.78	129	129	0.001	
Hump	Hump-to-tail distance	Single	0.984	0.977	0.989	123.989	129	129	0.001	1st
		Average/Cα	0.992	0.989	0.994	123.989	129	129	0.001	
	Hump length	Single	0.905	0.868	0.932	20.049	129	129	0.001	1st
		Average/Cα	0.950	0.929	0.965	20.049	129	129	0.001	
	Hump width	Single	0.989	0.985	0.992	182.709	129	129	0.001	1st
		Average/Cα	0.995	0.992	0.996	182.709	129	129	0.001	
	Hump heigth	Single	0.995	0.992	0.996	375.396	129	129	0.001	1st
		Average/Cα	0.997	0.996	0.998	375.396	129	129	0.001	
	Hump girth	Single	0.587	0.461	0.689	3.838	129	129	0.001	1st
		Average/Cα	0.739	0.632	0.816	3.838	129	129	0.001	
Rump and Tail	Rump length	Single	0.938	0.914	0.956	31.371	129	129	0.001	1st
		Average/Cα	0.968	0.955	0.977	31.371	129	129	0.001	
	Rump width	Single	0.984	0.978	0.989	124.652	129	129	0.001	1st
		Average/Cα	0.992	0.989	0.994	124.652	129	129	0.001	

Table 2. *Cont.*

Area	Measurements	Parameters	Intraclass Correlation	95% Confidence Interval Lower Bound	95% Confidence Interval Higher Bound	F Test with True Value 1	df1	df2	Sig	Round [a]
Rump and Tail	Tail length	Single	0.984	0.977	0.988	121.041	129	129	0.001	1st
		Average/Cα	0.992	0.988	0.994	121.041	129	129	0.001	
	Width af the base of the tail	Single	0.842	0.783	0.885	11.642	129	129	0.001	1st
		Average/Cα	0.914	0.879	0.939	11.642	129	129	0.001	
Extremiti es	Thigh perimeter	Single	0.618	0.500	0.714	4.239	129	129	0.001	2nd
		Average/Cα	0.764	0.666	0.833	4.239	129	129	0.001	
	Hock perimeter	Single	0.753	0.668	0.819	7.107	129	129	0.001	3rd
		Average/Cα	0.859	0.801	0.901	7.107	129	129	0.001	
	Fore cannon bone perimeter	Single	0.612	0.492	0.709	4.156	129	129	0.001	3rd
		Average/Cα	0.759	0.660	0.830	4.156	129	129	0.001	
	Rear cannon bone perimeter	Single	0.529	0.393	0.642	3.243	129	129	0.001	3rd
		Average/Cα	0.692	0.564	0.782	3.243	129	129	0.001	
Feet	Sole length	Single	0.718	0.623	0.792	6.097	129	129	0.001	1st
		Average/Cα	0.836	0.768	0.884	6.097	129	129	0.001	
	Length of toe dorsal line	Single	0.894	0.853	0.924	17.832	129	129	0.001	1st
		Average/Cα	0.944	0.921	0.960	17.832	129	129	0.001	
	Heel heigth	Single	0.977	0.968	0.984	86.753	129	129	0.001	1st
		Average/Cα	0.988	0.984	0.992	86.753	129	129	0.001	
	Foot perimeter	Single	0.486	0.343	0.607	2.894	129	129	0.001	3rd
		Average/Cα	0.654	0.511	0.756	2.894	129	129	0.001	

[a]First: Variables for which direct translation between methods was feasible; Second: Variables for which Bayesian regression modelling correction as a function of digital measurements and live body weight was performed (except for foot perimeter, for which live body weight did not report a significant effect ($p < 0.05$)); Third: Variables for which Bayesian regression modelling correction as a function of live body weight and natural logarithm correction addition was performed.

Bayesian linear regression modelling and second round of method comparison/repeatability and scale reliability

After the initial round of method comparison/repeatability and scale reliability, neck girth at caudal third, heart girth, thigh perimeter, hock perimeter, fore cannon bone perimeter, rear cannon bone perimeter, and foot perimeter, respectively, did not reach acceptable levels of scale reliability (Average/Cα < 0.600, Table 2). Hence, we subjected them to Bayesian Regression Modelling Correction as a function of live body weight (except for foot perimeter, for which a nonsignificant effect of live body weight was reported $p < 0.05$), and the second round of ICC computation was performed. We did not consider additional factors such as coat color or age, given no evidence for their significant effect was found ($p > 0.05$). Table 3 summarizes Bayesian unstandardized linear (β) regression coefficients posterior distribution statistics for each of the variables considered. Bayesian determination coefficients (R^2) or percentages of variance captured by each of the models and their respective BF are provided in Table 4. Models were considerably more probable than those which only comprised the intercept. Posterior predictive p values (pppvalues) for models were 0 < pppvalues < 1 and around 0.500, so therefore model fit was ensured (Table 5).

Table 3. Bayesian estimates of posterior distribution statistics for unstandardized linear regression coefficients for digital measurements and live body weight as regressors for the zoometric traits for which Average/Cronbach's alpha did not surpass 0.600 at direct translation in the first round.

Zoometric trait (=y)	Parameter	Posterior Mode	Mean	Variance	95% Credible Interval Lower Bound	95% Credible Interval Upper Bound
Corrected Neck girth: caudal third	Intercept	40.713	40.713	214.839	11.938	69.488
	Neck girth: caudal third	0.347	0.347	0.013	0.125	0.570
	Live body weight	0.088	0.088	0.000	0.054	0.121
Corrected Heart girth	Intercept	76.511	76.511	48.808	62.796	90.227
	Heart girth	-0.017	-0.017	0.001	-0.081	0.046
	Live body weight	0.111	0.111	0.000	0.092	0.130
Corrected Thigh circumference	Intercept	44.180	44.180	30.676	33.307	55.053
	Thigh circumference	0.217	0.217	0.007	0.059	0.376
	Live body weight	0.039	0.039	0.000	0.021	0.058
Corrected Hock circumference	Intercept	13.005	13.005	11.842	6.250	19.761
	Hock circumference	0.335	0.335	0.008	0.162	0.508
	Live body weight	0.025	0.025	0.000	0.015	0.036

Table 3. *Cont.*

Zoometric trait (=y)	Parameter	Posterior Mode	Mean	Variance	95% Credible Interval Lower Bound	95% Credible Interval Upper Bound
Corrected Fore cannon bone perimeter	Intercept	10.646	10.646	2.169	7.755	13.537
	Fore cannon bone perimeter	0.247	0.247	0.005	0.104	0.390
	Live body weight	0.006	0.006	0.000	0.001	0.010
Corrected Rear cannon bone perimeter	Intercept	9.392	9.392	1.684	6.844	11.939
	Rear cannon bone perimeter	0.225	0.225	0.003	0.111	0.340
	Live body weight	0.009	0.009	0.000	0.005	0.013
Corrected Foot perimeter	Intercept	33.356	33.356	21.631	24.226	42.487
	Foot perimeter	0.260	0.260	0.016	0.015	0.506

Table 4. Bayes factor model summary for correction models comprising digital measurements and live body weight, except for foot perimeter, for which only digital measurement was used as a regressor, to estimate for on-field zoometric measurements in Canarian camels.

Zoometric trait (=y)	Corrected neck girth: caudal third	Corrected Heart girth	Corrected Thigh circumference	Corrected Hock circumference	Corrected Fore cannon bone perimeter	Corrected Rear cannon bone perimeter	Corrected Foot perimeter
Correction Method	Bayesian regression and Natural logarithm	Bayesian regression and Natural logarithm	Bayesian regression	Bayesian regression and Natural logarithm	Bayesian regression and Natural logarithm	Bayesian regression and Natural logarithm	Bayesian regression and Natural logarithm
Regressors	Live body weight and Digital Imaging measurement for neck girth: caudal third	Live body weight and Digital Imaging measurement for Heart girth	Live body weight and Digital Imaging measurement for Thigh circumference	Live body weight and Digital Imaging measurement for Hock circumference	Live body weight and Digital Imaging measurement for Fore cannon bone perimeter	Live body weight and Digital Imaging measurement for Rear cannon bone perimeter	Digital Imaging measurement for Foot perimeter
Round	3rd	3rd	2nd	3rd	3rd	3rd	3rd
Equation	y=40.713+ 0.347*(Neck girth: caudal third)+0.088 *(Live body weight)+ ln(Neck girth: caudal third)	y=76.511+ (0.017) *(Heart girth)+0.111 *(Live body weight)+ ln(Heart girth)	y=44.18+ 0.217 *(Thigh circumference)+0.039* (Live body weight)	y=13.005+ 0.335*(Hock circumference)+0.025* (Live body weight)+ ln(Hock circumference)	y=10.646+ 0.247*(Fore cannon bone perimeter)+ 0.006*(Live body weight)+ ln(Fore cannon bone perimeter)	y=9.392+ 0.225*(Rear cannon bone perimeter)+ 0.009*(Live body weight)+ ln(Rear cannon bone perimeter)	y=33.356+ 0.260*(Foot perimeter)+ ln(Foot perimeter)

Table 4. *Cont.*

Zoometric trait (=y)	Corrected neck girth: caudal third	Corrected Heart girth	Corrected Thigh circumference	Corrected Hock circumference	Corrected Fore cannon bone perimeter	Corrected Rear cannon bone perimeter	Corrected Foot perimeter
Regression Sum of Squares	11540.442	12611.463	3226.575	1504.485	114.180	182.118	162.324
Regression df	2.000	2.000	2.000	2.000	2.000	2.000	1.000
Regression Mean Square	5770.221	6305.731	1613.288	752.242	57.090	91.059	162.324
F	20.168	67.975	23.580	33.454	11.409	23.354	4.409
Sig.	0.000	0.000	0.000	0.000	0.000	0.000	0.038
Residual Sum of Squares (RSS)	36336.003	11781.220	8689.017	2855.697	635.487	495.174	4712.808
Residual df	127.000	127.000	127.000	127.000	127.000	127.000	128.000
Residual Mean Square	286.110	92.766	68.417	22.486	5.004	3.899	36.819
Bayes Factor (BF)	269,937.547	6.39×10^{17}	3,356,913.557	2.93×10^{9}	252.807	2,850,184.198	0.597
R	0.491	0.719	0.520	0.587	0.390	0.519	0.182
Bayesian R Square	0.241	0.517	0.271	0.345	0.152	0.269	0.033
Bayesian Adjusted R Square	0.229	0.509	0.259	0.335	0.139	0.257	0.026
SE	16.915	9.631	8.271	4.742	2.237	1.975	6.068
Monte Carlo standard error (MCSE)	279.508	90.625	66.839	21.967	4.888	3.809	36.252
Bayesian Information Criterion (BIC)	95,207.940	76,173.431	71,028.278	52,222.907	26,827.621	22,611.369	60,684.398

LN: Natural logarithm; SE: Standard error.

Table 5. Predictive Posterior p-Values (pppvalues) for correction models comprising digital measurements and live body weight, except for foot perimeters, for which only digital measurement was used as a regressor to estimate for on-field zoometric measurements in Canarian camels.

Variables for which a correction was issued	P(T>=T_obs) Predictive Posterior p-Values
Corrected Neck girth: caudal third	0.496
Corrected Heart girth	0.459
Corrected Thigh circumference	0.495
Corrected Hock circumference	0.495
Corrected Fore cannon bone perimeter	0.494
Corrected Rear cannon bone perimeter	0.497
Corrected Foot perimeter	0.497
P(T>=T_obs) close to 0 or 1 indicates lack of fit.	

Natural logarithmic correction for perimeters and girths and third round of method comparison/repeatability and scale reliability

Afterwards, all the variables except for thigh perimeters had not reached acceptable levels of scale reliability (Average/Cα < 0.600, Table 2). Therefore, natural logarithm was added to their equation, and the third round of ICC computation was used.

Final outputs for method comparison/repeatability and scale reliability

After Bayesian linear regression modeling and natural logarithmic correction, all methods proved to be highly repeatable and reliable, as suggested by the values of ICC and 95% CI for average measurements (Average/Cα) for all the zoometric measurements that were made. Finally, the resulting equations are reported in Table 4. Linear zoometrics always reported excellent repeatability values over 0.836 (for sole length average measurements ICC) with high 95%CI lower bounds over 0.768. Although perimeters and girths reported lower average measurements ICC, values were always higher than 0.654 (for foot perimeter average measurements ICC), which suggested good repeatability, while also presenting a reasonable 95%IC lower bound over 0.511. A summary of the results obtained after the three rounds of ICC calculation (single and average measurements/Cα) and 95%CI is reported in Table 1. Dispersion statistics for the measurements collected on-field and those extracted from digital imaging methods after correction are reported in Supplementary Table S3.

Discussion

Apart from the time reduction, personnel requirements, and handlers' safety improvement implicit in digital imaging zoometrics, a lower expected random error is obtained when these are compared to on-field measurements. This improved accuracy, reliability, and repeatability is not only supported by our results (Tables 2 and 5, Supplementary Table S3), but also by literature references highlighting a greater dispersion of the zoometric data collected with traditional instruments on-field against those extracted from digital image-based methods (Gaudioso et al., 2014; Huang et al., 2018; Negretti et al., 2007).

This may be ascribed to the difficulty for the animals to remain completely immobile during on-field measurement collection, which could add undesired noise to the data. As a drawback of image-based zoometric measurements, rigorous efforts may need to be made by operators to hold animals in the correct aplomb at a completely static position while keeping the photographic and camel midsagittal planes parallel (Rahagiyanto & Adhyatma, 2021).

In line with these preliminary arguments, collateral factors such as the image resolution, the accuracy of the distance measurement from the camera to the animal (focal plane), hair length and extension, coat color, and the fat condition of the animal, may need to be controlled before and during the zoometric measurements extraction from digital images to ensure that data depicts the real morphometry of the individuals as far as possible (Collins & Gazley, 2017; Muir et al., 2013; Negretti et al., 2007; Pérez-Ruiz et al., 2020; Waite et al., 2007).

The correspondence between on-field and image-based zoometrics methods was evaluated via the average measurements intraclass correlation coefficient (ICC)/Cronbach's alpha (Cα) (Colli et al., 2013). Method correspondence was considered acceptable when a limit value of 0.6 ICC/Cα was reached (Abu-Zidan et al., 2012). This limit was attained for all the measurements except for 'Neck girth: caudal third', 'Thoracic girth', 'Thigh perimeter', 'Hock perimeter', 'Fore cannon bone perimeter', 'Rear cannon bone perimeter', and 'Foot perimeter' at the first round (direct extrapolation). These findings were compared with those of Pezzuolo et al. (2018) and Pérez-Ruiz et al. (2020), who reported a particularly large relative error in digital three- dimensional zoometric measurements when compared to on-field three-dimensional measurements. Hence, the need for a correction methodology for digital three-dimensional measurements was suggested.

The basis for this lack of initial correspondence (in the first round) between three-dimensional measurements may be based on the fact that for their on-field collection, the participation of at least two operators is generally required. This, in turn, results in an unbalanced placement of the corresponding measuring instrument at different transverse planes in the homologous contralateral regions. By contrast, linear measurements are generally made by the same operator who controls the exact position of the instrument used for the measurement and is only performed on one side of the animal, which reduces the probability of finding morphological variance throughout the measured area.

As a result, the second round of correction was necessary to enhance method correspondence for the measurements for which acceptable levels had not been attained in the first round. A Bayesian linear regression was applied between manual and non-contact measurements, considering body weight as the most critical influencing parameter.

Evidence of body weight is a source for such quantitative differences between on-field and digital imaging-based three-dimensional measurements found, as suggested by the lack of evidence of significance and CV values. According to literature, the circular perimeter of the area to be measured can intrinsically vary along its length depending on the regional adiposity (Jensen, Danielsen, & Tauson, 2016) and the muscular development of the region (Albertí et al., 2005), which are both directly related to body weight. Indeed, Boujenane (2019) referenced that such a strong relationship between zoometry and weight could have been expected, since the estimation of the latter relies on chest and hump girth apart from height to withers via its estimation formula.

Once the digital measurement was multiplied by the coefficients obtained and the intercept value-added, the ICC between on-field and the corrected digital measurement improved only for the variable of 'Thigh perimeter'. Hence, the third round of correction was necessary to improve correspondence for the remaining measurements for which acceptable levels had not been reached. The correspondence between on-field and digital measurements was achieved after applying an additional correction consisting of the sum of the natural logarithm of the digital measurement (third round).

The fact that a linear regression model was enough to obtain a corrected digital measurement with acceptable correspondence for on-field thigh perimeter could be explained under the assumption that this area, given its location, hardly varies in its muscular tonus if no strong movements are carried out. This lack of variability does not distort skewness values; hence, the logarithmic correction does not improve correspondence values.

By contrast, for 'Neck girth: caudal third' and 'Thoracic girth', continuous respiratory movements may cause slight perimeter variations in the photographs taken during on-field evaluations, altering skewness properties and perhaps making it necessary to consider a natural logarithmic correction factor.

This could also be applied to the rest of the variables, that is, 'Hock perimeter, 'Fore cannon bone perimeter', 'Rear cannon bone perimeter', and 'Foot perimeter'. The implicit difficulty to restrain camels in a completely static position may induce temporary size changes in these local areas. Specifically, the pressure that the fore and rear limbs have to cope with depends on the particular position of the animal aplomb at the moment of measure collection (photo taking).

This may derive from the fact that the musculoskeletal systems involved in maintaining the posture are incapable of maintaining limbs in a perfect and unique stationary position, with the consequent increase in local muscle temperature due to rising blood flow and the transient oscillation of the distal limbs to the resonant frequency of heartbeats producing muscle tremor (Lakie, 2010; Marsden et al., 1969). This translates into a source of increased skewness, data dispersion, and noise, which is corrected, as suggested by literature, via the addition of natural logarithms of the zoometric measurement to the equation.

Conclusions

The efficiency, repeatability, and accuracy of the on-field zoometric methods that are routinely considered for zoometric characterization in dromedaries can be enhanced through the use of digital imaging techniques. On-field and digital imaging zoometric extrapolation results in comparatively improved performance of the latter, due to the reduced dispersion of the data extracted from photographs. However, mathematical correction methods may be needed for three-dimensional measurements to reach acceptable levels of on-field/digital imaging methods correspondence. Body weight is the main source of bias in perimeter digital zoometric extraction if other factors such as age and coat color are controlled. All zoometric perimeters collected on-field should be regressed against body weight, except for foot perimeter, to ensure acceptable levels of correspondence are attained. Additionally, we summed the natural logarithms of the particular measurements which could be affected by spontaneous movements (breathing or proprioception) to correct for derived skewness distortion. The present method offers a time and economically affordable alternative, which saves the drawbacks derived from the lack of consideration of three-dimensional measurements that routinely occur in digital imaging zoometrics. The high degree of correspondence between methods makes this tool valid for its standardized implementation in camel zoometric characterization, while it may be translatable to other species.

Supplementary materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/math10193453/s1, Table S1. Commonly used thresholds to define significance of evidence through Bayes factor (BF); Table S2. Model validity and accuracy parameters definition and interpretation; Table S3. Descriptive statistics and dispersion measurements for digital imaging and on-field zoometric variables in Canarian camels.

Author contributions: Conceptualization, C.I.P., F.J.N.G. and J.V.D.B.; Data curation, C.I.P. and F.J.N.G.; Formal analysis, C.I.P., F.J.N.G. and J.V.D.B.; Funding acquisition, E.C., M.E.C.V. and J.V.D.B.; Investigation, C.I.P. and F.J.N.G.; Methodology, C.I.P. and F.J.N.G.; Project administration, E.C., M.E.C.V. and J.V.D.B.; Resources, E.C., M.E.C.V. and J.V.D.B.; Software, C.I.P. and F.J.N.G.; Supervision, F.J.N.G., E.C., M.E.C.V. and J.V.D.B.; Validation, F.J.N.G. and J.V.D.B.; Visualization, E.C. and M.E.C.V.; Writing—original draft, C.I.P. and F.J.N.G.; Writing—review & editing, F.J.N.G., E.C., M.E.C.V. and J.V.D.B. All authors have read and agreed to the published version of the manuscript.

Funding: The present research was carried out in the financing framework of the international project CA.RA.VA.N—'Toward a Camel Transnational Value Chain' (Reference APCIN-2016-00011-00-00) and during the coverage period of a predoctoral contract (FPU Fellowship) funded by the Spanish Ministry of Science and Innovation.

Data availability statement: Data will be made available from first author upon reasonable request.

Acknowledgments: The authors would also like to thank 'Aires Africanos' Eco-tourism Company, Oasis Park Fuerteventura, and 'Camelus' Camellos de Almería, for their direct technical help and assistance.

Conflicts of interest: The authors declare no conflict of interest.

Ethics declaration statement: All farms included in the study followed specific codes of good practices and therefore, the animals received humane care in compliance with the national guide for the care and use of laboratory and farm animals in research. Written consent from the owners was obtained for their participation. The study was conducted in accordance with the Declaration of Helsinki. The Spanish Ministry of Economy and Competitivity through the Royal Decree Law 53/2013 and its credited entity, the Ethics Committee of Animal Experimentation from the University of Córdoba, permitted the application of the protocols present in this study as cited in the 5th section of its 2nd article, as the animals assessed were used for credited zootechnical use. This national Decree follows the European Union Directive 2010/63/UE, from the 22 September of 2010.

References

Abdallah, H. R., & Faye, B. (2012). Phenotypic classification of Saudi Arabian camel (*Camelus dromedarius*) by their body measurements. *Emirates Journal of Food and Agriculture*.

Abdullahi, I. A., Musa, H. A.-H., & Jibril, A. (2012). Scrotal circumference and testicular morphometric characteristics of the camel (*Camelus dromedarius*) in the semi-arid environment of northern Nigeria. *International Journal of Morphology*, 30(4), 1369-1372.

Abu-Zidan, F. M., Eid, H. O., Hefny, A. F., Bashir, M. O., & Branicki, F. (2012). Camel bite injuries in United Arab Emirates: a 6 year prospective study. *Injury*, 43(9), 1617-1620.

Al-Atiyat, R. M., Suliman, G., AlSuhaibani, E., El-Waziry, A., Al-Owaimer, A., & Basmaeil, S. (2016). The differentiation of camel breeds based on meat measurements using discriminant analysis. *Tropical animal health and production*, 48(5), 871-878.

Albertí, P., Ripoll, G., Goyache, F., Lahoz, F., Olleta, J., Panea, B., & Sañudo, C. (2005). Carcass characterisation of seven Spanish beef breeds slaughtered at two commercial weights. *Meat Science*, 71(3), 514-521.

Alexander, M., & Kusleika, R. (2016). *Excel 2016 Formulas*: John Wiley & Sons.

Alhajeri, B. H., Alaqeely, R., & Alhaddad, H. (2019). Classifying camel breeds using geometric morphometrics: a case study in Kuwait. *Livestock Science*, 230, 103824.

Alhajeri, B. H., Alhaddad, H., Alaqeely, R., Alaskar, H., Dashti, Z., & Maraqa, T. (2021). Camel breed morphometrics: current methods and possibilities. *Transactions of the Royal Society of South Australia*, 1-22.

Analla, M. (1998). Model validation through the linear regression fit to actual versus predicted values. *Agricultural Systems*, 57(1), 115-119.

Arora, J. S. (2017). Chapter 14 - Practical Applications of Optimization. In *Introduction to Optimum Design (Fourth Edition)* (pp. 601-680) (J. S. Arora, Ed.): Academic Press.

Ayadi, M., Aljumaah, R. S., Samara, E. M., Faye, B., & Caja, G. (2016). A proposal of linear assessment scheme for the udder of dairy camels (*Camelus dromedarius* L.). *Tropical animal health and production*, 48(5), 927-933.

Azzaro, G., Caccamo, M., Ferguson, J. D., Battiato, S., Farinella, G. M., Guarnera, G. C., Puglisi, G., Petriglieri, R., & Licitra, G. (2011). Objective estimation of body condition score by modeling cow body shape from digital images. *Journal of Dairy Science*, 94(4), 2126-2137.

Babu, K. (2015). Natural textile fibres: Animal and silk fibres. In *Textiles and Fashion* (pp. 57-78): Elsevier.

Bao, L., Gneiting, T., Grimit, E. P., Guttorp, P., & Raftery, A. E. (2010). Bias correction and Bayesian model averaging for ensemble forecasts of surface wind direction. *Monthly Weather Review*, 138(5), 1811-1821.

Bayarri, M. J., Berger, J. O., Forte, A., & García-Donato, G. (2012). Criteria for Bayesian model choice with application to variable selection. *The Annals of statistics*, 40(3), 1550-1577.

Beanland, C., Schneider, Z., LoBiondo-Wood, G., & Haber, J. (1999). *Nursing research: Methods, critical appraisal and utilization*: Elsevier.

Bell, C. M., Hindell, M. A., & Burton, H. R. (1997). Estimation of body mass in the southern elephant seal, *Mirounga leonina*, by photogrammetry and morphometrics. *Marine mammal science*, 13(4), 669-682.

Bewley, J., Peacock, A., Lewis, O., Boyce, R., Roberts, D., Coffey, M., Kenyon, S.J., & Schutz, M. (2008). Potential for estimation of body condition scores in dairy cattle from digital images. *Journal of Dairy Science*, 91(9), 3439-3453.

Bitaraf Sani, M., Hosseini, S. A., Asadzadeh, N., Ghavipanje, N., Afshin, M., Jasouri, M., Banabazi, M.H., Esmaeilkhanian, S., Harofte, J.Z., Naderi, A.S., & Burger, P. (2022). A New Approach in the Evaluation of Dairy Camels: Using Test Day Milk and Morphometric Records. *Dairy*, 3(1), 78-86.

Boujenane, I. (2019). Comparison of body weight estimation equations for camels (*Camelus dromedarius*). *Tropical animal health and production*, 51(4), 1003-1007.

Brewer, K. R. (2002). *Combined survey sampling inference: Weighing Basu's elephants*: Oxford University Press.

Çağlı, A., & Yılmaz, M. (2021). Determination of some body measurements of camels with three-dimensional modeling method (3D). *Tropical animal health and production*, 53(6), 1-12.

Carlin, J. (2019). *Solutions to some exercises from Bayesian Data Analysis*: Columbia Press.

Cervantes, I., Baumung, R., Molina, A., Druml, T., Gutiérrez, J., Sölkner, J., & Valera, M. (2009). Size and shape analysis of morphofunctional traits in the Spanish Arab horse. *Livestock Science*, 125(1), 43-49.

Chandrupatla, T. R., & Osler, T. J. (2010). The perimeter of an ellipse. *Mathematical Scientist*, 35(2).

Clyde, M., Cetinkaya-Rundel, M., Rundel, C., Banks, D., Chai, C., & Huang, L. (2019). Chapter 7. Bayesian Model Choice. In *An Introduction to Bayesian Thinking*: BookDown.

Colli, L., Perrotta, G., Negrini, R., Bomba, L., Bigi, D., Zambonelli, P., Verini Supplizi, A., Liotta, L., & Ajmone-Marsan, P. (2013). Detecting population structure and recent demographic history in endangered livestock breeds: the case of the Italian autochthonous donkeys. *Animal genetics*, 44(1), 69-78.

Collins, K. S., & Gazley, M. F. (2017). Does my posterior look big in this? The effect of photographic distortion on morphometric analyses. *Paleobiology*, 43(3), 508-520.

Corp., I. (2017a). *IBM SPSS Statistics Algorithms*. In Version 25.0 ed., pp. 110. Armonk, NY: IBM Corp.

Corp., I. (2017b). *IBM SPSS Statistics for Windows (Version 25.0)*. Armonk, NY: IBM Corp.

Creswell, J. W. (2010). *Educational research: Planning, conducting, and evaluating quantitative (4th ed.)*: Prentice Hall Upper Saddle River.

de Bruyn, P., Bester, M., Carlini, A., & Oosthuizen, W. (2009). How to weigh an elephant seal with one finger: a simple three-dimensional photogrammetric application, *Aquatic Biology*, 5, 31–39.

de Kock, M. E., O'Donovan, D., Khafaga, T., & Hejcmanová, P. (2021). Zoometric data extraction from drone imagery: the Arabian oryx (*Oryx leucoryx*). *Environmental Conservation*, 48(4), 295-300.

De Wet, L., Vranken, E., Chedad, A., Aerts, J.-M., Ceunen, J., & Berckmans, D. (2003). Computer-assisted image analysis to quantify daily growth rates of broiler chickens. *British poultry science*, 44(4), 524-532.

Depaoli, S., & Van de Schoot, R. (2017). Improving transparency and replication in Bayesian statistics: The WAMBS-Checklist. *Psychological methods*, 22(2), 240.

Doğan, N. Ö. (2018). Bland-Altman analysis: A paradigm to understand correlation and agreement. *Turkish Journal of Emergency Medicine*, 18(4), 139-141.

Dorantes-Coronado, E., Torres-Hernández, G., Hernández-Mendo, O., & Rojo-Rubio, R. (2015). Zoometric measures and their utilization in prediction of live weight of local goats in southern México. *SpringerPlus*, 4(1), 1-8.

Drton, M., & Plummer, M. (2017). A Bayesian information criterion for singular models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 79(2), 323-380.

Fleiss, J. L., & Cohen, J. (1973). The equivalence of weighted kappa and the intraclass correlation coefficient as measures of reliability. *Educational and psychological measurement*, 33(3), 613-619.

Gaudioso, V., Sanz-Ablanedo, E., Lomillos, J., Alonso, M., Javares-Morillo, L., & Rodríguez, P. (2014). "Photozoometer": A new photogrammetric system for obtaining morphometric measurements of elusive animals. *Livestock Science*, 165, 147-156.

Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., & Rubin, D. B. (2013). *Bayesian data analysis*: CRC press.

Gelman, A., Goodrich, B., Gabry, J., & Vehtari, A. (2019). R-squared for Bayesian regression models. The *American Statistician*, 73(3), 307-309.

George, D., & Mallery, P. (2003). *Reliability analysis. SPSS for Windows, step by step: a simple guide and reference (14th ed.)*: Allyn & Bacon.

Geweke, J. (1996). Variable selection and model comparison in regression. Proceedings of the Fifth Valencia International Meetings on Bayesian Statistics.

Gherissi, D. E., Lamraoui, R., Chacha, F., & Gaouar, S. B. S. (2022). Accuracy of Image Analysis for Linear Zoometric Measurements in Dromedary Camels. *Tropical Animal Health and Production*, 54(4), 232.

González Ariza, A., Arando Arbulu, A., Navas González, F. J., Ruíz Morales, F. d. A., León Jurado, J. M., Barba Capote, C. J., & Camacho Vallejo, M. E. (2019). Sensory preference and professional profile affinity definition of endangered native breed eggs compared to commercial laying lineages' eggs. *Animals*, 9(11), 920.

Hall, P., & Maiti, T. (2006). Nonparametric estimation of mean-squared prediction error in nested-error regression models. *The Annals of Statistics*, 34(4), 1733-1750.

Hayes, A. F., Glynn, C. J., & Huge, M. E. (2012). Cautions Regarding the Interpretation of Regression Coefficients and Hypothesis Tests in Linear Models with Interactions. *Communication Methods and Measures*, 6(1), 1-11.

Heck, D. (2019). A Caveat on the Savage-Dickey Density Ratio: The Case of Computing Bayes Factors for Regression Parameters. *British Journal of Mathematical and Statistical Psychology*, 72, 316-333.

Huang, L., Li, S., Zhu, A., Fan, X., Zhang, C., & Wang, H. (2018). Non-contact body measurement for qinchuan cattle with LiDAR sensor. *Sensors*, 18(9), 3014.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S., & Bermejo, J. V. (2020a). Zoometric characterization and body condition score in Canarian camel breed. *Archivos de zootecnia*, 69(265), 14-21.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S., & Bermejo, J. V. (2020b). Biokinematics and applied thermography in the Canarian camel breed. *Archivos de zootecnia*, 69(265), 102-107.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Barba Capote, C. J., & Delgado Bermejo, J. V. (2020). Effect of Research Impact on Emerging Camel Husbandry, Welfare and Social-Related Awareness. *Animals*, 10(5), 780.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., González Ariza, A., & Delgado Bermejo, J. V. (2021). A tool for functional selection of leisure camels: Behaviour breeding criteria may ensure long-term sustainability of a European unique breed. *Research in Veterinary Science*, 140, 142-152.

Jeffreys, H. (1961). *Theory of Probability (3rd edition)*: Oxford University Press.

Jensen, R. B., Danielsen, S. H., & Tauson, A.-H. (2016). Body condition score, morphometric measurements and estimation of body weight in mature Icelandic horses in Denmark. *Acta Veterinaria Scandinavica*, 58(1), 19-23.

Kaplan, D., & Depaoli, S. (2012). Bayesian structural equation modeling. In *Handbook of structural equation modeling* (R. H. Hoyle, Ed.) (pp. 650–673): The Guilford Press.

Kass, R. E., & Raftery, A. E. (1995). Bayes factors. *Journal of the American Statistical Association*, 90(430), 773-795.

Kerje, S., Lind, J., Schütz, K., Jensen, P., & Andersson, L. (2003). Melanocortin 1-receptor (MC1R) mutations are associated with plumage colour in chicken. *Animal genetics*, 34(4), 241-248.

Köhler-Rollefson, I. (2022). Camel biodiversity—and how to conserve it. *Animal frontiers*, 12(4), 17-19.

Koo, T. K., & Li, M. Y. (2016). A Guideline of Selecting and Reporting Intraclass Correlation Coefficients for Reliability Research. *Journal of chiropractic medicine*, 15(2), 155-163.

Lakie, M. (2010). The influence of muscle tremor on shooting performance. *Experimental physiology*, 95(3), 441-450.

Lee, M., & Wagenmakers, E. (2013). *Bayesian data analysis for cognitive science: A practical course*: Cambridge University Press.

Liang, F., Paulo, R., Molina, G., Clyde, M. A., & Berger, J. O. (2008). Mixtures of g priors for Bayesian variable selection. *Journal of the American Statistical Association*, 103(481), 410-423.

Marsden, C., Meadows, J., Lange, G., & Watson, R. (1969). The role of the ballistocardiac impulse in the genesis of physiological tremor. *Brain*, 92(3), 647-662.

Meghelli, I., Kaouadji, Z., Yilmaz, O., Cemal, İ., Karaca, O., & Gaouar, S. (2020). Morphometric characterization and estimating body weight of two Algerian camel breeds using morphometric measurements. *Tropical animal health and production*, 52(5), 2505-2512.

Morey, R., & Rouder, J. (2015). BayesFactor 0.9. 12-2. *Comprehensive R Archive Network*.

Motulsky, H. J., & Brown, R. E. (2006). Detecting outliers when fitting data with nonlinear regression–a new method based on robust nonlinear regression and the false discovery rate. *BMC bioinformatics*, 7(1), 123.

Muir, A., Vecsei, P., Pratt, T., Krueger, C., Power, M., & Reist, J. (2013). Ontogenetic shifts in morphology and resource use of cisco *Coregonus artedi*. *Journal of fish biology*, 82(2), 600-617.

Negretti, P., Bianconi, G., Bartocci, S., Terramoccia, S., & Verna, M. (2008). Determination of live weight and body condition score in lactating Mediterranean buffalo by Visual Image Analysis. *Livestock Science*, 113(1), 1-7.

Negretti, P., Bianconi, G., & Finzi, A. (2007). Visual image analysis to estimate morphological and weight measurements in rabbits. *World Rabbit Science*, 15(1), 37-41.

Nunnally, J. C., & Bernstein, I. (1994). *The Role of University in the Development of Entrepreneurial Vocations: A Spanish Study*: McGraw-Hill New York.

O'Malley, B. P., Schmitt, J. D., Holden, J. P., & Weidel, B. C. (2021). Comparison of Specimen-and Image-Based Morphometrics for Cisco. *Journal of Fish and Wildlife Management*, 12(1), 208-215.

Padalino, B., Monaco, D., & Lacalandra, G. M. (2015). Male camel behavior and breeding management strategies: How to handle a camel bull during the breeding season? *Emirates Journal of Food and Agriculture*, 338-349.

Pallant, J. (2020). *SPSS survival manual: A step by step guide to data analysis using IBM SPSS*: Routledge.

Parés, C., & Sañudo, C. (2009). *Valoración morfológica de animales domésticos*: Editorial Sañudo.

Pérez-Ruiz, M., Tarrat-Martín, D., Sánchez-Guerrero, M. J., & Valera, M. (2020). Advances in horse morphometric measurements using LiDAR. *Computers and Electronics in Agriculture*, 174, 105510.

Pezzuolo, A., Guarino, M., Sartori, L., & Marinello, F. (2018). A feasibility study on the use of a structured light depth-camera for three-dimensional body measurements of dairy cows in free-stall barns. *Sensors*, 18(2), 673.

Pizarro Inostroza, M. G., Navas González, F. J., Landi, V., León Jurado, J. M., Delgado Bermejo, J. V., Fernández Álvarez, J., & Martínez Martínez, M. d. A. (2020a). Bayesian Analysis of the Association between Casein Complex Haplotype Variants and Milk Yield, Composition, and Curve Shape Parameters in Murciano-Granadina Goats. *Animals*, 10(10), 1845.

Pizarro Inostroza, M. G., Navas González, F. J., Landi, V., León Jurado, J. M., Delgado Bermejo, J. V., Fernández Álvarez, J., & Martínez Martínez, M. d. A. (2020b). Software-Automatized Individual Lactation Model Fitting, Peak and Persistence and Bayesian Criteria Comparison for Milk Yield Genetic Studies in Murciano-Granadina Goats. *Mathematics*, 8(9), 1505.

Pizarro Inostroza, M. G., Navas González, F. J., Landi, V., León Jurado, J. M., Delgado Bermejo, J. V., Fernández Álvarez, J., & Martínez, M. d. A. M. (2020). Goat Milk Nutritional Quality Software-Automatized Individual Curve Model Fitting, Shape Parameters Calculation and Bayesian Flexibility Criteria Comparison. *Animals*, 10(9), 1693.

Proffitt, K. M., Garrott, R. A., Rotella, J. J., & Lele, S. (2008). Using form analysis techniques to improve photogrammetric mass-estimation methods. *Marine mammal science*, 24(1), 147-158.

Puig-Diví, A., Escalona-Marfil, C., Padullés-Riu, J. M., Busquets, A., Padullés-Chando, X., & Marcos-Ruiz, D. (2019). Validity and reliability of the Kinovea program in obtaining angles and distances using coordinates in 4 perspectives. *PloS one*, 14(6), e0216448.

Rahagiyanto, A., & Adhyatma, M. (2021). A Review of Morphometric Measurements Techniques on Animals Using Digital Image Processing. *Food and Agricultural Sciences: Polije Proceedings Series*, 3(1), 67-72.

Rouder, J. N., & Morey, R. D. (2012). Default Bayes factors for model selection in regression. *Multivariate Behavioral Research*, 47(6), 877-903.

Rouder, J. N., Morey, R. D., Speckman, P. L., & Province, J. M. (2012). Default Bayes factors for ANOVA designs. *Journal of Mathematical Psychology*, 56(5), 356-374.

Rouder, J. N., Speckman, P. L., Sun, D., Morey, R. D., & Iverson, G. (2009). Bayesian t tests for accepting and rejecting the null hypothesis. *Psychonomic bulletin & review*, 16(2), 225-237.

Shrader, A. M., Ferreira, S. M., & Van Aarde, R. J. (2006). Digital photogrammetry and laser rangefinder techniques to measure African elephants. *South African Journal of Wildlife Research*, 36(1), 1-7.

Singaraju, G. S., Js, Y. P., Mandava, P., Ganugapanta, V. R., Teja, N. R., & Jn, P. R. (2020). Data Set For Computation Of Maxillary Arch Perimeter With Ramanujan's Equation For Ellipse In Different Skeletal Malocclusions. *Data in Brief*, 32, 106079.

StataCorp. (2017). *Stata Statistical Software (Version 15)*. College Station, TX.

States, E. I. A. o. t. U. (1989). *Commercial Buildings Energy Consumption Survey: Commercial buildings energy consumption and expenditures*: Michigan State University.

Sueur, C., Kuntz, C., Debergue, E., Keller, B., Robic, F., Siegwalt-Baudin, F., Richer, C., Ramos, A., & Pelé, M. (2018). Leadership linked to group composition in Highland cattle (*Bos taurus*): Implications for livestock management. *Applied Animal Behaviour Science*, 198, 9-18.

Waite, J. N., Schrader, W. J., Mellish, J.-A. E., & Horning, M. (2007). Three-dimensional photogrammetry as a tool for estimating morphometrics and body mass of Steller sea lions (*Eumetopias jubatus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 64(2), 296-303.

White, R., Schofield, C., Green, D., Parsons, D., & Whittemore, C. (2004). The effectiveness of a visual image analysis (VIA) system for monitoring the performance of growing/finishing pigs. *Animal Science*, 78(3), 409-418.

Yakubu, A., Ladokun, A., & Adua, M. (2011). Bioprediction of body weight from zoometrical traits of non-descript goats using linear and non-linear models in North Central Nigeria. *Livestock Research for Rural Development*, 23, 6.

Zellner, A., & Siow, A. (1980). Posterior odds ratios for selected regression hypotheses. *Trabajos de estadística y de investigación operativa*, 31(1), 585-603.

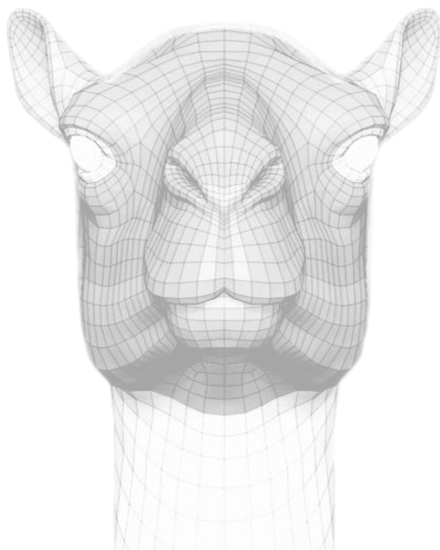
2.2 Evidences of subpopulation diversification and traces of introgression within Canarian camel breed zoometric standard: scope and opportunities for selection

Carlos Iglesias Pastrana[1], Francisco Javier Navas González[1], Elena Ciani[2], Antonio González Ariza[3], Sergio Nogales Baena[1] and Juan Vicente Delgado Bermejo[1]

[1]Department of Genetics, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain

[2]Department of Biosciences, Biotechnologies and Environment, Faculty of Veterinary Sciences, University of Bari 'Aldo Moro', 70121 Bari, Italy

[3]Centro Agropecuario Provincial de Córdoba, Diputación Provincial de Córdoba, 14071 Córdoba, Spain



Quality indicator information provided on the publication
Latest information available (2022)

Status of the manuscript: Submitted

Journal (year, volume, page(s)): *Italian Journal of Animal Science*

International database in which it is indexed: Journal of Citation Reports (JCR)

Thematic area in the reference database: Veterinary Sciences

Impact index of the journal in the year of the article's publication: 2.5

Rank/number of thematic area journals: 25/143 (Q1)

Abstract

Extant diversity for phenotypic traits is an essential criterion to be considered when ordering priorities for conservation and improvement of animal genetic resources. Concretely, the characterization of the distinctive body morphometry of a particular group of animals can aid at design selective breeding programmes given the strong correlation between body morphology and productive function. The present research aims to characterize an endangered autochthonous camel breed ('Canarian Camel'), mainly relegated to leisure riding, for its body morphology with a double objective: explore the phenotypic diversity and structure of the breed for zoometric traits, and assess the zoometric profile of this genetic resource that supports its differentiation from other camel breeds. Overall, the results highlight the existence of a high degree of genetic diversity for zoometric traits in an endangered autochthonous breed with traditional in situ breeding schemes, which predicts the success on the implementation of genetic improvement schemes for such functional characteristics. This phenotypic diversity in body morphology could also be a tool for the evaluation of new functional niches within the efforts of functional valorization of this camel breed for its sustainable conservation. Body morphology traits in the studied camel breed are significantly influenced by sex, physiological status and coat colour.

Keywords

Body morphology, sexual dimorphism, epistasis, phenotypic diversity, selective breeding, dromedary camel

Introduction

Livestock biodiversity is the result of the complex process of evolution trough which domestic animals have been maintained over time in human-influenced scenarios with differential raising and environmental conditions. Artificial selection and the natural mechanisms responsible for the dynamics of genetic change in live populations (mutation, genetic drift, gene flow, and natural selection) underlie the biological divergence among farm animal resources (Eusebi, Martinez, & Cortes, 2020; Hoffmann, 2011).

The comprehensive knowledge of the genetic heritage of a particular population, breed or variety is of primary interest for owners and stakeholders to understand the impact of the historical background of such animal aggrupation in its current status and functionality, but also for the evaluation of possible functional avenues (Ovaska et al., 2021). The later becomes possible, on the one hand, through the contrasted comparison of the studied population with those similar, nearest phylogenetic neighbors (De la Barra, Martínez, & Carvajal, 2016). In addition, the estimation of the patent genetic variation within the interest population, provides useful information in its adaptive potential to challenging issues (Kardos et al., 2021).

Concretely, the zoometric characterization aims to explore the distinctive morphometry of a particular group of animals with reference to their functionality (Brito et al., 2021). Body morphological characteristics, annexed with formal registers of the individual functional performance, sex and phaneroptic (i.e., coat colour and particularities), serve for the calculation of factor-correlated variability that may drive the definition and application of selection criteria (Toalombo Vargas et al., 2020; Yusuff & Fayeye, 2016). Additionally, when genealogical records are available, the components of heritability for traits of interest can be estimated (Poyato-Bonilla et al., 2021). In turn, zoometrics constitutes a key method for driving decisions on animal breeding with improvement, utilization and conservation purposes (Assan, 2015).

Among livestock species, camels remain extensively disregarded for breed characterization based on morphometric assessment, despite it is widely known the strong correlation between body morphology and productive function (Iglesias et al., 2020a). Actually, the existing literature on the phenotypic and genotypic variability of camel species for morphometric traits is by far less numerous compared to other domestic livestock (Alhaddad & Alhajeri, 2019; Alhajeri, Alaqeely, & Alhaddad, 2019; Babelhadj et al., 2017). However, it is manifest a positive tendence in camel demographics and geographical distribution (Faye, 2022), together with the increase in the socio-economic interest for production due to their relatively recent progressive appreciation as sustainable species (Iglesias Pastrana et al., 2020a). Being that so, the study of the existent morphometrics phenotypic variability in camels comes up as a pivotal prerequisite for assessing the variations within and between populations, hence to conserve camel biodiversity worldwide through the effective selection for specialized traits and the revalorization of endangered resources (Iglesias et al., 2020b; Köhler-Rollefson, 2022). Besides, when molecular tools are not affordable, morphological characterization trough discriminant analysis constitute the most reliable alternative option (Ceccobelli et al., 2016).

Contextually, the Canarian camel (*Camelus dromedarius*), a local breed mostly based in the Canary Islands (Spain) and the unique along Europe, is threatened. Since its arrival at the archipelago around 1405, local dromedaries were subjected to anthropogenic selection for the performance of rural labours and work loading activities. Later, these animals were functionally relegated to leisure activities within tourism industry, niche that continues to be the major income source for this local breed and responsible for its survival till present (Pastrana et al., 2021). Linked to the reproductive isolation from other camel populations by officially health-based legislations, this local camel genetic heritage could differentiate from its source of origin (North Africa), as it was probed by Schulz et al. (2010). These authors performed the first genotyping study of this animal population that leaded its official declaration as a singular breed in 2012 (Iglesias Pastrana et al., 2020b).

Several particularities in the physical conformation of the Canarian breed (greater muscle development at fore and hind quarters, and chest depth) have been identified as the main attributes that permits its differentiation with ease from the camels inhabiting the North of Africa and were the fundamental basis for the proposal of a first breed standard within the official breeding programme (Fernández de Sierra & Fabelo Marrero, 2017; Schulz, 2008). Though, it does not exist any morphometric characterization that assess the distribution of phenotypic variability or subdivision between different populations of the breed, and thus the identification of the genetic groups that could act as reservoirs of genetic variability.

To this aim, the present research conducts an extended morphological characterization of Canarian dromedaries by means of canonical discriminant analysis to (1) explore the phenotypic diversity and structure of the breed, and (2) assess the phenotypic profile of this autochthonous genetic resource that supports its differentiation from other camel breeds. The definition of the breed standard conformation traits and its phenotypic variability, will aid at the adaptation of breeding strategies with sustainable conservation and genetic improvement purposes.

Material and methods

Definition of zoometric parameters

In order to establish a comprehensive database of zoometric measurements for camels throughout the entire month of September 2019, we conducted an extensive literature review on the subject. This review was conducted using the Google Scholar search engine (https://scholar.google.com/) and was accessed on September 1, 2019. This method has been employed in previous studies for efficient data extraction (Iglesias Pastrana et al., 2020a). From this literature search, we identified six relevant papers related to camel zoometrics, spanning the years 1994 to 2019 (Iglesias, Navas, Ciani, Arbulu, et al., 2020). To augment the list of measurements obtained from these documents, we incorporated other pertinent variables related to camel functional development as outlined by Alhajeri et al. (2021). After compiling this variable list, we identified a total of 30 zoometric measurements to be collected in the field and subsequently extracted from digital images. Detailed results and definitions of the zoometric parameters considered in this study can be found in Iglesias Pastrana et al. (2022).

Animal sample

The collection of zoometric data took place between September 2019 and August 2020 and involved 130 individuals of the 'Canarian Camel' breed, consisting of 58 females and 72 males. These camels were located in three representative breeding locations within Spain: Huelva (Doñana National Park, coordinates 36.972330, −6.427498), Almería (coordinates 36.902180, −2.429520), and Fuerteventura (coordinates 28.186777, −14.158361). To ensure the suitability of the animals for the study, thorough clinical examinations were conducted to assess their well-being and eligibility. Furthermore, only non-pregnant female camels were included in the study to avoid potential bias in zoometric measurements in the thoracoabdominal region due to pregnancy (Yakubu et al., 2011). Both age and live weight did not follow a normal distribution ($p < 0.05$). The live weight was calculated using the formula (Equation 1) proposed by Boujenane (2019):

$$\text{Live Weight} = 6.46 \times 10^{-7} \, (HW + ChG + HG)^{3.17}$$

where HW represents height at the withers, ChG denotes chest girth, and HG signifies hump girth.

Each of the 30 zoometric measurements collected from each animal was obtained from its left side, following the procedures outlined in Iglesias et al. (2020a), Iglesias Pastrana et al. (2022), and Alhajeri et al. (2021).

The age of female Canarian dromedary camels in the study spanned from 40 to 423 months, while male Canarian dromedary camels ranged in age from 18 to 385 months. Regarding live weight, female Canarian dromedary camels exhibited weights ranging from 327.03 to 687.13 Kg, while their male counterparts weighed between 342.72 and 777.56 Kg.

Sampling

To minimize potential bias attributed to hair length and texture, we selected the end of the molting season, which spans a six-to-eight-week period starting in late spring (Babu, 2015), as the sampling moment. A flowchart summarizing the research methodology can be found in Iglesias Pastrana et al. (2022).

On-field zoometrics

For on-field measurements, the animals were positioned in a static upright stance, with their heads naturally raised and bodies correctly aligned (parallel fore and hind legs perpendicular to the ground with toes in line). Measurements were taken on a flat and firm ground surface using a non-elastic measuring tape. All operators underwent training, with the first operator responsible for on-field measurement collection and subsequent digital image measurement extraction. The second operator assisted in collecting zoometric measurements, while a third operator recorded the results and held a one-meter measuring bar for reference during digital zoometric extraction, following the procedures outlined in Iglesias Pastrana et al. (2022).

Image-assisted zoometrics

Three photographs (front, lateral, and back views perpendicular to the camera) were captured for each animal just before the on-field zoometric evaluation. The second operator took these photographs for subsequent digital imaging analysis, while the third operator held a one-meter measuring bar along the same midline as the animal's body to serve as a reference for distance calibration in the computer measurement software used for digital imaging zoometrics. The obtained images were digitally processed using Kinovea 0.95 (Free Software Foundation, Inc., Boston, MA). Zoometric linear measurements were recorded in pixels by drawing a straight line between two points in the image, which was then automatically converted to centimeters following calibration using the measuring bar as a reference through the software's Calibrate option (Iglesias et al., 2020a). Puig-Diví et al. (2019) previously reported Kinovea software to be a valid and reliable tool for accurate measurements at distances of up to 5 meters from the object and at angles ranging from 90° to 45°.

Image collection was conducted on an open, firm, and flat ground surface, with lighting conditions carefully chosen to ensure the animal was not in a shaded area or exposed to light that might distort image capture. The animal's color was considered to prevent any distortion or misregistration of measurements due to background color. The camera was positioned at a standardized height of 1 meter on a camera stand, 4 meters away from the camel's center of balance. This distance and height allowed for capturing the entire animal being evaluated. Procedures outlined in Iglesias et al. (2020b) were followed to ensure the animal's correct position, including marking standard lines on the ground before taking photographs to confirm proper alignment. Zoometric measurements were manually extracted from the photographs by a trained operator using a digital camera (Sony DSC-RX100 SENSOR CMOS Exmor 1.0 of 20.1 MP, F1.8–4.9, Zoom 20–100, Optical Zoom 3.6×, 3″ LCD Screen Image stabilizer) in standard mode, using the Joint Photographic Experts Group (JPEG) compression format.

Observational sample

As suggested by Iglesias Pastrana et al. (2022), digital imaging zoometry and zoometry on live animals can be reliably translated and used interchangeably or simultaneously. For this reason, we decided to use both on-live animal zoometric measurements and digital imaging-based zoometric measurements as dependent variables in the statistical analysis developed further in the present study.

Statistical analysis

Following the methodology outlined in González Ariza et al. (2022), we initially used a discriminant canonical analysis to create a tool for evaluating the most optimal linear combinations of zoometric traits (either on-live animals or digital imaging based), phaneroptics (eye colour, coat colour, and coat particularities), sex, and sexual status (neutering) within and between the three locations in which Canarian dromedary camels can be found in Spain (Doñana National Park, Almería, and Fuerteventura (served as independent variables in our analysis.

Our dependent variables consisted of zoometric traits (either on-live animals or digital imaging based), as previously described. Additionally, we considered factors such as phaneroptics (eye colour, coat colour, and coat particularities), sex and sex status in the analysis due to these variables being reported to condition dromedary camel zoometry in literature (Alhajeri et al., 2021; Babu, 2015; Pigière & Henrotay, 2012; Tandoh & Gwaza, 2017). These variables, interlinked with genetics and environmental factors, contribute significantly to the variation in zoometric measurements among dromedary camels. Researchers have unveiled intriguing associations between sex, castration status, and specific zoometric parameters, highlighting the profound influence of hormonal factors on growth and development. Moreover, the role of coat and eye colour in camel adaptation to diverse climates and ecosystems is a compelling avenue of study. As a result, these characteristics may serve as visual indicators of potential adaptations and genetic diversity. Investigating their impact on zoometry provides valuable insights into the complex interplay of genetics, environment, and physiological responses that shape the physical attributes of dromedary camels. Understanding these conditioning effects not only contributes to our knowledge of camel biology but also has practical implications for camel management, selective breeding, and conservation strategies (Alhaddad & Alhajeri, 2019). For these reasons we decided to considered them as dependent variables in our discriminant analysis.

For the classification, prediction, interpretation, and manipulation of observations related to the aforementioned dependent variables, we employed the Chi-squared automatic interaction detection (CHAID) decision tree method. This approach allowed us to discretely analyze the independent variables and their relationship to the three locations where Canarian dromedary camels are bred.

To assess the reliability of the CHAID decision tree model, we conducted cross-validation to evaluate its predictive performance when applied to new data samples, comparing it to the training sample. This assessment helped us determine how effectively the model generalized to unseen data. We used ten-fold cross-validation to validate the CHAID decision tree and assess whether the selected predictors effectively explained differences across three locations where Canarian dromedary camels inhabit.

Results

A summary of descriptive statistics for zoometric traits in 'Canarian Camel' breed can be consulted in Table 1.

After conducting 3 rounds of multicollinearity analyses, the variables included in the discriminant canonical analysis are those outlined in Table 2.

Pillai's trace criterion reported a significant difference across locations (Pillai's trace criterion: 1.5648, F (Observed value): 19.6869, F (Critical value): 1.3075, df1: 800, df2: 438, p-value< 0,0001), confirming the validity of the discriminant canonical analysis.

Out of the two functions identified through discriminant analysis, two were found to be significant for their discriminant ability (Table 3). Among these, the F1 function exhibited the highest discriminatory power, with an eigenvalue of 0.5374, explaining 83.84% of the variance.

The various variables examined in this study were ranked based on their discriminative capacity. An evaluation of the equality of group means of the dependent variables involved in the discriminant canonical analysis is presented in Table 4.

Higher values of F and lower values of Wilks' Lambda indicate greater discriminating power. The analysis revealed that Hump heigth, Tail length, Hump length, Neck length: dorsal line, Body length, Head length, Thigh perimeter, Hump girth, Rump length, Neck girth: cranial third, Ear length, Neutering status, Coat colour, Heart girth, Rump width, Head width, Neck girth: middle third, Chest width, Sole length, Length of toe dorsal line, Heel height, Hock perimeter, Sex, Neck length: ventral line, Hump-to-tail distance and Hump width made highly significant contributions (P < 0.01) to the discriminant functions when locations were the clustering criteria.

Standardized discriminant coefficients were used to assess the relative weight of each dependent variable across the two significantly established discriminant functions (Supplementary Table S1).

A Press' Q value of 467.40 (n = 260; n' = 251; K = 3) was computed for zoometric traits (either on-live animals or digital imaging based), phaneroptics (eye or coat colour) and sex and sexual status, indicating that predictions can be considered better than chance at a 95% confidence level (Chan, 2005).

Table 1. Descriptive statistics for zoometric traits in Canarian camel breed.

Zoometric trait	***Minimum (cm)***	***Maximum (cm)***	**Mean (cm)**	**Standard deviation (cm)**	**Coefficient of Variation (%)**
Head length	36.5	67	53.87	5.78	10.72
Head width	24	36.1	26.3	3.27	12.45
Ear length	4.5	14.3	10.88	1.55	14.29
Ear width	3.7	10.5	7.74	1.21	15.62
Neck length: dorsal line	158	178	122.80	16.50	13.43
Neck length: ventral line	54.6	128.7	105.83	9.89	9.34
Neck girth: cranial third	49.58	103.26	75.67	9.09	12
Neck girth: middle third	46.92	116.43	74.12	10.39	14.02
Neck girth: caudal third	86.44	152.27	119.51	13.32	11.15
Chest width	35.4	98.5	51.31	6.76	13.18
Heart girth	69.84	165.43	137.1	12.20	8.90
Height at withers	158	203.2	184.40	101.06	54.8
Body length	95	193	160.3	15.72	9.80
Hump-to-tail distance	30.9	81.5	49.91	7.37	14.77
Hump length	18.6	113.5	81.31	14.28	17.56
Hump width	12.9	173	80.09	14.02	17.5
Hump heigth	26.3	92.7	62.17	13.2	21.23
Hump girth	76.42	209.6	141.72	26.18	18.47
Rump length	30.2	57.4	43.07	4.90	11.37
Rump width	26.5	53.1	38.20	5.53	14.48
Tail length	27.6	65.5	52.85	7.65	14.47
Width at the base of the tail	8.1	21.3	12.57	2.1	16.71
Thigh perimeter	47.14	103.35	75.42	9.68	12.83
Hock perimeter	28.01	55.3	41.46	4.92	11.85
Fore cannon bone perimeter	8.12	23.2	17.43	3.50	20.01
Rear cannon bone perimeter	10.37	24.85	19.63	3.45	17.56
Sole length	13	24.6	18.92	2.04	10.78
Length of toe dorsal line	6	44.50	14.3	3.27	22.9
Heel height	4.56	53	7.84	4.14	52.81
Foot perimeter	25.4	54.9	41	5.1	12.45

Table 2. Summary of the value of tolerance and VIF after multicollinearity analysis of zoometric traits (either on-live animals or digital imaging based), phaneroptics (eye colour and coat colour) sex, and sexual status in Canarian camel breed.

Statistic	Tolerance ($1-R^2$)	VIF (1/Tolerance)
Hump width	0.8809	1.1352
Height at withers	0.8658	1.1550
Heel height	0.7222	1.3847
Length of toe dorsal line	0.6812	1.4679
Coat colour – Ashed	0.6577	1.5204
Coat colour – Black	0.6379	1.5676
Coat colour - White	0.5902	1.6944
Head width	0.5846	1.7105
Hump-to-tail distance	0.5690	1.7576
Eye colour – Brownish with blue spots	0.5545	1.8033
Eye colour - Brown	0.5342	1.8718
Chest width	0.5109	1.9572
Neck girth: caudal third	0.4778	2.0931
Neck length: dorsal line	0.4715	2.1207
Width at the base of the tail	0.4505	2.2200
Neck girth: cranial third	0.4501	2.2219
Neck girth: middle third	0.4383	2.2816
Sole length	0.4358	2.2945
Neck length: ventral line	0.4333	2.3081
Hump length	0.4313	2.3185
Rump width	0.4270	2.3421
Tail length	0.4115	2.4303
Hock perimeter	0.4064	2.4604
Hump height	0.4064	2.4608
Coat colour - Blonde	0.3925	2.5475
Coat colour - Bay	0.3617	2.7644
Ear width	0.3516	2.8445
Heart girth	0.3400	2.9414
Coat colour - Cinnamon	0.3111	3.2145
Ear length	0.3033	3.2968
Hump girth	0.3012	3.3206
Rear cannon bone perimeter	0.2998	3.3360
Neutered - No	0.2921	3.4240
Rump length	0.2917	3.4285
Coat colour – Chestnut	0.2896	3.4525
Thigh perimeter	0.2650	3.7734
Sex – Male	0.2649	3.7752
Foot perimeter	0.2530	3.9518
Body length	0.2336	4.2804
Head length	0.2258	4.4287

Interpretation thumb rule: VIF ≥ 5 (highly correlated); 1 < VIF < 5 (moderately correlated); VIF = 1 (not correlated).

Table 3. Canonical discriminant analysis efficiency parameters to determine the significance of each canonical discriminant function.

Test functions	Canonical Correlation	Eigenvalue	Variance discrimination(%)	Bartlett's statistic	P-value
1 through 2	0.9377	7.2867	76.9755	776.9583	0.001
2	0.8279	2.1796	23.0245	274.7274	0.001

Table 4. Results for the tests of equality of group means to test for difference in the means across sample groups once redundant variables have been removed.

Variable	Wilk's Lambda	F	P-value	Rank
Hump heigth	0.5988	86.1083	<0.0001	1
Tail length	0.6599	66.2208	<0.0001	2
Hump length	0.7238	49.0383	<0.0001	3
Neck length: dorsal line	0.7343	46.4963	<0.0001	4
Body length	0.7852	35.1437	<0.0001	5
Head length	0.8024	31.6458	<0.0001	6
Thigh perimeter	0.8042	31.2925	<0.0001	7
Hump girth	0.8135	29.4504	<0.0001	8
Rump length	0.8154	29.0960	<0.0001	9
Neck girth: cranial third	0.8282	26.6649	<0.0001	10
Ear length	0.8494	22.7841	<0.0001	11
Neutered – Yes	0.8618	20.6069	<0.0001	12
Coat colour – Bay	0.8639	20.2422	<0.0001	13
Heart girth	0.8671	19.7001	<0.0001	14
Rump width	0.8683	19.4942	<0.0001	15
Coat colour – Ashed	0.8705	19.1103	<0.0001	16
Head width	0.8866	16.4413	<0.0001	17
Neck girth: middle third	0.8966	14.8817	<0.0001	18
Coat colour – Chestnut	0.9059	13.3537	<0.0001	19
Chest width	0.9075	13.0949	<0.0001	20
Sole length	0.9397	8.2511	0.0003	21
Length of toe dorsal line	0.9398	8.2364	0.0003	22
Heel height	0.9509	6.6388	0.0015	23
Hock perimeter	0.9523	6.4418	0.0019	24
Sex – Female	0.9542	6.1680	0.0024	25
Coat colour – Blonde	0.9563	5.8769	0.0032	26
Coat colour – Black	0.9569	5.7816	0.0035	27
Neck length: ventral line	0.9577	5.6693	0.0039	28
Hump-to-tail distance	0.9681	4.2277	0.0156	29
Hump width	0.9756	3.2129	0.0419	30
Coat colour – Cinnamon	0.9784	2.8337	0.0606	
Eye colour – Brownish with blue spots	0.9856	1.8772	0.1551	
Eye colour – Brown	0.9878	1.5811	0.2077	
Coat colour – Roan	0.9880	1.5672	0.2106	
Foot perimeter	0.9897	1.3434	0.2628	

Table 4. *Cont.*

Variable	Wilk's Lambda	F	P-value	Rank
Neck girth: caudal third	0.9906	1.2132	0.2989	
Rear cannon bone perimeter	0.9926	0.9534	0.3868	
Width at the base of the tail	0.9960	0.5145	0.5984	
Height at withers	0.9990	0.1289	0.8792	
Ear width	0.9997	0.0409	0.9600	

df1=80;df2=438

Calculation of centroids for different locations was conducted. The relative positions of each centroid were determined by substituting the mean values for the observations represented in each of the two detected discriminant functions (F1 and F2). Territorial map depicting the Canarian dromedary camels in the canonical discriminant analysis sorted across locations and the results for the functions at the centroids are presented in Figure 1. This figure depicts the separation among the animals comprising the three locations considered in this study.

To perform variable selection, we employed regularized forward stepwise multinomial logistic regression algorithms. In this process, we regulated the priors based on group sizes calculated using the prior probability function of commercial software (SPSS Version 26.0 for Windows, SPSS, Inc., Chicago, IL). This approach ensured that groups with varying sample sizes did not unduly impact the classification quality, thereby enhancing the reliability of our analysis (Marín Navas et al., 2021).

The utilization of the same sample size across groups, as employed in this study, is known to provide robust results. In this context, previous research has indicated that a minimum sample size of at least 20 observations per every 4 or 5 predictors is advisable. Additionally, it is recommended that the maximum number of independent variables should not exceed n-2, where n represents the sample size. This approach helps mitigate potential distortions in the analysis (Marín Navas et al., 2021; Poulsen & French, 2008),.

Consequently, the present study used a 6 or 7 times higher ratio between observations and independent variables than those described above, which renders discriminant approaches efficient.

CHAID decision tree is presented in Supplementary Figure 1.

Discussion

Domestic camel population (dromedaries or one-humped camels, and Bactrian or double-humped camels) has been revealed to display a relatively low genomic diversity (structural variation) (Burger, Ciani, & Faye, 2019). However, notorious phenotypic variability induced by adaptive plasticity to heterogeneous environments, anthropogenic

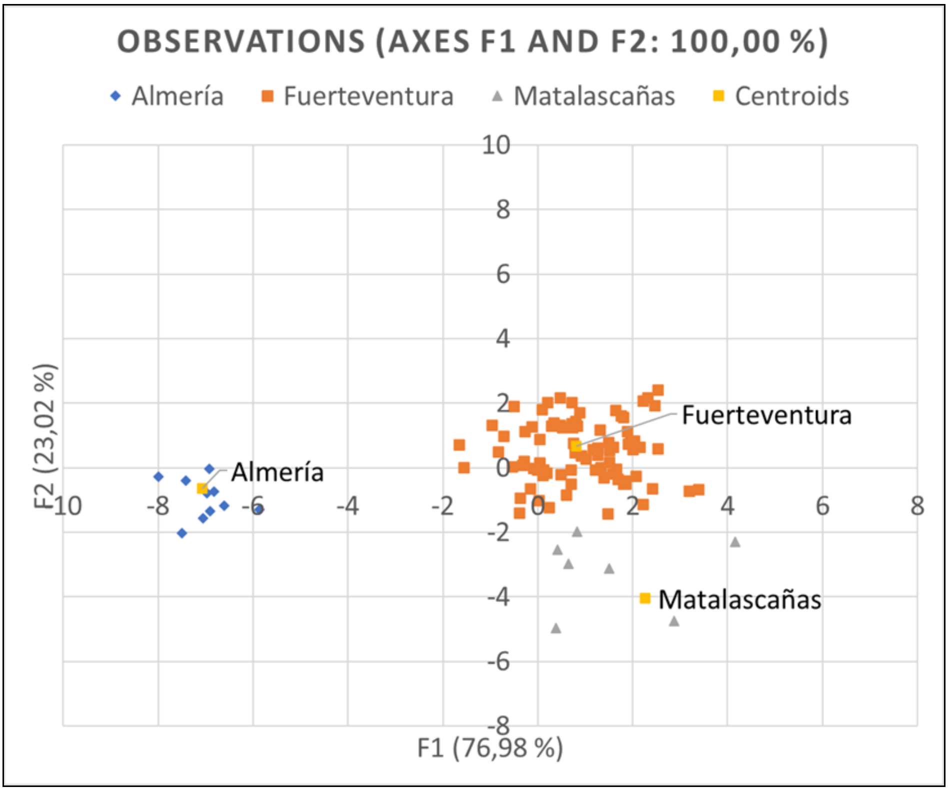


Figure 1. Territorial map depicting the Canarian dromedary camels in the canonical discriminant analysis sorted across breeding locations.

selection pressure and geographical mixing does exist in these livestock species (Faye, 2022). As stated by Goswami et al. (2022), diversity in morphological characteristics and diversity in number of species are not closely related in mammals. In this scenario, the accurate estimation of the levels of phenotypic diversity within and between camel populations, will help to adapt control and selection strategies for the prevention and minimisation of detrimental loss of such variability (Singh & Verma, 2018).

Breed-specific and comparative phenotypic variability for morphological traits: influencing factors

In the present research, focused on the morphological characterization of a unique endangered dromedary camel breed ('Canarian Camel'), the coefficient of variation (CV) in the data ranged between 8.90 and 54.80%. This wide range of variation is indicative of substantial population heterogeneity for body morphology traits and predicts the success on the implementation of genetic improvement schemes for such characteristics. High values of phenotypic variability offer further scope to improve genetic resources upon through selection with rapid response (Azimi, Marker, & Bhattacharjee, 2017). Except for Bekele et al. (2018), Chniter et al. (2013) and Bello et al. (2022), who reported CV between 3-13 %, 5-11% and 7-30% for morphometric traits in camels from Ethiopia, Tunisia and Nigeria respectively, any of the other existing morphological characterizations of camels did not specifically calculate this normalized measure of data variability. Then, scientists, stakeholders and animal breeders are ignoring a statistical figure that would allow them to make an accurate comparison between and within different camel populations for body morphology phenotypes, thus limiting the opportunities for empirical conservation and sustainable improvement global camel biodiversity.

Focusing on the specific background of the present work, several factors both methodological issues and animal-dependent features, can be potentially explaining the obtention of large general CV values in our data set. First, sampling an animal population in which a wide range of ages is represented, would intrinsically influence the consistency of data (Melesse et al., 2022). Moreover, sex and sex status showed a significant discriminating power. Specifically, females and neutered animals were those animal groups within the differences for body morphometrics were more evident. The Canarian camel breed is indeed reported to exhibit modest sexual dimorphism for the general size of the animals and some local body regions (Fernández de Sierra & Fabelo Marrero, 2017), condition that could be affected to a greater extent in a contemporaneous scene given the progressive relegation of females from leisure tourism to milk production (Iglesias Pastrana et al., 2021). Additionally, the time of castration of camels is demonstrated to have a great impact on their body development, being the animals neutered after reaching sexual maturity those that will develop a wider and robust physico-anatomical structure and working endurance (Faye, 1997; Pigière & Henrotay, 2012; Ucko & Dimbleby, 2007). Lastly, given the huge variety recognized for phaneroptic traits such as coat colour in the studied camel breed, it is expected for this qualitative attribute to have a great effect on the dimension of body measurement traits on the basis of the correlations between zoometrics and coat type (Sánchez-Guerrero et al., 2019). In particular, the coat phenotypes 'bay', 'blonde', 'black,' 'ashed' y 'chestnut', were the coat colour categories that presented larger differences for body morphology traits between individuals. Other qualitative attributes such as eye colour, did not explain in a significant manner the differences for morphological characteristics between animals in the studied population, although this categorical character is evidenced to impact other criterion of functional interest complementary to zoometric traits in working animals' breeding such as leadership behaviour (Iglesias Pastrana et al., 2021).

If the measured variables are aggregated into qualitative categories, the mean CV are 35.78% for heights, 14.86% for widths, 13.92% for girths/perimeters, and 13.70% for lengths. In the breed-specific context of the current investigation, these findings are almost in accordance with the historical and genetic history of the Canarian camel. Compared with its ancestors, this dromedary is a little shorter but broader than the Western Sahara camel (Schulz, 2008). The physical effort required for their working performance in rural labours since their arrival in the Canary Islands, that required them to carry out more traction than large displacements, led to the Canarian camels having developed muscles, firm limbs and well planted on the ground. On the contrary, the camels from the Western Sahara are characterized by a light body and long limbs, more suitable for long journeys and development of higher speeds. Additionally, the importation of camels from the North of Africa to the archipelago until the official prohibition of this practice for health reasons at the end of last century and before the institutional declaration of the local population as a singular camel breed nearly two decades after (Fernández de Sierra & Fabelo Marrero, 2017), irremediably has a footprint on the contemporary genetic structure of the Canarian camel breed. Hence, the increased variation in heights and widths in our study sample could be explained by the large variability that it might display depending on the degree of kinship of each of the individuals measured with the respective founder line, and inflated by the differential intraherd functional selection across generations and production environments.

When compared to previous related morphological characterizations, both similar and contrasting results are identified. Fatih et al. (2021) have recently reported that the sex and breed fixed factor explain the differences between eight Pakistan working camel breeds mainly for morphological widths and lengths. Further, Alhajeri et al. (2019) founded a main effect of the breed for torso length and shape when exploring the morphometric variation of six common Arabian Peninsula camel breeds. Other authors encountered that wither height, thoracic and abdominal circumferences, length of the head and length of the neck were the variables that explained in a greater proportion the differences between and within two different Algerian camel's populations (Belkhir, Chehma, & Faye, 2013). Similar to this, Meghelli et al. (2020) found a significant effect of sex and breed mostly for lengths and circular perimeters in other two different camel breeds raised in Algeria. On the contrary, Bello et al. (2022) recently encountered significant morphometric variation attributed to the oroclimatic conditions at rearing location in four different strains of camels from North-Western Nigeria, being the heights and widths the measurements with the highest CV. In the case of dromedaries from southern Tunisia, Chniter et al. (2013) observed increased CV for lengths and widths, followed by perimeters and heights. This last tendence is identical to that observed for multipurpose camels reared in Ethiopia (Bekele et al., 2018).

The main conclusion derived from the comparison between our results and those obtained in these last cited studies, is that the set of morphological characteristics that allow explaining with greater precision the differences between breeds or populations of camels, will be strongly correlated with their main functionality. For example, in the case of working animals (i.e., Canarian and Pakistan camels), the height and positioning of the limbs as well as the length and width of the head, neck and anterior and posterior joints, are decisive for excellent functional performance and account for almost the total variation among individuals (Kefena et al., 2011; Vicente et al., 2014). On the other hand, animals destined for meat, milk and other by-products, as is the case of the camel populations evaluated in the Arabian Peninsula, Algeria, Tunisia and Ethiopia, are mainly selected for local and general lengths and depth indexes (Figueiredo Filho et al., 2016; Pourlis, 2020). So, the differential inclusion of morphological traits within selection schemes, modulated by the genetic structure and history of each particular breed or population, and overall expressed as different productive yields, might explain the relatively high level of heterogeneity for the respective discriminating traits.

Phenotypic diversification between and within Canarian camel subpopulations

Considering the fact that the intensity of artificial selection applied within this breed is low due to its state of relative functional emergency and the breeding strategies have hardly been based on pedigree management because of the low rate of completeness of genealogical records, it could be expected to observe little phenotypic variability rates. However, the reality is the exact opposite. Therefore, it could be assumed that the effect of migration, genetic drift and natural selection, together with the evolutionary changes caused by the exploitation of this breed in different geographical environments with slight peculiarities (Iglesias Pastrana et al., 2020b), may have resulted in its genetic structuring among separated subpopulations, as shown by the results of the cluster analysis.

The canonical analysis identified two discriminant functions that explained 76,98% and 23,02% of total variance. Furthermore, the value of Wilk's Lambda in the study sample was 0,0380 (3.85%), which in turn indicates that nearly the total variability encountered in the cluster analysis (96.15%) can be attributed to differences between the subpopulations studied. In fact, the genetic homogeneity within each subpopulation is further supported by the relatively high value of the correct classification of individual camels into their respective source population (96.54%).

The very little proportion of animals that were not correctly classified to their source population within the discriminant analysis, might be then a signature of genetic introgression or mix of individuals between subpopulations. This finding can be explained in reference to the gene flow arising from the exportation of some animals mostly from the eastern Canary Islands to mainland Spain in a scenario of reintroduction (Iglesias Pastrana et al., 2020b). In this regard, the ongoing exchange of animals between productive environments should be exhaustively controlled so that the magnitude of introgression does not further increase and the phenotypic variation rates for key morphological and ecological traits within and between subpopulations continues to be high enough to guarantee the successful local adaptation to particular climatic and/or orographic conditions (Melesse et al., 2022). Marker-assisted selection, when available, constitutes the best approach for this precision breeding (Eggen, 2012).

In the present study, significant differences were detected between subpopulations for the mean values of all the morphological traits considered, except for 'ear width', 'height at withers', 'width at the base of the tail', 'neck girth: caudal third', 'rear cannon bone perimeter' and 'foot perimeter'. Specifically, the thigh muscle, one of the main differentiating features between the Canarian camel and its ancestors, is also one of the main characteristics that allow discriminate between the subpopulations of the breed considered in this research. The animals from Almeria, followed in descending order by the animals of Fuerteventura and Matalascañas, are those Canarian dromedaries that have the greater muscle development in this body area. This finding could be explained on the basis of the larger efforts that the animals reared in this location have to deal with higher inclined, heterogeneous and abrupt grounds during the leisure activities they perform (Cervelló-Royo & Peiró-Signes, 2015; Martínez Raya & González-Sánchez, 2020), linked to the fact that most of them are imported from the island of Lanzarote, where the animals are used to working on slightly abrupt grounds (Carracedo, 2014). In addition, the growth of the muscle-skeletal system is susceptible to be affected by the protocol used for training camels for the performance of leisure works in each productive environment (i.e, time duration of training sessions, number of sessions per week and maximum permissible load weights, among other factors) (Matsuura et al., 2013).

For the rest of the evaluated morphological characters with discriminating potential, different sets of variables broadly characterize and differentiate each subpopulation. The dromedaries from Fuerteventura have the widest and longest head, ears, rump and tail. By contrast, the camels reared in both subpopulations of the mainland Spain, have particular characteristics for hump dimensions. The dromedaries reared in Matalascañas have the tallest but globally smaller hump, being this last attribute indirectly inferred from their highest values for the variable 'hump-to-tail distance'. In Almeria, the dromedary camels have the longest hump and the widest anterior torso, being this attribute in close relationship with the abovementioned greater muscle development in the posterior part of the body in this subpopulation for environment-mediated functional reasons.

Globally, it is common to find animals whose height exceeds body length as well as some quantitative differences between sexes for the proportion of certain local body regions in this camel breed. With a slightly lower height at the withers, males have a larger head, a forehead often divided into two well-defined fat pads, a thicker anterior torso, larger overall hump size, and thicker and stronger extremities. These differences between sexes for morphological traits would be explained by both hormone-mediated effects and the sex-biased selection within this breed since males are supposed to possess more physical strength for greater working performance (Schulz, 2008).

The contemporaneous efforts to promote the milk production potential of Canarian female camels (Pastrana et al., 2021), can be expected to further increase this phenotypic differentiation in the short term. In this paradigm, special attention should be paid when designing selective breeding programs by considering the magnitude of the correlations between morphological characters and milk yield, so that the selection criteria and pressure to be implemented cannot have undesired effects on the current genetic structure and viability of the breed.

Exploration of future potential niches basing on interbreed similarity

The long-term sustainable conservation of the Canarian camel breed not only requires the immediate enforcement of selective breeding programmes for its major functional dimension (leisure tourism) but also the constitution of potential alternative niches that could aid at the diversification of the products and/or services obtained from this livestock population. With this aim, a general comparison of morphological traits between Canarian camels and other camel populations already characterized for body measurements, may lead to a preliminary evaluation of niche opportunities.

Concerning the length of the neck, body and hump, Canarian camels are quite similar to pack, beauty and riding camels from Sudan (Ishag, Eisa, & Ahmed, 2011; Ishag et al., 2010), Pakistan (Fatih et al., 2021) and India (Mehta, Bhardwaj, & Sahani, 2007). Such similarities would be explained by the influence of the length of these local body regions on the maintenance of postural balance and propulsion during riding and loading activities (Harris, 2017).

In regard of the general depth of the anterior third (neck circumference and chest circumference), they are similar to food production camels from Africa (Belkhir et al., 2013; Chniter et al., 2013; Meghelli et al., 2020), India (Mehta et al., 2007), Saudi Arabia (Abdallah & Faye, 2012; Al-Hazmi, Ghandour, & ElGohar, 1994), and Afghanistan and Pakistan (Raziq, Tareen, & De Verdier, 2011). It is widely known that these particular body dimensions are significantly correlated with productive life and efficiency in livestock species (Marković et al., 2019; Sawa et al., 2013).

Canarian camel then shares similarities for body morphological characteristics with other camel breeds and populations with different functional destinies and reared in distant geographic regions. This evidence suggests the possibilities to exploit new niches in a scenario of opportunity. For example, the potential participation of this native camel breed in beauty contests, animal-assisted interventions for the treatment of functional motor disabilities in humans, and food production.

Conclusions

Despite the low intensity of artificial selection and limited pedigree management in Canarian dromedaries, notable phenotypic diversification for zoometric traits was observed between and within subpopulations of this camel breed. However, slight genetic introgression between subpopulations, likely influenced by gene flow resulting from the exportation of animals from Canary Islands to mainland Spain, did also exist. Sex and physiological status significantly impacted zoometric traits, with females and neutered animals displaying the most pronounced within-group differences in body morphometrics. Sexual dimorphism for zoometrics in this camel breed can be attributed to both hormone-mediated effects and sex-biased selection favoring greater physical strength in males. Male dromedaries exhibits larger head size, divided forehead fat pads, thicker anterior torso, larger hump size, thicker and stronger extremities, and slightly lower height at the withers compared to their counterparts. Furthermore, gene epistasis can be inferred on behalf of the significant variation in body morphology traits between different coat colour phenotypes. The ongoing exchange of animals between productive environments should be exhaustively controlled so that the magnitude of introgression does not further increase and the phenotypic variation rates for key morphological and ecological traits within and between subpopulations continues to be high enough to guarantee the successful local adaptation to particular climatic and/or orographic conditions. Additionally, a meta-analysis that calculates the coefficient of variation (CV) for body morphological traits evaluated in different camel populations, will produce valuable information for researchers and breeders on the magnitude of heterogeneity for such characteristics within and between camel populations, and thus the scope for conservation and genetic improvement of global camel biodiversity.

Author contributions: Conceptualization, C.I.P., F.J.N.G. and J.V.D.B.; Data curation, C.I.P., F.J.N.G. and S.N.B.; Formal analysis, C.I.P., F.J.N.G., A.G.A. and J.V.D.B.; Funding acquisition, E.C. and J.V.D.B.; Investigation, C.I.P., F.J.N.G., A.G.A. and S.N.B.; Methodology, C.I.P. and F.J.N.G.; Project administration, E.C. and J.V.D.B.; Resources, E.C. and J.V.D.B.; C.I.P., F.J.N.G., A.G.A. and S.N.B.; Supervision, F.J.N.G., E.C. and J.V.D.B.; Validation, C.I.P., F.J.N.G., A.G.A. and S.N.B.; Visualization, E.C.; Writing—original draft, C.I.P. and F.J.N.G.; Writing—review & editing, F.J.N.G., E.C. and J.V.D.B. All authors have read and agreed to the published version of the manuscript.

Funding: The present research was carried out in the financing framework of the international project CA.RA.VA.N—'Toward a Camel Transnational Value Chain' (Reference APCIN-2016-00011-00-00) and during the covering period of a predoctoral contract (FPU Fellowship) funded by the

Spanish Ministry of Science and Innovation and was developed under the context a Ramón y Cajal Post-Doctoral fellowship financially supported by MCIN/AEI/10.13039/501100011033 and European Union "NextGenerationEU"/PRTR" (Recovery, Transformation and Resilience Plan—Funded by the European Union—NextGenerationEU).

Data availability statement: The data presented in this study are available on request from the first author.

Acknowledgments: The authors would also like to thank 'Aires Africanos' Eco-tourism Company, Oasis Park Fuerteventura, and 'Camelus' Camellos de Almería, for their direct technical help and assistance.

Conflicts of interest: The authors declare no conflict of interest.

Ethics declaration statement: All farms included in the study followed specific codes of good practices and therefore, the animals received humane care in compliance with the national guide for the care and use of laboratory and farm animals in research. Written consent from the owners was obtained for their participation. The study was conducted in accordance with the Declaration of Helsinki. The Spanish Ministry of Economy and Competitivity through the Royal Decree Law 53/2013 and its credited entity, the Ethics Committee of Animal Experimentation from the University of Córdoba, permitted the application of the protocols present in this study as cited in the 5th section of its 2nd article, as the animals assessed were used for credited zootechnical use. This national Decree follows the European Union Directive 2010/63/UE, from the 22 September of 2010.

References

Abdallah, H. R., & Faye, B. (2012). Phenotypic classification of Saudi Arabian camel (*Camelus dromedarius*) by their body measurements. *Emirates Journal of Food and Agriculture*.

Al-Hazmi, M., Ghandour, A., & ElGohar, M. (1994). A study of the biometry of some breeds of Arabian camel (*Camelus dromedarius*) in Saudi Arabia. *Science*, 6(1).

Alhaddad, H., & Alhajeri, B. H. (2019). Cdrom archive: a gateway to study camel phenotypes. *Frontiers in genetics*, 10, 48.

Alhajeri, B. H., Alaqeely, R., & Alhaddad, H. (2019). Classifying camel breeds using geometric morphometrics: A case study in Kuwait. *Livestock Science*, 230, 103824.

Alhajeri, B. H., Alhaddad, H., Alaqeely, R., Alaskar, H., Dashti, Z., & Maraqa, T. (2021). Camel breed morphometrics: Current methods and possibilities. *Transactions of the Royal Society of South Australia*, 145(1), 90-111.

Assan, N. (2015). Prospects for utilization of the relationship between zoometrical measurements and performance traits for poultry and livestock genetic improvement in developing countries. *Scientific Journal of Animal Science*, 4(11), 124-132.

Azimi, A. M., Marker, S., & Bhattacharjee, I. (2017). Genotypic and phenotypic variability and correlation analysis for yield and its components in late sown wheat (Triticum aestivum L.). *Journal of pharmacognosy and phytochemistry*, 6(4), 167-173.

Babelhadj, B., Benaissa, A., Adamou, A., Tekkouk-Zemmouchi, F., Raache, S., Babelhadj, T., & Guintard, C. (2017). Morphozoometric approach of female camels (*Camelus dromedarius* L.) of the Algerian Sahraoui and Targui populations. *Revue d'Élevage et de Médecine Vétérinaire des Pays Tropicaux*, 70(2), 65-69.

Babu, K. (2015). Natural textile fibres: Animal and silk fibres. In *Textiles and fashion* (pp. 57-78): Elsevier.

Bekele, B., Kebede, K., Tilahun, S., & Serda, B. (2018). Phenotypic Characterization of Camels and their Production System in Yabello and Melka Soda Districts. *Ethiopian Journal of Agricultural Sciences*, 28(1), 33-49.

Belkhir, A. O., Chehma, A., & Faye, B. (2013). Phenotypic variability of two principal Algerian camel's populations (Targui and Sahraoui). *Emirates Journal of Food and Agriculture*, 231-237.

Bello, M. O., Ojo, O. A., Kabir, M., & Akinsola, O. M. (2022). Evaluation of the morphometric traits of camels (*Camelus dromedarius*) in North-Western Nigeria. *Nigerian Journal of Genetics*, 36(1), 62-70.

Boujenane, I. (2019). Comparison of body weight estimation equations for camels (*Camelus dromedarius*). *Tropical animal health and production*, 51, 1003-1007.

Brito, N. V., Lopes, J. C., Ribeiro, V., Dantas, R., & Leite, J. V. (2021). Biometric Characterization of the Portuguese Autochthonous Hens Breeds. *Animals*, 11(2), 498.

Burger, P. A., Ciani, E., & Faye, B. (2019). Old World camels in a modern world–a balancing act between conservation and genetic improvement. *Animal Genetics*, 50(6), 598-612.

Carracedo, J. C. (2014). The 1730–1736 eruption of Lanzarote, Canary Islands. In *Landscapes and landforms of Spain* (pp. 273-288): Springer.

Ceccobelli, S., Di Lorenzo, P., Panella, F., Lasagna, E., & Sarti, F. M. (2016). Morphological and genetic characterisation of Pagliarola breed and its genetic relationships with other three indigenous Italian sheep breeds. *Italian Journal of Animal Science*, 15(1), 47-54.

Cervelló-Royo, R., & Peiró-Signes, Á. (2015). Environmental impact of coastline tourism development in Spain. *Sustainability, social responsibility, and innovations in the hospitality industry*, 151-170.

Chan, Y. (2005). Biostatistics 303. Discriminant analysis. *Singapore medical journal*, 46(2), 54.

Chniter, M., Hammadi, M., Khorchani, T., Krit, R., Benwahada, A., & Hamouda, M. B. (2013). Classification of Maghrebi camels (*Camelus dromedarius*) according to theirtribal affiliation and body traits in southern Tunisia. *Emirates Journal of Food and Agriculture*, 625-634.

De la Barra, R., Martínez, M., & Carvajal, A. (2016). Morphostructural relationships and productive functionality of sheep breeds used for terminal crossbreeding in Chile. *International Journal of Morphology*, 34, 958-962.

Eggen, A. (2012). The development and application of genomic selection as a new breeding paradigm. *Animal Frontiers*, 2(1), 10-15.

Eusebi, P. G., Martinez, A., & Cortes, O. (2020). Genomic tools for effective conservation of livestock breed diversity. *Diversity*, 12(1), 8.

Fatih, A., Celik, S., Eyduran, E., Tirink, C., Tariq, M. M., Sheikh, I. S., Faraz, A., & Waheed, A. (2021). Use of MARS algorithm for predicting mature weight of different camel (*Camelus dromedarius*) breeds reared in Pakistan and morphological characterization via cluster analysis. *Tropical animal health and production*, 53(1), 1-14.

Faye, B. (1997). *Guide de l'élevage du dromadaire*: Sanofi.

Faye, B. (2022). Is the camel conquering the world? *Animal Frontiers: the Review Magazine of Animal Agriculture*, 12(4), 8-16.

Fernández de Sierra, G., & Fabelo Marrero, F. J. (2017). *El camello canario*: Asociación de Criadores del Camello Canario.

Figueiredo Filho, L. A. S., Do Ó, A. O., Sarmento, J. L. R., Santos, N. P. D. S., & Torres, T. S. (2016). Genetic parameters for carcass traits and body size in sheep for meat production. *Tropical animal health and production*, 48(1), 215-218.

González Ariza, A., Arando Arbulu, A., Navas González, F. J., León Jurado, J. M., Delgado Bermejo, J. V., & Camacho Vallejo, M. E. (2022). Data mining-based discriminant analysis as a tool for the study of egg quality in native hen breeds. *Scientific Reports*, 12(1), 15873.

Goswami, A., Noirault, E., Coombs, E. J., Clavel, J., Fabre, A.-C., Halliday, T. J., Churchill, M., Curtis, A., Watanabe, A., Simmons, N. B., Beatty, B.L., Geisler, J.H., Fox, D.L., & Felice, R.N. (2022). Attenuated evolution of mammals through the Cenozoic. *Science*, 378(6618), 377-383.

Harris, S. E. (2017). *Horse Gaits, Balance, and Movement: The natural mechanics of movement common to all breeds*: Souvenir Press.

Hoffmann, I. (2011). Livestock biodiversity and sustainability. *Livestock Science*, 139(1-2), 69-79.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S. and Delgado, J. V. (2020a). Zoometric characterization and body condition score in Canarian camel breed. *Archivos de zootecnia*, 69(265), 14-21.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S. and Delgado, J. V. (2020b). Biokinematics and applied thermography in the Canarian camel breed. *Archivos de zootecnia*, 69(265), 102-107.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Barba Capote, C. J., & Delgado Bermejo, J. V. (2020a). Effect of research impact on emerging camel husbandry, welfare and social-related awareness. *Animals*, 10(5), 780.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Nogales Baena, S., & Delgado Bermejo, J. V. (2020b). Camel Genetic Resources Conservation through Tourism: A Key Sociocultural Approach of Camelback Leisure Riding. *Animals*, 10(9), 1703.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Arando Arbulu, A., & Delgado Bermejo, J. V. (2021). The Youngest, the Heaviest and/or the Darkest? Selection Potentialities and Determinants of Leadership in Canarian Dromedary Camels. *Animals*, 11(10), 2886.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Camacho Vallejo, M. E., & Delgado Bermejo, J. V. (2022). Bayesian Linear Regression and Natural Logarithmic Correction for Digital Image-Based Extraction of Linear and Tridimensional Zoometrics in Dromedary Camels. *Mathematics*, 10(19), 3453.

Ishag, I., Eisa, M., & Ahmed, M. (2011). Phenotypic characteristics of Sudanese camels (*Camelus dromedarius*). *Livestock Research for Rural Development*, 23(24), 4.

Ishag, I., Reissmann, M., Peters, K., Musa, L., & Ahmed, M. (2010). Phenotypic and molecular characterization of six Sudanese camel breeds. *South African Journal of Animal Science*, 40(4).

Kardos, M., Armstrong, E. E., Fitzpatrick, S. W., Hauser, S., Hedrick, P. W., Miller, J. M., Tallmon, D.A., & Funk, W. C. (2021). The crucial role of genome-wide genetic variation in conservation. *Proceedings of the National Academy of Sciences*, 118(48), e2104642118.

Kefena, E., Beja-Pereira, A., Han, J., Haile, A., Mohammed, Y., & Dessie, T. (2011). Eco-geographical structuring and morphological diversities in Ethiopian donkey populations. *Livestock Science*, 141(2-3), 232-241.

Köhler-Rollefson, I. (2022). Camel biodiversity—and how to conserve it. *Animal Frontiers*, 12(4), 17-19.

Marín Navas, C., Delgado Bermejo, J. V., McLean, A. K., León Jurado, J. M., Rodriguez de la Borbolla y Ruiberriz de Torres, A., & Navas González, F. J. (2021). Discriminant canonical analysis of the contribution of Spanish and Arabian purebred horses to the genetic diversity and population structure of Hispano-Arabian horses. *Animals*, 11(2), 269.

Marković, B., Dovč, P., Marković, M., Radonjić, D., Adakalić, M., & Simčič, M. (2019). Differentiation of some Pramenka sheep breeds based on morphometric characteristics. *Archives animal breeding*, 62(2), 393-402.

Martínez Raya, A., & González-Sánchez, V. M. (2020). Efficiency and sustainability of public service obligations on scheduled air services between Almeria and Seville. *Economic research-Ekonomska istraživanja*, 33(1), 2751-2760.

Matsuura, A., Irimajiri, M., Matsuzaki, K., Hiraguri, Y., Nakanowatari, T., Yamazaki, A., & Hodate, K. (2013). Method for estimating maximum permissible load weight for Japanese native horses using accelerometer-based gait analysis. *Animal Science Journal*, 84(1), 75-81.

Meghelli, I., Kaouadji, Z., Yilmaz, O., Cemal, İ., Karaca, O., & Gaouar, S. (2020). Morphometric characterization and estimating body weight of two Algerian camel breeds using morphometric measurements. *Tropical animal health and production*, 52(5), 2505-2512.

Mehta, S., Bhardwaj, B., & Sahani, M. (2007). Status and conservation of Mewari and Jaisalmeri camels in India. *Animal Genetic Resources/Resources génétiques animales/Recursos genéticos animales*, 40, 87-101.

Melesse, A., Yemane, G., Tade, B., Dea, D., Kayamo, K., Abera, G., Mekasha, Y., Betsha, S., & Taye, M. (2022). Morphological characterization of indigenous goat population in Ethiopia using canonical discriminant analysis. *Small Ruminant Research*, 206, 106591.

Ovaska, U., Bläuer, A., Kroløkke, C., Kjetså, M., Kantanen, J., & Honkatukia, M. (2021). The Conservation of Native Domestic Animal Breeds in Nordic Countries: From Genetic Resources to Cultural Heritage and Good Governance. *Animals*, 11(9), 2730.

Pastrana, C. I., González, F. J. N., Ciani, E., Ariza, A. G., & Bermejo, J. V. D. (2021). A tool for functional selection of leisure camels: Behaviour breeding criteria may ensure long-term sustainability of a European unique breed. *Research in Veterinary Science*, 140, 142-152.

Pigière, F., & Henrotay, D. (2012). Camels in the northern provinces of the Roman Empire. *Journal of Archaeological Science*, 39(5), 1531-1539.

Poulsen, J., & French, A. (2008). *Discriminant function analysis*. San Francisco State University: San Francisco, CA.

Pourlis, A. (2020). Ovine mammary morphology and associations with milk production, milkability and animal selection. *Small Ruminant Research*, 184, 106009.

Poyato-Bonilla, J., Sánchez-Guerrero, M. J., Cervantes, I., Gutiérrez, J. P., & Valera, M. (2021). Genetic parameters for canalization analysis of morphological traits in the Pura Raza Español horse. *Journal of Animal Breeding and genetics*, 138(4), 482-490.

Puig-Diví, A., Escalona-Marfil, C., Padullés-Riu, J. M., Busquets, A., Padullés-Chando, X., & Marcos-Ruiz, D. (2019). Validity and reliability of the Kinovea program in obtaining angles and distances using coordinates in 4 perspectives. *PloS one*, 14(6), e0216448.

Raziq, A., Tareen, A., & De Verdier, K. (2011). Characterization and significance of Raigi camel, a livestock breed of the Pashtoon pastoral people in Afghanistan and Pakistan. *Journal of Livestock Science*, 2, 1-9.

Sánchez-Guerrero, M. J., Negro-Rama, S., Demyda-Peyras, S., Solé-Berga, M., Azor-Ortiz, P. J., & Valera-Córdoba, M. (2019). Morphological and genetic diversity of Pura Raza Español horse with regard to the coat colour. *Animal Science Journal*, 90(1), 14-22.

Sawa, A., Bogucki, M., Krężel-Czopek, S., & Neja, W. (2013). Relationship between conformation traits and lifetime production efficiency of cows. *International Scholarly Research Notices*, 2013.

Schulz, U. (2008). *El camello en Lanzarote*: Aderlan.

Schulz, U., Tupac-Yupanqui, I., Martínez, A., Méndez, S., Delgado, J. V., Gómez, M., Dunner, S., & Cañón, J. (2010). The Canarian camel: a traditional dromedary population. *Diversity*, 2(4), 561-571.

Singh, N., & Verma, O. (2018). Genetic variability, heritability and genetic advance in rice (*Oryza sativa* L.) under salt stressed soil. *Journal of pharmacognosy and phytochemistry*, 7(3), 3114-3117.

Tandoh, G., & Gwaza, D. (2017). Sex dimorphism in the one hump-camel (*Camelus dromedarius*) from selected populations in Nigeria. *Journal of Applied Life Sciences International*, 15(3), 1-10.

Toalombo Vargas, P. A., Navas González, F. J., Landi, V., León Jurado, J. M., & Delgado Bermejo, J. V. (2020). Sexual dimorphism and breed characterization of Creole hens through biometric canonical discriminant analysis across Ecuadorian agroecological areas. *Animals*, 10(1), 32.

Ucko, P. J., & Dimbleby, G. W. (2007). *The domestication and exploitation of plants and animals*: Transaction Publishers.

Vicente, A., Carolino, N., Ralão-Duarte, J., & Gama, L. (2014). Selection for morphology, gaits and functional traits in Lusitano horses: I. Genetic parameter estimates. *Livestock Science*, 164, 1-12.

Yusuff, A., & Fayeye, T. (2016). Effects of age, sex, season and breed on the body weight and zoometric characteristics of extensively managed Nigerian goats. *Nigerian Journal of Agriculture, Food and Environment*, 12(4), 1-6.

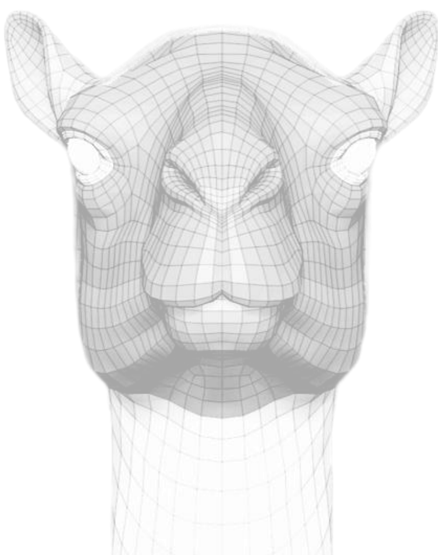
2.3 Optimization and validation of a linear appraisal scoring system for physical fitness-linked zoometric traits in dromedary camels

Carlos Iglesias Pastrana[1], Francisco Javier Navas González[1], Elena Ciani[2], José Manuel León Jurado[3] and Juan Vicente Delgado Bermejo[1]

[1]Department of Genetics, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain

[2]Department of Biosciences, Biotechnologies and Environment, Faculty of Veterinary Sciences, University of Bari 'Aldo Moro', 70121 Bari, Italy

[3]Centro Agropecuario Provincial de Córdoba, Diputación Provincial de Córdoba, 14071 Córdoba, Spain



Quality indicator information provided on the publication
***Latest information available (2022)**

Status of the manuscript: Submitted

Journal (year, volume, page(s)): *Research in Veterinary Science*

International database in which it is indexed: Journal of Citation Reports (JCR)

Thematic area in the reference database: Veterinary Sciences

Impact index of the journal in the year of the article's publication: 2.4

Rank/number of thematic area journals: 29/143 (Q1)

Abstract

In a similar vein to the development of alternative and efficient methods for extracting precise zoometric measurements of live animals from digital images, it is feasible to explore the validation and optimization of reliable linear appraisal scales. These scales would enable the objective description of the biological range for zoometric measurements across the animal population, while enhancing the efficiency of both human resources and economic and time investment that are needed to this aim. The primary objective of the present study is to optimize a protocol for the linear appraisal of physical fitness-linked zoometric traits in dromedary camels mostly dedicated to leisure riding. Furthermore, the replicability of linear trait data and their potential to predict zoometric variability in this animal species were assessed. This validation process is crucial for endorsing the proposed protocol. None of the zoometric variables is susceptible of discarding due to their ability to explain the variability observed in the sample. Nevertheless, several zoometric variables lacked statistically significant representation across one or more levels within the linear appraisal scale. Therefore, a proposal for optimizing the linear appraisal scale involves reducing the number of initially proposed linear categories for these variables. The lowest levels of agreement between raters were found for apical body regions, which are more prone to continuous movement during animal evaluation. This scale optimization and validation would speed up morphological evaluation of large animal samples, aiding in the selection of superior individuals for breeding.

Keywords

Phenotypic assessment, morphological trait, physical aptitude, scale dimensionality reduction, intraclass correlation coefficient, *Camelus dromedarius*

Introduction

The morphological conformation of domestic animals has been gaining recognition over the years due to the increasing evidence of the significant relationship between zoometric traits and productive function (Anisimova et al., 2018; Kugonza et al., 2011; Sánchez-Guerrero et al., 2016). Although purely aesthetic criteria have been commonly used to define the harmony between the different body regions and their adjustment to the standard of breed purity (Holloway, 2005), the functional type criteria are more useful for livestock selection programs. These criteria put special attention to those morphological aspects that are known to determine a better adaptation of the animals to the productive demands to which they are subjected and thus a higher performance (Dahiya, Kumar, & Kumar, 2020; El-Gendy et al., 2014).

In this context, linear appraisal scoring system is an evaluation method that seeks to collect predictive and objective information on morpho-functional characters through the independent visual assessment of each of them and the subsequent translation of their biological variability based on a predefined species-specific point scale (Janssens & Vandepitte, 2004). The range of this scale of points must be wide enough so that all the possibilities of expression of the evaluated characteristics are collected, which must be well defined and be relatively easy to appreciate in order to minimize the subjectivity that could appear when the assessment is carried out by different observers (Breen, 2009; Janssens et al., 2004; Vostrý et al., 2009).

Analogously to the validation of alternative efficient techniques for extracting zoometric measurements of live individuals from images (Gaudioso et al., 2014), it may exist the possibility to validate reliable linear appraisal scales that allow describing the biological range for zoometric measurements across the population. Thereby, the tasks aimed at the morphological evaluation of large animal samples with a view to the selection of elite individuals for breeding, would be speeded up at the same time that the required human and economic resources optimized.

With this aim, Fernández Álvarez, León Jurado, Navas González, Iglesias Pastrana, and Delgado Bermejo (2020) proposes a simplification of the on-farm panel of zoometric variables and the linear appraisal protocol while seeking for the lowest loss of accuracy for dairy goats (Pares-Casanova, Sinfreu, & Villalba, 2013; Vincent et al., 2014). Panel optimization and validation through the assessment of statistically significant correlations between zoometric measurements and linear trait data, can ensure the reliable capacity of linear appraisal scores to reproduce the existing phenotypic variability within corresponding zoometric traits. Similarly, for sport horses, Gómez et al. (2006) found that the zoometric measurements registered were related to the linear type traits that represented.

Based on the above applied attempts, the statistical optimization and validation of a linear appraisal system could enhance the effective and affordable construction of large data repositories of phenotypic information for other livestock such as camels, which are relatively disregarded for morphometrics evaluation because of their often-strong temper that can compromise integrity of operators (Alhajeri et al., 2021). Given the contemporaneous growing interests for the breeding and production of camels (Iglesias Pastrana et al., 2020a), it becomes imperative to build protocols that allow data collection with the least possible contact with live animals. These methods will lead to greater efficiency in the tasks of characterization of camel breeds, which in turn contribute to the knowledge of the phenotypic variability for morphometric traits in these animals and the design of adapted selection and conservation strategies (Köhler-Rollefson, 2022).

Consequently, the present study is intended to optimize a protocol implemented for the linear appraisal of dromedary camels dedicated to leisure riding activities. Further, the replicability of the linear trait data as their potential to predict for physical fitness-related zoometric variability in this animal species is evaluated to validate such protocol. Hence, resources optimization at phenotype collection and the maximization of productive objectives in the mid-to-short term will be reached. To the authors' best knowledge, this is the first report on the cross-validation of linear appraisal system scores and zoometric measurements in dromedary camels.

Material and methods

Definition of zoometric parameters

We conducted a comprehensive literature review on the subject to establish a robust database of zoometric measurements in camels throughout the entire month of September 2019. The bibliographic analysis was carried out using the Google Scholar search engine (https://scholar.google.com/) (accessed on 1 September 2019), a method employed in previous studies for efficient data extraction (Iglesias Pastrana et al., 2020a). Following this document search, we identified six papers related to camel zoometrics, regardless of the measuring methodology used, published between 1994 and 2019 (Iglesias et al., 2020a). We augmented the list of measurements found in these documents with other relevant variables pertaining to camel functional development (Alhajeri et al., 2021). After compiling the variable list, we determined a total of 30 zoometric measures to collect in the field and later extract from digital images. Results and the definition of zoometric parameters considered can be consulted in Iglesias Pastrana et al. (2022).

Animal sample

Zoometric data collection occurred between September 2019 and August 2020 and involved 130 Canarian camel breed individuals, comprising 58 females and 72 males. These camels were situated in three representative locations where Canary camels are bred: Huelva (Doñana National Park, coordinates 36.972330, −6.427498), Almería (coordinates 36.902180, −2.429520), and Fuerteventura (coordinates 28.186777, −14.158361), all within Spain. To ensure the suitability of the animals for the study, thorough clinical examinations were conducted, ensuring the animals' well-being and eligibility. Additionally, to mitigate potential bias stemming from the animals' sexual status at the time of sampling, sexually immature individuals below 3 years of age were excluded. Furthermore, only non-pregnant female camels were included in the study to prevent potential bias in zoometric measurements in the thoracoabdominal region due to pregnancy (Yakubu, Ladokun, & Adua, 2011). Both age and live weight did not adhere to a normal distribution ($p < 0.05$). Live weight was computed using the formula (Equation 1) proposed by Boujenane (2019):

$$\text{Live Weight} = 6.46 \times 10^{-7} (HW + ChG + HG)^{3.17}$$

where HW represents height at the withers, ChG denotes chest girth, and HG signifies hump girth.

Each of the 30 zoometric measurements collected from each animal was obtained from its left side, following the procedures outlined in Iglesias et al. (2020a), Iglesias Pastrana et al. (2022), and Alhajeri et al. (2021).

Females were from 40 to 423 months old, while males age ranged from 18 to 385 months. Live body weight ranged from 327.03 to 687.13 for female Canarian dromedaries, while male Canarian dromedaries weighted from 342.72 to 777.56 kg

Sampling

To minimize potential bias attributed to hair length and texture, we selected the end of the molting season, which spans a six-to-eight-week period starting in late spring (Babu, 2015), as the sampling moment. Iglesias Pastrana et al. (2022) provides a flowchart summarizing the research methodology.

On-field zoometrics

Live animal-based measurement sampling was conducted with the animals in a static upright position, their heads naturally raised, and their bodies correctly aligned (parallel fore and hind legs perpendicular to the ground with toes in line). Measurements were taken on a flat and firm ground surface using a non-elastic measuring tape. All operators underwent training. The first operator was responsible for on-field measurement collection and digital image measurement extraction. The second operator assisted the first operator in collecting zoometric measurements, while a third operator recorded the results of the zoometric evaluation and held a one-meter measuring bar for reference during digital zoometrics extraction as described in Iglesias Pastrana et al. (2022).

Image-assisted zoometrics

Three photographs (front, lateral, and back views perpendicular to the camera) were taken for each animal just before on-field zoometric evaluation. The second operator captured these three photographs for subsequent digital imaging analysis. The third operator held a one-meter measuring bar along the same midline as the animal's body to serve as a reference for distance calibration in the computer measurement software used for digital imaging zoometrics while taking these photographs. The obtained images were digitally processed using Kinovea 0.95 (Free Software Foundation, Inc., Boston, MA). Zoometric linear measurements were recorded in pixels by drawing a straight line between two points in the image, which was then automatically converted to centimeters following calibration using the measuring bar as a reference through the software's Calibrate option (Iglesias et al., 2020b). Puig-Diví et al. (2019) previously reported Kinovea software to be a valid and reliable tool for accurate measurements at distances of up to 5 meters from the object and at angles ranging from 90° to 45°.

Image collection was conducted on an open, firm, and flat ground surface, with light conditions chosen to ensure the animal was not placed in a shaded area or one that might distort image capture due to light exposure. Consideration was given to the animal's color to prevent any distortion or misregistration of measurements due to background color. The camera was positioned at a standardized height of 1 meter on a camera stand, 4 meters away from the camel's center of balance. This distance and height allowed for capturing the entire animal being evaluated. We followed the procedures outlined in Iglesias, Navas, Ciani, Arbulu, et al. (2020) to ensure the animal's correct position, including marking standard lines on the ground before taking photographs to confirm proper alignment. Image capture was performed using a digital camera (Sony DSC-RX100 SENSOR CMOS Exmor 1.0 of 20.1 MP, F1.8–4.9, Zoom 20–100, Optical Zoom 3.6×, 3″ LCD Screen Image stabilizer) in standard mode, using the Joint Photographic Experts Group (JPEG) compression format. A trained operator manually extracted zoometric measurements from the photographs.

Linear Appraisal System (LAS) for Canarian camel breed

Zoometric measurements were assigned to each of the five levels in a linear appraisal scale. Hence, each animal's LAS registry comprised one score from 1 to 5 for each of the thirty zoometric traits measured.

Afterwards, for the development of the actual Canarian dromedary camels linear appraisal scale used, these thirty linear appraisal traits were reduced to twenty different linear appraisal regions to fit the linear appraisal system that is normally used as shown in literature (Parkinson, 2011; Yilmaz & Ertugrul, 2014) (Table 1).

Sexual dimorphism in dromedary camels, like in many species, is evident in various aspects of their zoometry and morphology (Tandoh & Gwaza, 2017). Male dromedaries or bulls tend to be larger and heavier, with more robust bodies and often have a distinctive hump shape. Their necks are thicker, and they may possess a more pronounced dewlap (a loose flap of skin) under their neck. In contrast, female camels or cows generally have a slenderer build and smaller humps.

Table 1. Detailed equivalences of the scales used and the translation process from zoometric traits to LAS scores in Canarian cows, bulls and geldings.

Region	Linear appraisal traits[1]	Zoometric measurements
Head	Head length and head profile	Head length
	Head Width and forehead	Head width
	Eyelashes, cheek, beard, and lips	Head length and Head width
	General size of the ears and hair in the anterior side of the ears	Ear length and Ear width
	Spatial disposition of the ears	Head width, Ear length and Ear width
Neck	Neck	Neck length: dorsal line, Neck length: ventral line, Neck girth: cranial third, Neck girth: middle third and Neck girth: caudal third
Trunk	Trunk	Chest width and Heart girth
	Height at withers vs. rump height	Height at withers (stature)
	Height at withers vs. body length	Body length
Hump	Hump-to-tail distance	Hump-to-tail distance
	General size of the hump	Hump length, Hump width, Hump heigth and Hump girth
	Ventral part of the hump and curly hair in the anterior part of the hump	Hump width, Hump heigth and Hump girth
Rump and Tail	Rump length and rump angle	Rump length
	Rump width	Rump width
	Tail length	Tail length
	Width at the base of the tail	Width at the base of the tail
Thorax, Dorsum and Rump	Angularity of the trunk and posterior third	Chest width, Heart girth, Rump length and Rump width
Extremities	Extremities	Thigh perimeter, Hock perimeter, Fore cannon bone perimeter and Rear cannon bone perimeter
	Muscles of the thigh and buttock, and straight hair in flank	Thigh perimeter and Hock perimeter
Feet	Feet	Sole length, Length of toe dorsal line, Heel heigth and Foot perimeter

[1]Linear appraisal traits were obtained after averaging all the zoometric measurements defining them as shown in this table.

On the other hand, the sexual status of the animals conditions their zoometry (Pigière & Henrotay, 2012). Castration can indeed influence the morphology of dromedary camels, although the extent of these changes may vary depending on when the castration is performed. When a male dromedary camel is castrated at a young age, before sexual maturity, the removal of the testes prevents the production of testosterone, a hormone that plays a significant role in the development of secondary sexual characteristics. As a result, these castrated males, known as steers or geldings, tend to have a less pronounced hump, a more slender and less muscular body, and a milder disposition compared to intact males. However, if castration is performed after sexual maturity, some secondary sexual characteristics, such as a large neck and dewlap, may already be established, and castrated males may retain some of these features. Therefore, the timing of castration can influence the extent to which it conditions the morphology of dromedary camels (Alhajeri et al., 2021). For these reasons a separate scale was develop for each gender and sexual status. All regions were evaluated in all animals with independence of their gender or sexual status.

Each linear appraisal level represents how close the animal resembles the reference values found in the population on average.

As no official linear appraisal system has been developed and implemented up to the date, the first approaches to a linear appraisal system published were used as a reference to develop the one in this study (Iglesias et al. 2020a; Parkinson, 2011; Yilmaz & Ertugrul, 2014). A detailed description of the scales used and the translation process from zoometric traits to LAS scores in Canarian camel cows, bulls and geldings can be consulted in Supplementary Table S1. The reduction process of the linear appraisal system was developed by averaging certain combinations of all the linear appraisal traits obtained from zoometric measurements (Table S1) basing upon the equivalences reported in Table 1. The qualitative definition of each of the levels on this reduced linear appraisal scale is shown in Table 2.

Statistical analysis

Dimensionality reduction: Zoometric/Linear Appraisal System optimization

The optimization of the LAS used in Canarian camels was performed using Principal Component Analysis (PCA). PCA can be used to perform an efficient selection of the minimum number of zoometric traits able to capture the highest fraction possible of variability for a given set of traits. Birth data for all animals was provided by each owner and registered at inspection of the animals' sanitary status prior to field experiences. Zoometric data collection was performed using a zoometric stick, a zoometric compass, and a tape measure. All measurements were recorded once by the same person to avoid inter-recorder effects. Descriptive statistics were calculated for each of the 30 zoometric variables studied and Spearman's correlation coefficients were computed for all possible combinations of the same. A significant Spearman's correlation between the two variables in a pair may result when the two variables involved in the comparison are monotonically related, even if they share a nonlinear relationship (Bishara & Hittner, 2012). The correlation matrix for the variables must contain at least two correlations of |0.30| or greater (Walde, 2020) in absolute value which is the minimum magnitude for variables to be suitable for structure detection, hence for PCA to be valid. As a "rule of thumb" for interpreting Spearman rho, 0 to ±0.20 could be considered negligible,

Table 2. Definition of Linear Appraisal Scale levels in Canarian cows, bulls and geldings.

Linear trait	Descriptors
Head length	1=too short; 3=proportional length with the rest of the body; 5=too long
Head width	1=too narrow; 3=width proportional with the rest of the body; 5=too wide
Head profile	1=very concave; 3=uniformly straight; 5=markedly straight
Forehead (fat pad divided into two hemispheres, especially in males)	1=not bulging; 3=slightly bulging; 5=noticeably bulging
Overall, ear size	1=very small, not extending beyond the fronto-temporal line; 3=ears as two equal halves in length, divided at the fronto-temporal level; 5=very large
Spatial position of ears	1=ears pressed against the head and backward; 3=ears in an upright position; 5=too much space between ears and head
Inner ear hair	1=absent; 3=somewhat present; 5=too abundant
Eyelashes	1=too short; 3=eyelash length equal to the diameter of the open eye; 5=too long, extending beyond the diameter of the open eye
Cheeks	1=very gaunt with very visible regional bone features; 3=normal muscular development without noticeable bone features; 5=too bulky
Whiskers	1=absent; 3=medium length not exceeding the anatomical boundary of the muscles in a front view; 5=too long, exceeding the anatomical boundary of the muscles in a front view
Lips	1=very thin; 3=slightly thickened lip edges; 5=too thick
Neck	1=short, arched, and thick neck; 3=neck proportional to the rest of the body and head; 5=long, thin, and straight neck
Trunk	1=underdeveloped chest, narrow ribcage, and shallow trunk; 3=chest with evident muscular development and deep trunk; 5=hypertrophied chest, very wide ribcage, and excessively deep trunk
Withers height vs. Rump height	1=withers height much lower than rump height; 3=withers height equal to rump height; 5=withers height much higher than rump height
Withers height vs. Body length	1=withers height much greater than body length; 3=withers height equal to body length; 5=withers height much lower than body length
Limbs	1=limbs lacking harmony and weak; 3=strong, well-formed, and muscled limbs; 5=limbs too thick/robust
Feet	1=small and poorly formed feet; 3=feet proportional to limbs and the rest of the body and well-formed; 5=feet too large, hindering proper locomotion
Overall hump size	1=no hump; 3=occupies at least 1/3=of the dorsal line; 5=too large or occupies more than 2/3=of the dorsal line
Lower part of the hump	1=not bulging; 3=slightly bulging; 5=too bulging
Curly hair on the front of the hump	1=absent; 3=somewhat present; 5=too abundant
Hump-to-Tail distance	1=distance too short; 3=distance equivalent to at least 1/3=of the dorsal line length; 5=very significant distance or much greater than 2/3=of the dorsal line
Pelvis length	1=very short pelvis; 3=pelvis of approximate length to 1/3=of the dorsal line; 5=very long pelvis or length much greater than 2/3=of the dorsal line

Table 2. *Cont.*

Linear trait	Descriptors
Rump angle	1=rump markedly inclined or elevated (angle greater than 45º); 3=normal rump (angle of 45º); 5=rump very retracted (angle much less than 45º)
Rump width	1=pelvis too narrow; 3=pelvis of similar width to the chest; 5=pelvis very wide or wider than the chest
Muscles of the thigh and buttock	1=little/no development; 3=noticeable muscle development; 5=markedly developed/hypertrophied
Straight hair in flank	1=absent; 3=somewhat present; 5=excessively abundant
Tail length	1=too short; 3=the tail occupies at least 1/3=of the line connecting the ischial tuberosity and the ankle; 5=tail too long that extends beyond the ankle
Width at the base of the tail	1=too narrow, and the mucous membranes of the anogenital region can be seen; 3=width equal to that of the anogenital region, so the mucous membranes of the latter are not noticeably visible; 5=too wide and rests laterally on the musculature of the surrounding area
Angularity of the trunk and posterior third	1=lack of angularity and closed ribs; 3=intermediate angularity and separated ribs; 5=very pronounced angularity and separated ribs

±0.21 to ±0.40 weak, ±0.41 to ±0.60 moderate, ±0.61 to 0.80 strong, and ±0.81 to ±1.00 could be considered very strong (Akoglu, 2018).

Data for the PCA were generated from the variance-covariance matrix. Kaiser-Meyer-Olkin (KMO) test of sampling adequacy and Bartlett's test of sphericity were computed to establish the validity of the data set for structure detection (KMO's measure determines whether the common factor model is appropriate as it measures to what extend the original variables belong together). The KMO should be greater than 0.5 for a satisfactory factor analysis to proceed. Bartlett's test of sphericity tests the hypothesis that your correlation matrix is an identity matrix, which would indicate that your variables are unrelated and therefore unsuitable for structure detection. Small p-values (less than 0.05) of the significance level indicate that factor analysis may be useful for the analysis of our data (Center, 2019).

Communalities were assessed to determine which variables should be maintained or discarded from PCA. Initial Communalities are indicative of the total amount of variance that certain original variable shares with all other variables included in the analysis. Extraction communalities are estimates of the variability of each variable that can be accounted by the factors in the factor solution. Small values (close to zero) are indicative of variables that do not fit well within the factor solution, hence, should possibly be dropped from the analysis. Communalities after extraction (Field, 2013).

During the process of Exploratory Factor Analysis (EFA) utilizing Principal Axis Factoring with Promax rotation, Osborne, Costello, and Kellow (2008) have proposed that communalities exceeding 0.4 are considered acceptable. Conversely, Child (2006) advocates for a stricter criterion, suggesting that communalities below 0.2 should be discarded. In these regards, Field (2009) emphasized the importance of inter-item correlation, indicating that values should be above 0.3 for them to be acceptable.

The communalities are calculated as the sum of square factor loadings, and a factor loading value of at least 0.30 or 0.33 is often recommended as a cutoff point for retaining an item. This suggests that an item's communality can potentially be as low as 0.09, assuming it loads on only one factor. However, if factor loadings are sufficiently high and the total explained variance meets the required level, it may still be appropriate to retain items with communalities near 0.3, as the overall model fit and interpretability may outweigh strict communalities criteria.

Rotation of principal components was performed to transform components into a simple structure. The raw varimax criterion of the orthogonal rotation method was used for the rotation of the factor matrix. The varimax rotation aims to maximize the sum of variances of a quadratic weight. Furthermore, when varimax rotation is applied via Kaiser Normalization, it corrects for the bias derived from the fact that some factors may have high correlations with a small number of variables and zero correlations with the rest.

The cumulative proportion of variance criterion was finally used to determine the number of components to extract. Cronbach alpha statistic was used to confirm the reliability and validity of the reduced variable set. The concept of procedure validity can be understood as the degree to which a certain scale measures which indeed it claims to measure. Cronbach's alpha measure of validity assumes a high correlation among the elements measuring the same construct. The closer the value of alpha is to 1, the greater is the internal consistency of the analyzed elements. George and Mallery (2003) provided a thumb rule for the interpretation of Cronbach alpha which stablishes thresholds as follows; 0.9 value is excellent, 0.8 is good, 0.7 is acceptable, 0.6 is questionable, 0.5 is poor, and less than 0.5 is unacceptable. All statistical tests referred above were performed using SPSS Statistics for Windows statistical software, Version 25.0 (Corp., 2017).

PCA was used to discard variables which had a confounding nature, and as a result do not significantly contribute to the fraction of explained variability but significantly increase the likelihood of type I errors introducing bias as a result. Component loadings below |0.4| were ruled out provided their confounding nature. SPSS Statistics for Windows, Version 25.0, IBM Corp. (2017) furnishes you with loadings in the form of direct correlation coefficients. Nevertheless, it is worth noting that within the Social Sciences, any loading exceeding 0.3 is considered favorable, while a loading of 0.4 is categorized as moderate. Highly loaded variables (whose component loadings is equal or over |0.5|) in the same dimension may reveal strong common underlying correlations among those variables.

Linear Appraisal System validation

In the initial phase of our study, we calculated the intraclass correlation coefficient (ICC) based on multiple paired Cohen's κ tests to determine whether the variability in zoometric measurements was sufficiently represented by linear appraisal scales, for their validation.

There are no standard values for acceptable reliability using Intraclass Correlation Coefficient (ICC). A low ICC could not only reflect the low degree of rater or measurement agreement but also relate to the lack of variability among the sampled subjects, the small number of subjects, and the small number of raters being tested. As a rule of thumb, at least 30 heterogeneous samples and at least 3 raters should be involved whenever possible when conducting a reliability study. Under such conditions, we suggest that ICC values less than 0.5 are indicative of poor reliability, values between 0.5 and 0.75 indicate moderate reliability, values between 0.75 and 0.9 indicate good reliability, and values greater than 0.90 indicate excellent reliability (Koo & Li, 2016).

Following the guidelines established by Fleiss and Cohen (1973), we interpreted ICC values as follows: less than 0.4 (low), between 0.4 and 0.59 (reasonable), 0.6 to 0.74 (good), and 0.75 to 1.0 (excellent) to determine whether we achieved adequate levels of reproducibility and repeatability. We selected the "Two-Way Random" model, as recommended by Koo and Li (2016), and calculated 95% confidence intervals using the formula 95% kappa Confidence Interval (95%CI) = $\kappa \pm 1.96\ SE\kappa$, with the reliability analysis routine of SPSS Statistics for Windows, Version 25.0, IBM Corp. (2017).

Scale Reliability: Zoometric Traits vs Linear Appraisal

We assessed the reliability (internal consistency) of the linear appraisal extrapolation from zoometric measurements using intraclass correlation coefficient (ICC) based on multiple paired Cohen's κ tests and Cronbach's Alpha (Cα). Internal consistency, when applied to instrument comparison, estimates the average correlation among items within a test, with each item representing a measuring method (zoometric on-field evaluation and linear appraisal in our case). In this context, ICC and Cα signifies the reliability level of the scale being compared to a reference instrument (linear appraisal in relation to zoometric on-field analysis) and was used to determine whether the variability in zoometric measurements was sufficiently represented by linear appraisal scales, for their validation (Tavakol & Dennick, 2011).

As suggested by George (2011), we applied the following recommendations to evaluate Cα coefficients: >0.9 is excellent, >0.8 is good, >0.7 is acceptable, >0.6 is questionable, >0.5 is poor, and <0.5 is unacceptable. However, when comparing internal consistency between instruments, Pallant (2020) reported that a Cα value above 0.6 is considered highly reliable and acceptable (Bunting et al., 2019). Retaining variables with values above 0.5 has been suggested due to their ability to explain data variability.

It is important to note that while single measures of ICC determine how a randomly selected observation correlates with another random observation (in our case, how a zoometric measure from on-field evaluation correlates with its paired counterpart from linear appraisal), average ICC and Cα determine the average consistency when zoometry and linear appraisal are compared. Average measures help mitigate potential measurement errors that might affect specific measurements, preventing inaccurate reporting of instrument reliability and accuracy for the tested instrument (linear appraisal in our case).

Reproducibility and Repeatability: Intraobserver and Interobserver reliability

As suggested by Bunting et al. (2019), ICC serves as a reference method for assessing the reproducibility and reliability of numeric measurements organized into groups, such as different operators measuring the same variable in different animals or the same operator using different methods on different animals (interobserver reliability) and the same operator measuring or scoring the same animal multiple times (intraobserver reliability).

Then, we calculated the coefficients of variation (CV = SD/Mean × 100%) to measure reproducibility. We defined parameter reproducibility as excellent when CV was ≤10%, good when CV was between 10–20%, acceptable when CV was between 20–30%, and poor when CV was >30% (Aronhime et al., 2014).

Thus, once linear appraisal scales had been validated, CV (%), ICC and Cα were used again to determine if the judgments of the six different trained raters were in substantial internal and external agreement.

Results

Statistical assumption testing, zoometric, and linear appraisal records

Common parametric assumptions were violated; hence a nonparametric approach was suggested. Summary of descriptive statistics for zoometric traits derived from Linear appraisal and zoometric assessment in Canary Camels bulls, cows and gelded males is reported in Supplementary Table S2.

Dimensionality reduction: Linear Appraisal System optimization

Spearman's correlation coefficients between almost all pairs of linear appraisal derived zoometric traits in Canary Camels across genders and sexual statuses were over |0.3|, which supported the performance of Principal Components Analysis.

Kaiser-Meyer-Olkin Measure of Sampling Adequacy for principal component analysis on linear appraisal variables was 0.657, 0.641, 0.597 in Canarian camel cows, bulls and geldings does, respectively, and Bartlett's Test of Sphericity reported a highly statistically significant value of 0.001, for the three animal categories, hence correlation matrix was applicable and PCA results were valid. All communalities were over 0.565, 0.642, 0.436 for Canarian dromedary camel cows, bulls and geldings, respectively, hence no variable was dropped off from the PCA. Supplementary Table S3 report Linear Appraisal System Varimax with Kaiser Normalization Rotated Component loadings, eigenvalues, and percentage of variance explained for Canarian dromedary camel cows, bulls and geldings, respectively. Figure 1 represents eigenvalues across dimensions for Canarian dromedary camel cows, bulls and geldings, respectively.

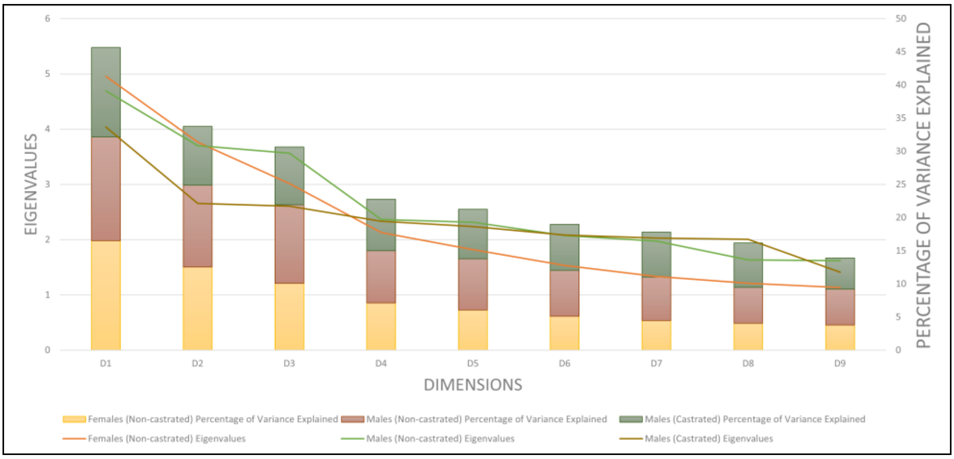


Figure 1. Representation of PCA eigenvalues for dimensions 1 to 9 (Dim. 1-9) for Linear Appraisal System (LAS) scores in Canarian Dromedary Camel cows, bulls and geldings.

After PCA, no trait was discarded from the panel of zoometric variables, thus all were used for the implementation of the Linear Appraisal system.

Linear Appraisal System validation, reproducibility and repeatability

The results demonstrated high reliability (Cronbach's alpha=0.7), as there was a statistically significant and acceptable agreement between zoometric measurements ranges and linear appraisal scales, thus linear appraisal scale was validated. The same acceptable agreement was also reported for each of the six appraisers' judgments when evaluating intraobserver reliability. Table 3 reports the results for interobserver reliability.

Table 3. Interobserver reliability of linear appraisal scales using ICC and Cronbach's alpha.

Interobserver reliability	Mean	Standard deviation	Coefficient of Variation (%)	ICC/Cronbach's alpha
Overall hump size	3.17	0.665	21	0.792
Neck	2.87	0.683	24	0.771
Curly hair on the front of the hump	3.52	0.946	27	0.759
Limbs	2.8	0.598	21	0.758
Hump-to-Tail distance	2.91	0.642	22	0.751
Angularity of the trunk and posterior third	0.295	0.550	19	0.743
Lower part of the hump	3.01	0.689	23	0.728
Head length	3.1	0.644	21	0.720
Overall, ear size	2.62	0.705	27	0.705
Trunk	3.07	0.648	21	0.688
Cheeks	2.76	0.585	21	0.681
Inner ear hair	2.72	0.838	31	0.676
Eyelashes	2.56	0.811	32	0.664
Withers height vs. Body length	2.77	0.586	21	0.664
Muscles of the thigh and buttock	3	0.834	28	0.608
Straight hair in flank	3.15	0.981	31	0.577
Withers height vs. Rump height	3.48	0.581	17	0.576
Spatial position of ears	2.68	0.769	29	0.565
Pelvis length	2.77	0.535	19	0.556
Whiskers	2.26	0.866	38	0.546
Lips	3.03	0.591	20	0.546
Rump width	3.02	0.604	20	0.499
Head width	3.03	0.396	13	0.494
Width at the base of the tail	2.98	0.426	14	0.472
Head profile	2.93	0.793	27	0.444
Tail length	3.02	0.461	15	0.436
Feet	2.91	0.418	14	0.432
Rump angle	2.8	0.786	28	0.382
Forehead (fat pad divided into two hemispheres, especially in males)	2.94	0.517	18	0.366

Discussion

The optimization and validation of a linear appraisal system as a methodological alternative to traditional on-field assessment of physical fitness-linked morphological traits in leisure dromedary camels, were performed using principal component and correlation analysis. As suggested by Reddy and Claridge (1994), such systematic approach to reducing the dimensionality of large datasets is fundamental to the pursuit of determining which are the reduced numbers of variables that explain the greater proportion of the variability found in a sample. Further, the level of resemblance between the measures within linear data cluster and zoometric scores was calculated to estimate the capacity of an artificially built linear appraisal system to capture the biological variability that exists in the study population for economically important zoometric traits.

First, the Cronbach's alpha value revealed substantial internal consistency and reliability in our data (Cronbach's alpha>0.7) (Tavakol & Dennick, 2011). This is indicative of moderate agreement between raters but also suggests that the animal and rater study samples are reasonably capable to capture and explain the existing internal variability for the morphological traits assessed (Koo & Li, 2016). In this sense, Melesse et al. (2022) remark the critical importance of sample size in morphological characterization researches given that it has to be large enough to differentiate genetic resources based on morphological traits in an accurate way and resemble the findings of molecular based studies when these last tools could not be feasible (Hassen et al., 2016).

With regard to the scale optimization, PCA identifies the existence of nine reorganized major categories or dimensions (Supplementary Table S3). Concerning the variability that was explained by each model, values of 69.65%, 71.33% and 79.78% were accounted for females, neutered males and bulls, respectively. For the three subgroups, the sets of variables that mostly explain the variability found in the data are those that are related to body general corpulence and the proportionality of specific local regions. This may be supported by the sex-separated breeding of Canarian dromedary camels for functional reasons (Iglesias Pastrana et al., 2021). Globally, it can be also concluded that no variable is redundant and thus susceptible to be discarded from any of the models, that is, they are all explanatory to a greater or lesser extent depending on the percentage of variance that explains the dimension or dimensions in which each variable is clustered. As suggested by Osborne et al. (2008), we established a value threshold of 0.4 for a variable's communality to be considered acceptable when indicating the proportion of each variable's variance that is explained by the principal components.

The qualitative aggrupation of explanatory variables slightly differs among animal subgroups, which can be explained on the basis of the sex-biased relative contribution of each specific construct to the global morphological value of each subgroup for utilitarian reasons. In the particular case of dromedary females and neutered males, the first dimension practically includes the same morphometric variables that are related to body general corpulence ('neck girth: caudal third', 'hump girth', 'thigh perimeter', 'hock perimeter', 'fore cannon bone perimeter', 'rear cannon bone perimeter', and 'foot perimeter' for females; and the same variables but including 'neck girth: middle third' and discarding 'hock perimeter' for neutered males); while for non-neutered males this dimension is at the third position ('neck girth: middle third', 'hump girth', 'thigh perimeter', 'fore cannon bone perimeter', 'rear cannon bone perimeter', and 'foot perimeter'). The relative importance of this dimension in both females and neutered males can be explained basing on the positive relationship between such morphological variables and milk yield (Pesántez-Pacheco et al., 2019) and riding performance (Faye, 1997; Pigière & Henrotay, 2012; Ucko & Dimbleby, 2007) of females and neutered males, respectively. Certain regional body proportions, namely 'head-neck junction' and 'neck-thorax junction' for females, and 'neck length and junction with thorax' for neutered males, additionally support these results basing on their reported genetic correlation with body size and milk yield (Alphonsus et al., 2010; Khan & Khan, 2016) and riding performance (Williamson & Payne, 1978; Zechner et al., 2001) in domestic species.

In contrast, non-neutered dromedary males are generally less corpulent (Pigière & Henrotay, 2012) and more difficult to handle for their often-strong temper (MacKay, VanHoy, & Lakritz, 2022) when compared to neutered dromedaries, which may translate both into a lower functional resistance and breeders' preference for working (Fenner et al., 2019; Iglesias Pastrana et al., 2021), and the highest contribution of other morphological traits to explain greater fractions of the variability in the specific dataset. Concretely, variables related to overall animal body proportion or harmony ('neck girth: cranial third', 'neck girth: middle third', 'heart girth', 'body length', 'hump length', 'hump width', 'hump girth', 'rump length', and 'thigh perimeter') explained the highest proportion of variation in bulls. These last specific dimensions can be encountered also for females in relatively less important positions (second position for overall body proportion and third position for body harmony) but they are absent for castrated males. The underlying basis of such finding can be the impact of body size and harmony traits on milk production in females (Ahlborn & Dempfle, 1992; Mingoas et al., 2017), and the correlations between harmonious body proportions and athletic performance in animals within the sport and leisure spheres (de Oliveira Bussiman et al., 2018; Gómez et al., 2016; Koenen, Aldridge, & Philipsson, 2004).

For dromedary bulls, although the body harmony was the most explanatory dimension of within-subgroup variability, we additionally encountered that dorsal length (fifth dimension) and anteroposterior proportionality (sixth dimension), have a non-negligible explanatory potential. They may be further implicated in the motion and the maintenance equilibrium during locomotion (ninth dimension) in these animal species for anatomical reasons. Contrary to other quadruped mammals and equal to giraffes, camels are particularly long-legged, so that the length, width and mobility of the neck are adapted to counteract the dorso-ventral balance of the limb's movements (Sharp, 2012).

Contextually, for neutered males, the apical balance ('neck girth: caudal third' and 'tail length'), in addition to neck length and body width at the anterior third ('neck length: dorsal line', 'neck length: ventral line', 'chest width', and 'heart girth'), are the dimensions that accounted for a greater proportion of the variability encountered within this animal subgroup when compared to bulls. This suggests that these regional morphological traits have a pivotal influence on the performance of neutered camels, the most preferred for riding activities, in account of the fact the animals have to maintain equilibrium while dealing with variable weight in their back. A major propulsion force is then also needed, as suggested by the greater relative importance of this dimension within this animal subgroup (sixth dimension) when compared to females and bulls (seventh dimension). Moreover, as they are disposed in caravans when performing leisure activities, the body language signals used by the animals for inter-individual communication are quite important for a secure experience and such condition can be ascribed to the identification of a specific dimension within PCA that comprises the size of some appendixes ('ear length, 'ear width', and 'tail length') widely known to be involved in non-verbal communication in animal species (Czycholl et al., 2020; Proctor & Carder, 2014; Westling, 2014). Besides, the proportions of the hump (i.e., overall size) are expected to affect the apical balance being the difficulties in maintaining the balance greater as long as the hump proportions increase, similarly to the reported deleterious effects of rider's size and position on equine gait balance and synchrony (Dyson et al., 2020; Dyson et al., 2022). Indeed, the variables 'hump-to-tail distance', 'hump length', 'hump width', 'hump height', and 'hump girth', are clustered together in our results. These dimensions lastly condition a good functional performance of the camel during the rides but also the customer satisfaction and return intention probability within this entertainment business (Iglesias Pastrana et al., 2020b).

Apart from these specific differences, both male subgroups share the same relative importance for dimensions comprising variables related to the disposition of gravity centre (second dimension), general equilibrium (fourth dimension) and aplombs (eight dimension). For females, these dimensions are inexistent. Indeed, despite sharing similar groups of morphological variables with both subgroups of males, female dromedaries appeared to display high inter-individual variability for morphometric traits that belong to general body proportion and some regional traits, namely the dimensionality of thoraco-abdominal region, but low variability for traits linked to aplombs and support. This is supported on the breeders' preference for females to be selected for milk production and the larger functional specialization and selection of male dromedaries towards riding activities. Furthermore, it could also be inferred that bulls would be morphologically more suitable for dressage/beauty activities while neutered males are more specialized for endurance riding activities.

After mapping the high-dimensionality initial dataset to a lower dimension space, the optimization of the scale further requires to corroborate that variability within each of the measured morphometric traits has a statistically significant representativeness across the five levels of the linear appraisal scale for each animal subgroup. The resulting distribution of study data in quantitative histograms and the descriptive statistics (i.e., minimum and maximum values) offers an exploratory but reliable interpretation for this statistical association. It can be easily visualized which are the variables that maintain notable representativeness of animals within the five levels but also those morphometric characters that display the greatest representativeness of animals concentrated in a shorter number of categories and thus proposed to be reduced to a fewer number of levels of linear traits (Supplementary Figure 1). Such a preliminary interpretation may need to be complemented by the values of Spearman rho for the correlation between the zoometric measurement and its corresponding level on the linear appraisal scale. As a rule of thumb, Spearman rho's values below the threshold of 0.81 are suggesting a progressively weak association between morphometric traits and its associated level within the LAS (Prion & Haerling, 2014).

Specifically, a lack of sample representativeness for one or more levels within the linear appraisal scale does exist for the variables 'ear length, 'ear width', 'neck length: dorsal line', 'chest width', 'body length', 'hump-to-tail distance', 'rump length', 'tail length', and 'length of toe dorsal line' for females; 'ear width', 'neck length: dorsal line', 'neck girth: caudal third', 'heart girth', 'body length', 'hump-to-tail distance', 'hump height', 'sole length', and 'foot perimeter' for bulls; 'head length', 'ear width', 'height at withers', 'rump length', 'hock perimeter', 'heel height', and 'foot perimeter' for castrated males. Additionally, the statistical correlation was denoted to be slightly lower for the variables 'heart girth' (Spearman's rho = 0.784, $p<0.0001$) and 'heel height' (Spearman's rho = 0.310, $p<0.05$) in castrated males and bulls, respectively.

Therefore, it can be summarized that all the morphometric variables considered in this study are maintained since they all have explanatory potential of the variability present in the sample. But, a proposal for the optimization of the scale goes through the numerical reduction of the initially proposed linear categories for the above cited variables given the fact that there is not enough representativeness of the sample in some of them. Hence, the present attempt for scale optimization reported quite conservative results, similarly to Fernández Álvarez et al. (2020), who only omitted one variable (rump angle) from the model.

Lastly, basing on the results obtained for interobserver reliability, the lowest levels of agreement between raters (ICC<0.5) (Koo & Li, 2016) pertained to the linear traits 'head profile', 'head width', 'forehead', 'rump angle, 'rump width', 'tail length', 'width at the base of the tail', 'feet', and 'angularity of the trunk and posterior third'. Such finding can be mostly associated to the fact that these traits are mainly apical body regions and thus more likely to move during the animal handling and restraining for on-field zoometric assessment and linear appraisal. Similar results are reported by Zechner et al. (2001) for horses.

Conclusions

The complete list of zoometric variables considered in the present study was retained since no variable was redundant, that is, they all have explanatory potential for the variability present in the animal sample. However, a numerical reduction of the initially designed linear categories for some zoometric variables is proposed, given the fact that no statistical representativeness for some linear categories did exist. Principal component analysis revealed differentiated sets of variables that explain the variability found for physical fitness-linked traits within each animal subgroup (sex and physiological status), which can be considered a reflection of the different breeding goals and management strategies carried out for purely utilitarian purposes in the studied camel breed. For dromedary females and neutered males, the greater fractions of within-subgroup variability are explained by those zoometric variables that are related to body general corpulence and apical balance. Contrastingly, variables related to overall animal body proportion or harmony are responsible for the highest proportion of variation in bulls. The relative importance of such dimensions within each subgroup may be supporting the correlations between the specific variables clustered and milk yield, and endurance riding/dressage performance in this animal species. Additionally, the lowest levels of agreement between raters were found for apical body regions, which are more prone to continuous movement during animal evaluation.

Author contributions: Conceptualization, C.I.P., F.J.N.G. and J.V.D.B.; Data curation, C.I.P., F.J.N.G. and J.M.L.J.; Formal analysis, C.I.P., F.J.N.G. and J.V.D.B.; Funding acquisition, E.C. and J.V.D.B.; Investigation, C.I.P. and F.J.N.G.; Methodology, C.I.P., F.J.N.G. and J.M.L.J.; Project administration, E.C. and J.V.D.B.; Resources, E.C. and J.V.D.B.; Software, C.I.P., F.J.N.G. and J.M.L.J.; Supervision, F.J.N.G., E.C. and J.V.D.B.; Validation, C.I.P., F.J.N.G. and J.M.L.J.; Visualization, E.C.; Writing—original draft, C.I.P. and F.J.N.G.; Writing—review & editing, F.J.N.G., E.C. and J.V.D.B. All authors have read and agreed to the published version of the manuscript.

Funding: The present research was carried out in the financing framework of the international project CA.RA.VA.N—'Toward a Camel Transnational Value Chain' (Reference APCIN-2016-00011-00-00) and during the covering period of a predoctoral contract (FPU Fellowship) funded by the Spanish Ministry of Science and Innovation and was developed under the context a Ramón y Cajal Post-Doctoral fellowship financially supported by MCIN/AEI/10.13039/501100011033 and European

Union “NextGenerationEU”/PRTR” (Recovery, Transformation and Resilience Plan—Funded by the European Union—NextGenerationEU).

Data availability statement: The data presented in this study are available on request from the first author.

Acknowledgments: The authors would also like to thank ‘Aires Africanos’ Eco-tourism Company, Oasis Park Fuerteventura, and ‘Camelus’ Camellos de Almería, for their direct technical help and assistance.

Conflicts of interest: The authors declare no conflict of interest.

Ethics declaration statement: All farms included in the study followed specific codes of good practices and therefore, the animals received humane care in compliance with the national guide for the care and use of laboratory and farm animals in research. Written consent from the owners was obtained for their participation. The study was conducted in accordance with the Declaration of Helsinki. The Spanish Ministry of Economy and Competitivity through the Royal Decree Law 53/2013 and its credited entity, the Ethics Committee of Animal Experimentation from the University of Córdoba, permitted the application of the protocols present in this study as cited in the 5th section of its 2nd article, as the animals assessed were used for credited zootechnical use. This national Decree follows the European Union Directive 2010/63/UE, from the 22 September of 2010.

References

Ahlborn, G., & Dempfle, L. (1992). Genetic parameters for milk production and body size in New Zealand Holstein-Friesian and Jersey. *Livestock Production Science*, 31(3-4), 205-219.

Akoglu, H. (2018). User's guide to correlation coefficients. *Turkish journal of emergency medicine*, 18(3), 91-93.

Alhajeri, B. H., Alhaddad, H., Alaqeely, R., Alaskar, H., Dashti, Z., & Maraqa, T. (2021). Camel breed morphometrics: Current methods and possibilities. *Transactions of the Royal Society of South Australia*, 145(1), 90-111.

Alphonsus, C., Akpa, G., Oni, O., Rekwot, P., Barje, P., & Yashim, S. (2010). Relationship of linear conformation traits with bodyweight, body condition score and milk yield in Friesian× Bunaji cows. *Journal of Applied Animal Research*, 38(1), 97-100.

Anisimova, E. I., Koshchaev, A. G., Nesterenko, A. A., Bakharev, A., Isaeva, A. G., Shuvaeva, T. M., & Kalashnikova, T. (2018). Comparative assessment of the relationship between intrabreed types of simmental cows and sectionized traits. *International Journal of Pharmaceutical Research*, 10(4), 604-610.

Aronhime, S., Calcagno, C., Jajamovich, G. H., Dyvorne, H. A., Robson, P., Dieterich, D., Fiel, M.I., Martel-Laferriere, V., Chatterji, M., Rusinek, H., & Taouli, B. (2014). DCE-MRI of the liver: effect of linear and nonlinear conversions on hepatic perfusion quantification and reproducibility. *Journal of Magnetic Resonance Imaging*, 40(1), 90-98.

Babu, K. (2015). Natural textile fibres: Animal and silk fibres. In *Textiles and fashion* (pp. 57-78): Elsevier.

Bishara, A. J., & Hittner, J. B. (2012). Testing the significance of a correlation with nonnormal data: comparison of Pearson, Spearman, transformation, and resampling approaches. *Psychological methods*, 17(3), 399.

Boujenane, I. (2019). Comparison of body weight estimation equations for camels (*Camelus dromedarius*). *Tropical animal health and production*, 51, 1003-1007.

Breen, E. (2009). A comparison of judging techniques and conformation traits in Irish draught horses. *Department of Life Science, Equine Science*.

Bunting, K. V., Steeds, R. P., Slater, L. T., Rogers, J. K., Gkoutos, G. V., & Kotecha, D. (2019). A practical guide to assess the reproducibility of echocardiographic measurements. *Journal of the American Society of Echocardiography*, 32(12), 1505-1515.

Center, I. K. (Producer). (2019, 12/05/2019). *KMO and Bartlett's test*. Retrieved from https://www.ibm.com/support/knowledgecenter/en/SSLVMB_24.0.0/spss/tutorials/fac_telco_kmo_01.html

Child, D. (2006). *The essentials of factor analysis*: A&C Black.

Corp., I. (2017). *IBM SPSS Statistics for Windows (Version 25.0)*. Armonk, NY: IBM Corp.

Czycholl, I., Hauschild, E., Büttner, K., Krugmann, K., Burfeind, O., & Krieter, J. (2020). Tail and ear postures of growing pigs in two different housing conditions. *Behavioural processes*, 176, 104138.

Dahiya, S., Kumar, S., & Kumar, M. (2020). Current status of research on linear type traits in Indian cattle and future strategies. *Tropical animal health and production*, 52, 2221-2232.

de Oliveira Bussiman, F., da Costa Perez, B., Ventura, R. V., e Silva, F. F., Peixoto, M. G. C. D., Vizoná, R. G., Chicaroni Mattos, E., Sterman Ferraz, J.B., Pereira Eler, J., Abdallah Curi, R., & de Carvalho Balieiro, J.C. (2018). Genetic analysis of morphological and functional traits in Campolina horses using Bayesian multi-trait model. *Livestock Science*, 216, 119-129.

Dyson, S., Ellis, A., Mackechnie-Guire, R., Douglas, J., Bondi, A., & Harris, P. (2020). The influence of rider: horse bodyweight ratio and rider-horse-saddle fit on equine gait and behaviour: A pilot study. *Equine Veterinary Education*, 32(10), 527-539.

Dyson, S., Martin, C., Bondi, A., & Ellis, A. (2022). The influence of rider skill on ridden horse behaviour, assessed using the Ridden Horse Pain Ethogram, and gait quality. *Equine Veterinary Education*, 34(7), e308-e317.

Gendy, M., Youssef, H., Saifelnasr, E., El-Sanafawy, H., & Saba, F. (2014). Relationship between udder characteristics and each of reproductive performance and milk production and milk composition in Zaraibi and Damascus dairy goats. *Egyptian Journal of Sheep and Goat Sciences*, 9(3), 95-104.

Faye, B. (1997). *Guide de l'élevage du dromadaire*: Sanofi.

Fenner, K., Caspar, G., Hyde, M., Henshall, C., Dhand, N., Probyn-Rapsey, F., Dashper, K., McLean, A., & McGreevy, P. (2019). It's all about the sex, or is it? Humans, horses and temperament. *PLoS One*, 14(5), e0216699.

Fernández Álvarez, J., León Jurado, J. M., Navas González, F. J., Iglesias Pastrana, C., & Delgado Bermejo, J. V. (2020). Optimization and Validation of a Linear Appraisal Scoring System for Milk Production-Linked Zoometric Traits in Murciano-Granadina Dairy Goats and Bucks. *Applied Sciences*, 10(16), 5502.

Field, A. (2009). *Discovering statistics using SPSS* (3rd edition): SAGE Books.

Field, A. (2013). *Discovering statistics using IBM SPSS statistics* (3rd edition): Sage.

Fleiss, J. L., & Cohen, J. (1973). The equivalence of weighted kappa and the intraclass correlation coefficient as measures of reliability. *Educational and psychological measurement*, 33(3), 613-619.

Gaudioso, V., Sanz-Ablanedo, E., Lomillos, J., Alonso, M., Javares-Morillo, L., & Rodríguez, P. (2014). "Photozoometer": A new photogrammetric system for obtaining morphometric measurements of elusive animals. *Livestock Science*, 165, 147-156.

George, D., & Mallery, M. (2003). Using SPSS for Windows step by step: a simple guide and reference.

George, D. (2011). *SPSS for windows step by step: A simple study guide and reference* (17.0 update). Pearson Education India.

Gómez, M., Gama, L., León, J., Fernández, J., Attalla, S., & Delgado, J. (2016). Genetic parameters for harmony and gaits in Hispano-Arabe horses estimated by Bayesian methods and restricted maximum likelihood. *Livestock Science*, 188, 159-165.

Gómez, M., Valera, M., Cervantes, I., Vinuesa, M., Peña, F., & Molina, A. (2006). Development of a linear type trait system for Spanish Purebred horses (preliminary analysis). Proceedings of the 57th Annual Meeting of the European Association for Animal Production, Antalya, Turkey.

Hassen, H., Rischkowsky, B., Termanini, A., Jessry, G., Haile, A., Baum, M., & Lababidi, S. (2016). Morphological and molecular genetic diversity of Syrian indigenous goat populations. *African Journal of Biotechnology*, 15(18), 745-758.

Holloway, L. (2005). Aesthetics, genetics, and evaluating animal bodies: locating and displacing cattle on show and in figures. *Environment and Planning D: Society and Space*, 23(6), 883-902.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S. and Delgado, J. V. (2020a). Zoometric characterization and body condition score in Canarian camel breed. *Archivos de zootecnia*, 69(265), 14-21.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S. and Delgado, J. V. (2020b). Biokinematics and applied thermography in the Canarian camel breed. *Archivos de zootecnia*, 69(265), 102-107.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Arando Arbulu, A., & Delgado Bermejo, J. V. (2021). The Youngest, the Heaviest and/or the Darkest? Selection Potentialities and Determinants of Leadership in Canarian Dromedary Camels. *Animals*, 11(10), 2886.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Barba Capote, C. J., & Delgado Bermejo, J. V. (2020a). Effect of research impact on emerging camel husbandry, welfare and social-related awareness. *Animals*, 10(5), 780.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Nogales Baena, S., & Delgado Bermejo, J. V. (2020b). Camel Genetic Resources Conservation through Tourism: A Key Sociocultural Approach of Camelback Leisure Riding. *Animals*, 10(9), 1703.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Camacho Vallejo, M. E., & Delgado Bermejo, J. V. (2022). Bayesian Linear Regression and Natural Logarithmic Correction for Digital Image-Based Extraction of Linear and Tridimensional Zoometrics in Dromedary Camels. *Mathematics*, 10(19), 3453.

Janssens, S., & Vandepitte, W. (2004). Genetic parameters for body measurements and linear type traits in Belgian Bleu du Maine, Suffolk and Texel sheep. *Small Ruminant Research*, 54(1-2), 13-24.

Janssens, S., Winandy, D., Tylleman, A., Delmotte, C., Van Moeseke, W., & Vandepitte, W. (2004). The linear assessment scheme for sheep in Belgium: breed averages and assessor quality. *Small Ruminant Research*, 51(1), 85-95.

Khan, M. A., & Khan, M. S. (2016). Genetic and phenotypic correlations between linear type traits and milk yield in Sahiwal cows. *Pakistan Journal of Agricultural Sciences*, 53(2).

Koenen, E., Aldridge, L., & Philipsson, J. (2004). An overview of breeding objectives for warmblood sport horses. *Livestock Production Science*, 88(1-2), 77-84.

Köhler-Rollefson, I. (2022). Camel biodiversity—and how to conserve it. *Animal Frontiers*, 12(4), 17-19.

Koo, T. K., & Li, M. Y. (2016). A guideline of selecting and reporting intraclass correlation coefficients for reliability research. *Journal of chiropractic medicine*, 15(2), 155-163.

Kugonza, D., Nabasirye, M., Mpairwe, D., Hanotte, O., & Okeyo, A. (2011). Productivity and morphology of Ankole cattle in three livestock production systems in Uganda. *Animal Genetic Resources/Resources génétiques animales/Recursos genéticos animales*, 48, 13-22.

MacKay, E., VanHoy, G., & Lakritz, J. (2022). Old World Camelids. *Medicine and Surgery of* Camelids, 621-643.

Melesse, A., Yemane, G., Tade, B., Dea, D., Kayamo, K., Abera, G., Mekasha, Y., Betsha, S., & Taye, M. (2022). Morphological characterization of indigenous goat population in Ethiopia using canonical discriminant analysis. *Small Ruminant Research*, 206, 106591.

Mingoas, K. J.-P., Awah-Ndukum, J., Dakyang, H., & Zoli, P. A. (2017). Effects of body conformation and udder morphology on milk yield of zebu cows in North region of Cameroon. *Veterinary world*, 10(8), 901.

Osborne, J. W., Costello, A. B., & Kellow, J. T. (2008). Exploratory factor analysis (EFA) is rightly described as both an art and a science, where researchers follow a series of ana-lytic steps involving judgments more reminiscent of qualitative inquiry, an interesting irony given the mathematical sophistication underlying EFA models'. *Best Practices in Quantitative Methods*, 86.

Pallant, J. (2020). *SPSS survival manual: A step by step guide to data analysis using IBM SPSS*: McGraw-hill education (UK).

Pares-Casanova, P.-M., Sinfreu, I., & Villalba, D. (2013). Application of varimax rotated principal component analysis in quantifying some zoometrical traits of a relict cow. *Korean Journal of Veterinary Research*, 53(1), 7-10.

Parkinson, J. (2011). What's a bigger draw than a camel fight? A camel beauty contest, of course. *Wall Street Journal*, 22.

Pesántez-Pacheco, J. L., Heras-Molina, A., Torres-Rovira, L., Sanz-Fernández, M. V., García-Contreras, C., Vázquez-Gómez, M., Feyjoo, P., Cáceres, E., Frías-Mateo, M., Hernández, F., Martínez-Ros, P., González-Martín, J.V., González-Bulnes, A., & Astiz, S. (2019). Maternal metabolic demands caused by pregnancy and lactation: association with productivity and offspring phenotype in high-yielding dairy ewes. *Animals*, 9(6), 295.

Pigière, F., & Henrotay, D. (2012). Camels in the northern provinces of the Roman Empire. *Journal of Archaeological Science*, 39(5), 1531-1539.

Prion, S., & Haerling, K. A. (2014). Making sense of methods and measurement: Spearman-rho ranked-order correlation coefficient. *Clinical Simulation in Nursing*, 10(10), 535-536.

Proctor, H. S., & Carder, G. (2014). Can ear postures reliably measure the positive emotional state of cows? *Applied Animal Behaviour Science*, 161, 20-27.

Puig-Diví, A., Escalona-Marfil, C., Padullés-Riu, J. M., Busquets, A., Padullés-Chando, X., & Marcos-Ruiz, D. (2019). Validity and reliability of the Kinovea program in obtaining angles and distances using coordinates in 4 perspectives. *PloS one*, 14(6), e0216448.

Reddy, T., & Claridge, D. (1994). Using synthetic data to evaluate multiple regression and principal component analyses for statistical modeling of daily building energy consumption. *Energy and buildings*, 21(1), 35-44.

Sánchez-Guerrero, M., Molina, A., Gómez, M., Peña, F., & Valera, M. (2016). Relationship between morphology and performance: Signature of mass-selection in Pura Raza Español horse. *Livestock Science*, 185, 148-155.

Sharp, N. C. (2012). Animal athletes: a performance review. *Veterinary Record*, 171(4), 87-94.

Tandoh, G., & Gwaza, D. (2017). Sex dimorphism in the one hump-camel (Camelus dromedarius) from selected populations in Nigeria. *Journal of Applied Life Sciences International*, 15(3), 1-10.

Tavakol, M., & Dennick, R. (2011). Making sense of Cronbach's alpha. *International journal of medical education*, 2, 53.

Ucko, P. J., & Dimbleby, G. W. (2007). The *domestication and exploitation of plants and animals*: Transaction Publishers.

Vincent, S., Araku, J., Ayongu, F., Chia, S., Momoh, O., & Yakubu, A. (2014). Redundancy elimination from morpho-stuctures of Nigerian Uda rams using principal component analysis. *Journal of Animal Production Advancements*, 14, 520-526.

Vostrý, L., Čapková, Z., Andrejsová, L., Mach, K., & Majzlík, I. (2009). Linear type trait analysis in Coldblood breeds: Czech-Moravian Belgian horse and Silesian Noriker. *Slovak Journal of Animal Science*, 42(3), 99-106.

Walde, J. (2020). Principal Components Analysis (PCA). In *Advanced Statistics*: Universität Innsbruck (Austria).

Westling, L. (2014). The zoosemiotics of sheep herding with dogs. In *The semiotics of animal representations* (pp. 31-52): Brill.

Williamson, G., & Payne, W. J. A. (1978). *An introduction to animal husbandry in the tropics*: Longman.

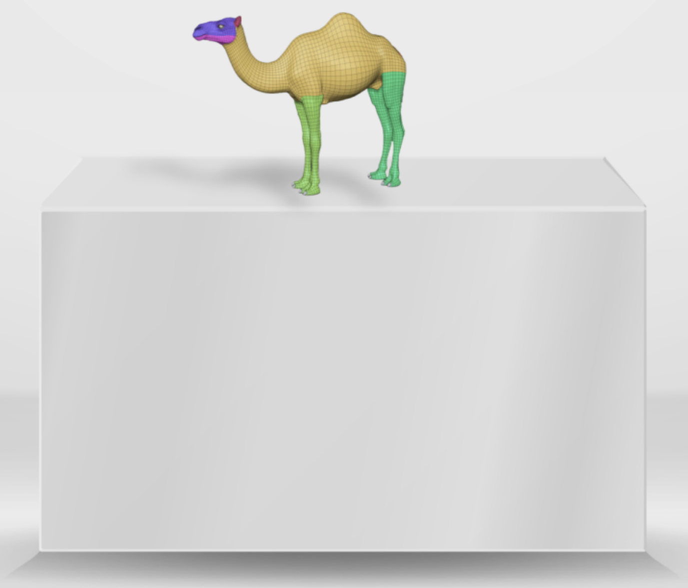
Yakubu, A., Ladokun, A., & Adua, M. (2011). Bioprediction of body weight from zoometrical traits of non-descript goats using linear and non-linear models in North Central Nigeria. *Livestock Research for Rural Development*, 23, 6.

Yilmaz, O., & Ertugrul, M. (2014). Camel wrestling culture in Turkey. *Türk Tarım ve Doğa Bilimleri Dergisi, 1(Özel Sayı-2)*, 1998-2005.

Zechner, P., Zohman, F., Sölkner, J., Bodo, I., Habe, F., Marti, E., & Brem, G. (2001). Morphological description of the Lipizzan horse population. *Livestock Production Science*, 69(2), 163-177.

CHAPTER 3

BIOMECHANICAL CHARACTERIZATION AND POST-EXERCISE EXAMINATION BY INFRARED THERMOGRAPHY OF 'CANARIAN CAMEL' BREED

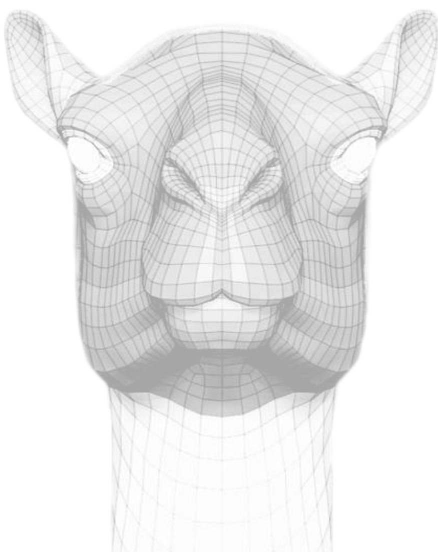


3.1 Determination of breeding criteria for gait proficiency in dromedary camels: a stepwise multivariate analysis of factors predicting overall biomechanical performance

Carlos Iglesias Pastrana[1], Francisco Javier Navas González[1], Elena Ciani[2], Carmen Marín Navas[1] and Juan Vicente Delgado Bermejo[1]

[1]Department of Genetics, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain

[2]Department of Biosciences, Biotechnologies and Environment, Faculty of Veterinary Sciences, University of Bari 'Aldo Moro', 70121 Bari, Italy



Quality indicator information provided on the publication
Latest information available (2022)

Status of the manuscript: Submitted

Journal (year, volume, page(s)): *Frontiers in Veterinary Science*

International database in which it is indexed: Journal of Citation Reports (JCR)

Thematic area in the reference database: Veterinary Sciences

Impact index of the journal in the year of the article's publication: 3.2

Rank/number of thematic area journals: 12/143 (D1)

Abstract

The previous literature on the biomechanics of camel gaits has not adequately addressed the performance and animal-dependent factors responsible for variability in animal locomotor performance with a high degree of accuracy. Consequently, there is a lack of specific breeding schemes based on empirical knowledge regarding the criteria to consider when selecting elite animals for this trait. To address this gap, we conducted curve fitting and discriminant canonical analysis. These analyses aimed to identify the mathematical function that best captures the dynamics of camel locomotion and to uncover which kinematic, animal morphometric, physiological, and phaneroptic-related variables significantly impact gait proficiency in dromedary camels primarily engaged in riding activities. The cubic function emerged as the most suitable mathematical model to represent the locomotive behavior of camels. Various factors were found to play a pivotal role in athletic performance in dromedary camels. These include angular measurements at the distal fore and rear extremity areas, pelvis inclination, relative volume of the hump, impact forces of the front limbs, post-neutering effects, as well as the kinematic behavior of the scapula, shoulder, carpus, hip, and foot. The outcomes of our functional data analysis can provide valuable insights for making informed breeding decisions aimed at enhancing customer satisfaction in camel riding activities. Furthermore, these findings can open avenues for exploring alternative applications, such as camel-assisted therapy. By leveraging this knowledge, we can work towards optimizing tasks that contribute to the functional enhancement of camels, thereby supporting their sustainable conservation.

Keywords

Gait performance, quantitative genetics, curve estimation regression models, discriminant analysis, breeding criteria, dromedary camel

Introduction

Although dromedary camels (*Camelus dromedarius*) were present in the Iberian peninsula since the Roman period (Moreno-Garcia et al., 2007), the Canarian archipelago is the only Spanish national territory in whose history, culture and ecology these animals have been strongly rooted for more than 600 years (Fernández de Sierra & Fabelo Marrero, 2017). The oldest records of the presence of dromedaries in the archipelago coincide with the historical chronicles relating to the process of European colonization of the eastern islands (Schulz, 2008). At the same time that they transported slaves and cattle from the African coasts, the feudal lords managed to introduce these animals to the islands. Due to its anatomical-physiological characteristics and its outstanding performance in fatigued draft works in the arid territories of the islands (Iglesias et al., 2020; Nelson, Bwala, & Nuhu, 2015), the camel has managed to perpetuate itself in them until present.

For centuries, the possession of a camel among local farmers was considered a symbol of status and social prosperity as well as a reinforcement of the family livelihood. Unfortunately, the mechanization of agriculture from the last third of the 20th century led to the progressive substitution of camels in rural labors and the migration of entrepreneurs to the tourism sector. Thus, the initiation of the activity of the National Paradors in the late 1950s and the emergence of tourism as an economic activity in the archipelago, contributed to the regression of the camel census in rural areas and their functional reorientation. That is, the main productive niche of the camel in the Canary Islands has since become tourist leisure, in which both animal behavior and physical conformation/performance has a notable impact (Iglesias Pastrana et al., 2020).

Considering the census of active breeders, the risk status assigned to the breed was endangered, a condition still in force today (Order AAA/251/2012; Spanish Ministry of Agriculture, Food and Environment). The lack of knowledge about the productive potentials and the under-utilization of local animal genetic resources in risk of extinction, places them in a scenario of special vulnerability. In this context, the investigation of the current and future potential that these resources have to ensure the sustenance of the human beings and the balance of the local environment, will help to promote existing productive niches as well as to define new ones.

The observable traits expressed by an organism are mainly governed by the inter-locus interaction (epistasis) of alleles for multiple single genes (Mackay, 2014). At livestock scenarios, the magnitude and impact of such complex genetic interactions are driven to a great extent both by historical and current uses of animal species, and the design and purposes of breeding programs. Indeed, epistatic genes are agreed to be a major feature in the genetic architecture of evolutionarily transcendent phenotypic variation (Caicedo et al., 2004). For the particular case of the relationships between physical attributes and gait performance in domestic animal species that are involved in moderately energy-demanding sport activities, scarce empirical information does exist. Being so, selective breeding schemes may be failing to reach genetic improvement but also interfering with the adaptive natural history of the animals (Fowler, 2011).

In the particular case of the Canarian camel, the present study pursues the biomechanical characterization of the breed by means of 2D video captures. Previous related research has performed basic analyses of biomechanics of camel gaits (Abdo et al., 2019; Dagg, 1974; Pfau, Parsons, & Wilson, 2006) and the elastic extension of tendons (Alexander et al., 1982), identified some environmental factors (e.g., sex and age) affecting the racing performance (Al-Shorepy, 2011), as well as studied the morphology of some parts of the distal skeleton (Abdo et al., 2019; Alsafy, El-Gendy, & Kamal, 2021; Badawy, 2011; El-Shafey & Kassab, 2013) and the pedal anatomy (Janis, Theodor, &

Boisvert, 2002). But no reference literature does report the exercise- and animal morphometrics and phaneroptic-related factors that are potentially responsible for oscillations in functional performance of camel locomotion to any degree of accuracy. Thus, the current research primarily aims to perform individual curve estimations through regression analysis to identify the model that best fits camel biomechanics. Afterwards, such curve fitting or functional data analysis approach will solve the need for stakeholders and breeders of identifying a model to describe the dynamics of camel locomotion, and detecting the location and magnitude of differences at gait performance within the evaluated function (Park et al., 2017).

As stated by Saastamoinen and Barrey (2000), the locomotor performance is the overall result of the combination of conformational, physiological and behavioral heritable traits. Indeed, the selection supported on these characters could overcome the generally low heritability of performance traits (Sánchez et al., 2013). Hence, the results obtained will aid at refining animal selection strategies and improving customer satisfaction for the main current functionality of this camel breed (leisure riding), but also the exploration of different alternatives in which to venture (i.e., assisted therapy) and with which reinforce the tasks of functional valorization for its sustainable conservation. The methodology proposed is expected to be translatable in a comparative manner to other camel populations involved in athletic activities.

Material and methods

Animal sample and data purge

A total of 130 Canarian dromedaries (72 males and 58 females; aged between 18 months and 35 years old), were included in this study. Gait evaluation was performed on all the animals but data collection and extraction was only feasible in those animals whom, first were able to develop any of the three specific gaits performed by dromedaries and described in literature, namely, walk, pace and gallop; second, from which two complete stride cycles could be collected and extracted. Animals who did not fulfill the aforementioned requirements were discarded from the database for further analysis. All animals were deemed healthy after clinical examination by a trained practitioner. No signs of pain or thoracolumbar vertebral alterations were observed.

As a result of this purging process, the number of animals producing data to be considered in statistical evaluations was as follows: 82 animals for walk, 97 for pace and 10 for gallop, respectively. There were some animals (n=60) which could be evaluated for more than one type of gait. The reduced number of animals which engaged into a galloping patterns may be ascribed to the fact that, as described in literature (Alexander, 1991; Janis et al., 2002; Maloiy, Rugangazi, & Rowe, 2009), these animals are inner energetic savers, hence rarely engage in faster patterns of movements except for very concrete situations in which their life may be compromised or threatened, or if trained to do it so as for instance it happens in trained, racing dromedaries.

Biometric variables and force mathematical determination

The development of gaits has not only been reported to considerably depend on the biometry of dromedaries but also on the relative forces that the animals are able to develop. For these reasons, the following variables were considered in the present study.

First, live weight was calculated using the formula by Boujenane (2019). Afterwards, pull force (maximum and minimum), load force (maximum and minimum), and maximum and minimum power were calculated following the methods described in Delgado et al. (2014).

Smoothened movement parameters are adjusted to trigonometric functions based on specific anatomical regions in both the forelimbs and hind limbs. Given the implication of angles shared between joints, eight angles were considered: angle 1 = cranial angle of the scapula-midway between acromion and head of humerus, angle 2 = midway between acromion and head of humerus-olecranon, angle 3 = olecranon-carpus, angle 4 = carpus-fetlock (metacarpophalangeal joint) on the forelimb, angle 5 = iliac crest-greater trochanter of the femur, angle 6 = greater trochanter of the femur-stifle (knee) joint, angle 7 = knee joint-tarsus, and angle 8 = tarsus-fetlock (metatarsophalangeal joint) on the hind limb, respectively.

The calculation of hump volume ($HV=0.07\ L \times B \times H$), hump weight ($HW= 0.45\ H - 13.8$), the ratio HW/HV (fat density), the proportion HV/BW, and the proportion HW/BW was performed using the methods described in Bengoumi et al. (2005). Additional indexes reported to condition the quality of movement and kinetics were also calculated, i.e., chest index, cefalic index, pelvic index, dactilothoracic index, weight in cannon index, conformation index, chest height index and compactness index upon the methods described in Susana Lopes et al. (2023).

Biokinematics variable’s units of measurement were set using Dunbar et al. (2008) as a reference.

Experimental setup and video recording

The image collection occurred on a level and solid open ground. Specific lighting conditions were selected to ensure that the animal was not situated in shadowed areas or under lighting that could distort the image capture. Additionally, the color of the animal was taken into account to prevent any potential distortion or misalignment caused by the background color.

To maintain consistency, the camera was positioned at a standardized height of 1 meter on a camera stand. This setup was situated 4 meters away from the center of balance of the camel. This configuration allowed for capturing the entire animal within the frame during the evaluation. To ensure proper alignment, we followed the guidelines presented in Iglesias et al. (2020), which involved marking standard lines on the ground before taking photographs to confirm the animal's correct positioning.

The image capture process utilized a digital camera (Sony DSC-RX100 SENSOR CMOS Exmor 1.0, 20.1 MP, F1.8–4.9, Zoom 20–100, Optical Zoom 3.6×, 3″ LCD Screen with Image Stabilizer; Sony Electronics, San Diego, CA, USA) in its standard mode. Cameras are strategically positioned to capture the observations without interfering with the animal's movement along the evaluation track. Dromedaries were recorded from two different views (side view and front view). The images were saved using the Joint Photographic Experts Group (JPEG) compression format.

Before recording, body length and height were measured, and masking tape squares (5 cm × 5 cm) were affixed to the dromedaries' bodies to serve as joint tracers reference points for data analysis. These markers were placed on the following left-side anatomical landmarks of the dromedaries: cranial angle of the scapula, midway between acromium and head of humerus, olecranon, carpus and fetlock (metacarpophalangeal joint) on the fore limb; the iliac crest, greater trochanter of femur, stifle (knee) joint, point of the hock (tarsus) and fetlock (metatarsophalangeal joint) on the hind limb, as shown in Figure 1. A trained operator visualized all video sequences and placed video tracers from video analysis software Kinovea software (Kinovea version 0.9.5; Kinovea Org., France). The same operator performed the potential replacement of joint tracers along the video sequences, when disagreement between real course and the course of the point of the software occurred.

A wooden pole (100 cm) was positioned parallel to the gait plane to provide a horizontal reference and calibration. The camera, mounted on a tripod, was adjusted to minimize parallax and ensure level alignment. Video footage was collected while the dromedaries engaged in their regular exercise routines, encompassing walking, pacing, and galloping.

Qualitative and quantitative stride-based gait analysis

The recording duration corresponds to the time taken by the animal to complete the circuit for each of the three gaits examined (walk, pace, and galloping) as shown in Figure 2. Two complete stride cycles were considered per animal. Stride-based gait

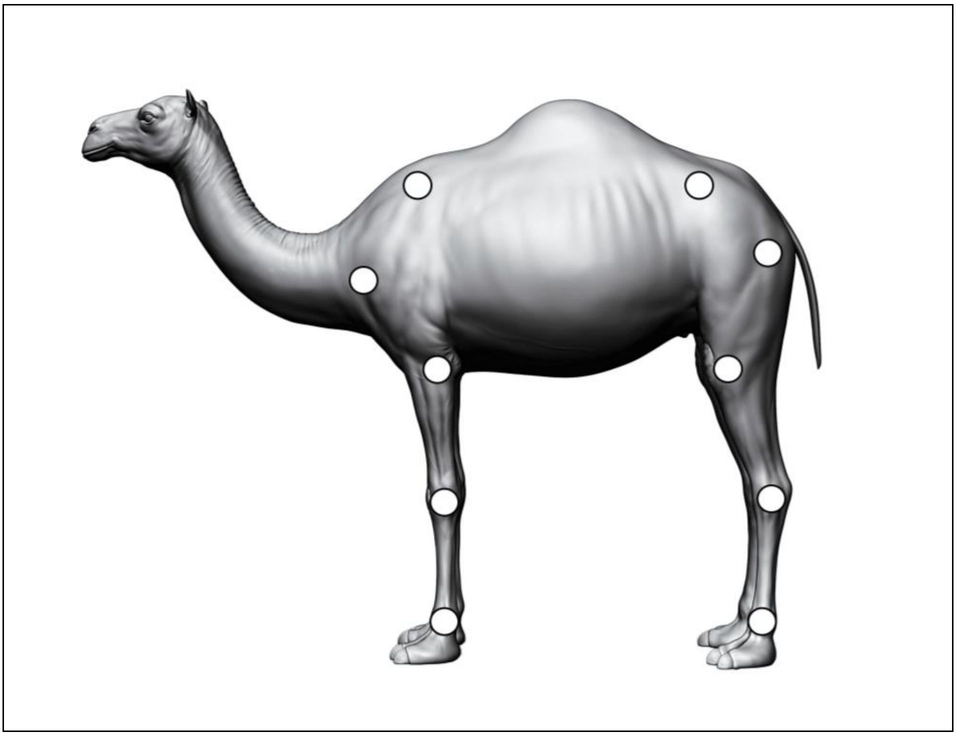


Figure 1. Graphical illustration of the anatomical disposition of masking tape squares (5 cm × 5 cm) at the dromedaries' bodies to serve as joint tracers reference points for gait analysis.

analysis generally considers the contact of the trailing hindfoot as the starting point of the stride cycle (Hildebrand, 1977). In the relative limb phase, the fraction of a stride in which the left forefoot, right hind, and right forefoot touchdown following the left hindfoot touchdown was calculated. It was calculated by counting the frames of the filmed motion sequences based on the method of Hildebrand (1980).

The individual locomotion process is assessed using a qualitative linear scale (1 to 5 points) described in Navas González et al. (2018). Gaits characterized by a lack of uniformity, which may be indicative of an absence of balance, cadence, or harmony, and poor limb development were attributed a score of 1. In contrast, animals receiving a score of 5 were observed to exhibit a harmonious, rhythmic, and seamlessly coordinated gait, with their bodily movements demonstrating a high degree of synchronicity.

Kinovea software (Kinovea version 0.9.5; Kinovea Org., France) was used to analyses video sequences and kinematic data extraction. With Kinovea images are calibrated using coordinate scales from the pictures, and the collected data undergoes leveling through three smoothing methods. Eleven kinematic variables were considered to characterize each of the gaits performed by the camels as a default. Biomechanics

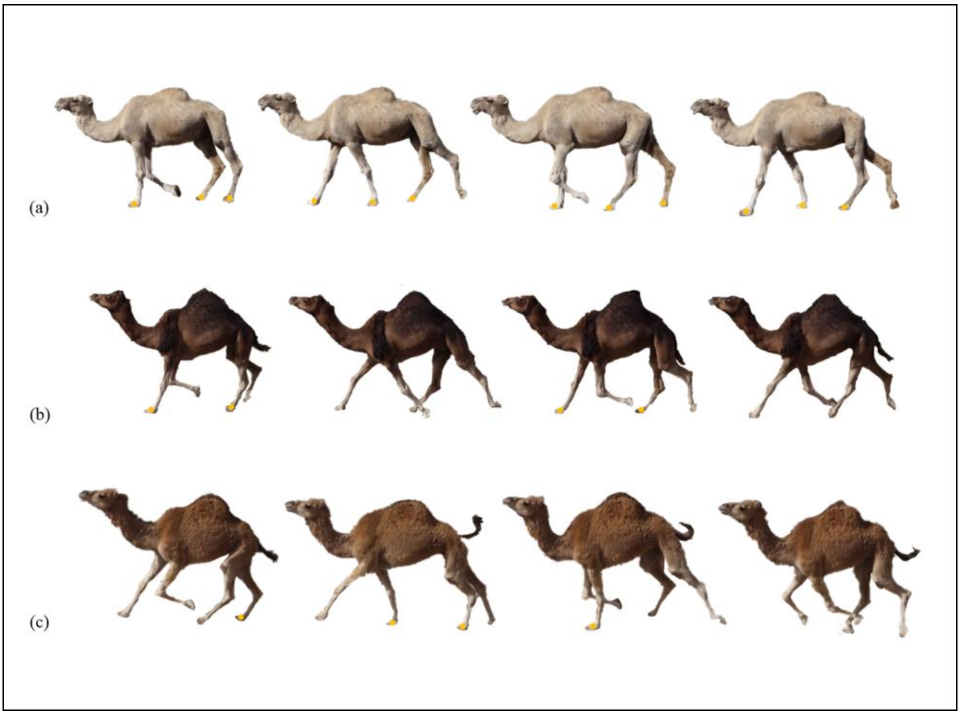


Figure 2. Graphical representation of the gait cycle during the walk (a), pace (b), and gallop (c) in dromedary camels. Yellow dots remarks which limbs are on the ground at each phase of the dromedary gait cycle.

parameters were as follows: acceleration, horizontal acceleration/position/velocity, total distance, total horizontal/vertical displacement, velocity, and vertical acceleration/position/velocity. An experienced researcher digitized anatomical landmarks to define body segments, including the lower lip, ear, withers (third thoracic vertebra), and tail base (dock). Segments' axes, such as the head, neck, and trunk, were established using these landmarks. Quantitative analysis was performed on trials where the head, neck, and trunk remained aligned in the sagittal plane. Various linear and angular variables related to head movement, including displacement and velocity, were calculated using specialized software tools.

Definition of cubic regression equations and coefficients

Individual curve estimation regression analysis to identify the model that best describes camel biomechanics parameters (acceleration, horizontal acceleration/position/velocity, total distance, total horizontal/vertical displacement, velocity, and vertical acceleration/position/velocity) was performed using the Curve Estimation routine of the Regression package of SPSS Statistics for Windows, Version

25.0, IBM Corp. (2017). The Curve Estimation routine in SPSS software produces curve estimation regression statistics and related plots for 11 different curve estimation regression models: linear, quadratic, compound, growth, logarithmic, cubic, S, exponential, inverse, power, and logistic, respectively. A generalized minimum adjusted R^2 value of over 0.7 was required in order for the model to be determined valid to capture data variability. The mathematical model that best fitted (comparatively superior average values of individual R^2;>0.7) the dynamics of locomotion of study animals was the cubic model. In these regards, parameter β0, β1, β2 and β3 of the curve for the variables of acceleration, horizontal acceleration/position/velocity, total distance, total horizontal/vertical displacement, velocity, and vertical acceleration/position/velocity, respectively per each of the limbs were considered as dependent variables in discriminant analysis.

In a cubic regression model, the equation takes the form:

$$y = \beta 0 + \beta 1x + \beta 2x^2 + \beta 3x^3 + \epsilon$$

where:

β0: This is the intercept term and represents the predicted value of y when x is 0. However, the interpretation of this term might not be as straightforward in some cases, depending on the range of your data and the context of your problem.

β1: This coefficient represents the change in the predicted y for a one-unit change in the linear term x. It captures the linear relationship between x and y, just like in a simple linear regression model.

β2: This coefficient represents the effect of the squared x on the predicted y. It indicates whether there is a curvature in the relationship between x and y. A positive β2 suggests an upward curvature, while a negative β2 suggests a downward curvature.

β3: This coefficient represents the effect of the cubed x on the predicted y. It introduces another level of curvature to the relationship between x and y. A positive β3 suggests that the curvature continues to be upward, while a negative β3 suggests a downward curvature.

Statistical analysis

Following the methodology on González Ariza et al. (2022), a discriminant canonical analysis was first used to develop a tool that evaluates the best possible linear combinations of Cubic regression unstandardized coefficients (β1, β2, and β3) within and between population clustering patterns each of the five levels in the linear appraisal of gaits as independent variables.

Dependent variables comprised biomechanics-related and biometrics variables, force and cubic regression coefficients, as aforedescribed. Additionally, sex, coat colour, coat particularities, eye colour, neutering status, owner and training regime (actively or not actively involved in desensitization protocols) were also considered in the analysis given their potential influence on gait quality development.

The Chi-squared automatic interaction detection (CHAID) decision tree method was used for classification, prediction, interpretation, and manipulation of the observation for the aforementioned dependent variables discretely categorized into the qualitative evaluation levels of gaits considered as the independent variables of this analysis.

To assess the reliability of the CHAID decision tree, cross-validation is conducted to measure the predictive performance when applied to new data samples compared to the training sample. This assessment helps determine how well the model generalizes to unseen data. Ten-fold cross-validation is utilized to validate the CHAID decision tree and evaluate whether the selected predictors effectively explain differences across the five qualitative evaluation levels of gaits.

Results

Discriminant canonical analysis model reliability

After 325 rounds of multicollinearity analyses, the variables retained in the discriminant canonical analyses are those presented in Table 1.

As unbalanced samples were used, and considerable number of variables was used the approximation of Rao for Wilks' Lambda test overcomes the robustness of other tests such as Pillai's trace test statistic in the case of heterogeneous variance. Wilks' Lambda statistic was highly statistically significant when Gait qualitative scale levels (Wilks' Lambda statistic: 0.001; F (Observed value): 4.202; F (Critical value): 3.258; df1: 736; df2: 7; P=0.025) was considered clustering criteria. Hence, the validity of the discriminant canonical analysis is ensured.

Five out of the thirteen functions revealed after the discriminant analysis were reported to be significant for their discriminant ability (Table 2). The discriminatory power of the F1 function was the highest in comparison to that reported for the rest of functions (eigenvalue of 6568.067, respectively; Figure 3) significantly explaining 89.72% of the variance. This framework makes F1 to F4 significantly explain 100% of the variability.

Canonical coefficients and loading interpretation

The different variables studied in this research were ranked according to their discriminating ability. A test of equality of group means of the dependent variables involved in the present discriminant canonical analysis was used as shown in Table 3. Standardized discriminant coefficients measure the relative weight of each dependent variable across the significant discriminant functions (Supplementary Table S1).

Table 1. Summary of the value of tolerance and VIF after multicollinearity analysis of biomechanical performance traits in Canarian camel breed.

Statistic	Tolerance (1-R^2)	VIF (1/Tolerance)
Angle 4	0.607	1.646
Proportion HV/BW	0.538	1.859
B3-Scapula Horizontal Acceleration	0.517	1.934
Angle 7	0.516	1.939
Angle 5	0.511	1.958
Chest height index	0.469	2.131
Weight in cannon index	0.447	2.238
B1-Iliac crest Horizontal Acceleration	0.443	2.255
B2-Fore fetlock Vertical acceleration	0.432	2.315
B2-Scapula Horizontal Velocity	0.425	2.353
B1-Hind fetlock Vertical velocity	0.424	2.361
B2-Carpus Total vertical displacement	0.393	2.547
B1-Knee Vertical acceleration	0.391	2.557
B3-Shoulder Acceleration	0.367	2.727
B2-Hip Horizontal Velocity	0.355	2.820
B2-Elbow Acceleration	0.354	2.824
Neutered-No	0.344	2.908
B2-Shoulder Horizontal Position	0.342	2.927
B2-Scapula Horizontal Position	0.337	2.964
B2-Iliac crest Horizontal Velocity	0.321	3.117
B2-Scapula Total vertical displacement	0.317	3.154
B1-Hip Horizontal Position	0.316	3.166
B2-Shoulder Vertical velocity	0.315	3.177
B2-Iliac crest Horizontal Position	0.308	3.243
B1-Knee Total vertical displacement	0.295	3.388
B2-Shoulder Horizontal Velocity	0.292	3.429
B2-Fore fetlock Acceleration	0.291	3.442
B3-Hip Vertical velocity	0.286	3.497
Body ratio	0.285	3.514
B2-Hip Total vertical displacement	0.275	3.641
B1-Hip Horizontal Acceleration	0.273	3.666
B1-Carpus Vertical velocity	0.260	3.844
B2-Iliac crest Total vertical displacement	0.257	3.897
B2-Hip Vertical acceleration	0.255	3.925
B3-Knee Vertical velocity	0.254	3.941
B2-Hind fetlock Vertical acceleration	0.250	3.995
B1-Elbow Vertical acceleration	0.249	4.021
B1-Elbow Vertical velocity	0.247	4.050
B3-Iliac crest Vertical velocity	0.240	4.166
B2-Elbow Horizontal Velocity	0.238	4.208
B2-Knee Acceleration	0.234	4.276
B1-Scapula Vertical acceleration	0.231	4.321
B1-Hind fetlock Total vertical displacement	0.217	4.606
B2-Tarsus Horizontal Velocity	0.212	4.713

Interpretation thumb rule: VIF ≥ 5 (highly correlated); 1 < VIF < 5 (moderately correlated); VIF = 1 (not correlated).

Table 2. Canonical discriminant analysis efficiency parameters to determine the significance of each canonical discriminant function.

Test functions	Canonical Correlation	Eigenvalue	Variance discrimination(%)	Bartlett's statistic	P-value
1 through 13	1.000	6568.067	89.720	2281.745	0.001
2 through 13	0.999	525.554	7.179	1459.868	0.001
3 through 13	0.997	153.996	2.104	873.964	0.001
4 through 13	0.993	72.981	0.997	402.406	0.001
5 through 13	0.000	0.000	0.000	0.000	0.001
6 through 13	0.000	0.000	0.000	0.000	1.000
7 through 13	0.000	0.000	0.000	0.000	1.000
8 through 13	0.000	0.000	0.000	0.000	1.000
9 through 13	0.000	0.000	0.000	0.000	1.000
10 through 13	0.000	0.000	0.000	0.000	1.000
11 through 13	0.000	0.000	0.000	0.000	1.000
12 through 13	0.000	0.000	0.000	0.000	1.000
13	0.000	0.000	0.000	0.000	1.000

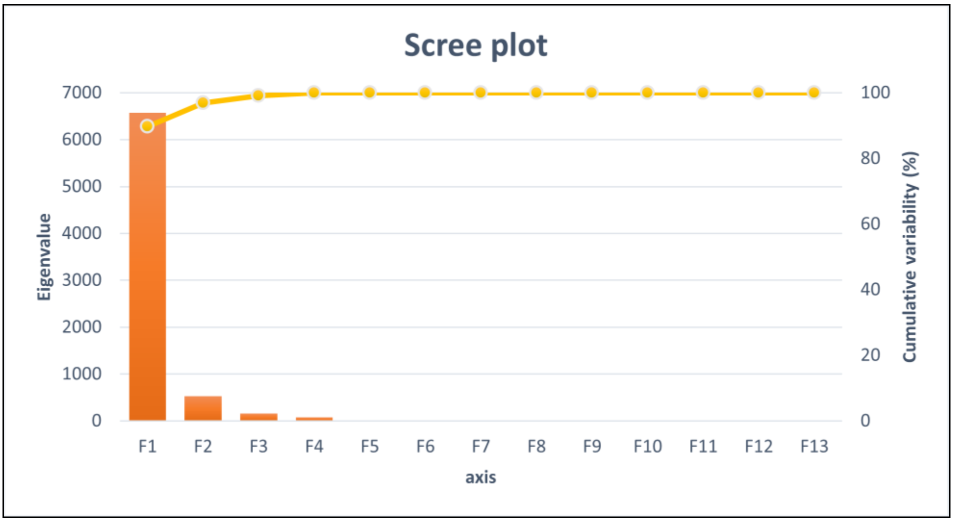


Figure 3. Canonical variable functions and their percentages of self-explained and cumulative variance.

A Press' Q value of 17.19 (n = 189; n' = 15; K = 5) was computed for qualitative gait evaluation levels. Thus, predictions can be considered to be better than chance at 95% (Chan, 2005).

Centroids from different levels for qualitative description of gait performance considered in this study are calculated. The relative position of each centroid is determined by substituting the mean value for the observations depicted in each of the

Table 3. Results for the tests of equality of group means to test for difference in the means across sample groups once redundant variables have been removed.

Variable	Wilk's Lambda	F	P-value	Rank
B1-Elbow Vertical velocity	0.769	13.822	<0.0001	1
B2-Iliac crest Horizontal Velocity	0.825	9.752	<0.0001	2
Neutered-No	0.845	8.411	<0.0001	3
B2-Shoulder Horizontal Velocity	0.864	7.244	<0.0001	4
Proportion HV/BW	0.867	7.080	<0.0001	5
B2-Hind fetlock Vertical acceleration	0.873	6.672	<0.0001	6
Weight in cannon index	0.882	6.154	0.000	7
B2-Carpus Total vertical displacement	0.891	5.635	0.000	8
B1-Knee Total vertical displacement	0.903	4.954	0.001	9
B1-Carpus Vertical velocity	0.910	4.566	0.002	10
B3-Shoulder Acceleration	0.911	4.504	0.002	11
B1-Hind fetlock Total vertical displacement	0.913	4.410	0.002	12
B1-Hip Horizontal Acceleration	0.917	4.172	0.003	13
B3-Knee Vertical velocity	0.918	4.107	0.003	14
B2-Scapula Total vertical displacement	0.923	3.855	0.005	15
B2-Elbow Horizontal Velocity	0.924	3.786	0.006	16
Body ratio	0.934	3.255	0.013	17
B2-Tarsus Horizontal Velocity	0.935	3.201	0.014	18
B3-Hip Vertical velocity	0.937	3.083	0.017	19
Angle 5	0.943	2.771	0.029	20
B1-Iliac crest Horizontal Acceleration	0.943	2.756	0.029	21
Angle 7	0.945	2.692	0.033	22
B2-Scapula Horizontal Velocity	0.946	2.613	0.037	23
B2-Hip Horizontal Velocity	0.947	2.552	0.041	24
B2-Hip Total vertical displacement	0.950	2.446	0.048	25
B3-Scapula Horizontal Acceleration	0.950	2.437	0.049	26
Angle 4	0.952	2.325	0.058	
B2-Knee Acceleration	0.953	2.272	0.063	
B1-Hip Horizontal Position	0.954	2.235	0.067	
B2-Fore fetlock Acceleration	0.954	2.211	0.069	
B2-Hip Vertical acceleration	0.954	2.198	0.071	
B3-Iliac crest Vertical velocity	0.957	2.082	0.085	
B2-Iliac crest Horizontal Position	0.958	2.037	0.091	
B1-Hind fetlock Vertical velocity	0.965	1.683	0.156	
B2-Iliac crest Total vertical displacement	0.965	1.662	0.161	
B2-Elbow Acceleration	0.965	1.658	0.162	
B2-Shoulder Horizontal Position	0.970	1.437	0.223	
B1-Elbow Vertical acceleration	0.970	1.400	0.236	
Chest height index	0.971	1.378	0.243	
B2-Shoulder Vertical velocity	0.974	1.237	0.297	
B1-Knee Vertical acceleration	0.981	0.904	0.463	
B2-Scapula Horizontal Position	0.981	0.874	0.480	
B1-Scapula Vertical acceleration	0.983	0.781	0.539	
B2-Fore fetlock Vertical acceleration	0.993	0.314	0.869	

df1=4;df2=184

five discriminant functions significantly detected (F1 to F5). Results for the functions at the centroids are reported in Table 4.

Table 4. Functions at the centroids for the thirteen discriminant functions detected in this study.

Function/Gait qualitative evaluation level	1	2	3	4	5
F1	-476.738	-52.340	40.573	-54.118	134.521
F2	108.758	-29.110	4.553	-11.968	62.230
F3	22.288	10.686	6.627	-17.247	-25.252
F4	1.326	-16.244	3.854	3.913	-23.801
F5	0.000	0.000	0.000	0.000	0.000
F6	0.000	0.000	0.000	0.000	0.000
F7	0.000	0.000	0.000	0.000	0.000
F8	0.000	0.000	0.000	0.000	0.000
F9	0.000	0.000	0.000	0.000	0.000
F10	0.000	0.000	0.000	0.000	0.000
F11	0.000	0.000	0.000	0.000	0.000
F12	0.000	0.000	0.000	0.000	0.000
F13	0.000	0.000	0.000	0.000	0.000

Data mining CHAID decision tree

CHAID decision tree is presented in Supplementary Figure 1.

Discussion

Following the premises of Maloiy et al. (2009), who stated that locomotory performance is essentially modulated by heritable characters, in lesser proportion by training, for both camels and equines, the present study has investigated which biomechanical and animal morphometric, physiology and phaneroptic related variables influence gait performance in dromedary camels primarily relegated to riding activities. As a preliminary requirement to effectively study these potential associations, it was identified the mathematical function that had the best fit to a series of data points obtained from the analysis of different gaits (walk, pace and galloping) in the studied dromedary camels. The mathematical model that best fitted (comparatively superior average values of individual R^2; ≥0.7) the dynamics of camel locomotion was the cubic function, whose end behavior at the graphs is determined by the sign of their leading coefficients. These results are in accordance with previous researches aimed at the mathematical and physical modelling of animal-like locomotion throughout the use of bioinspired robots (Bayraktaroglu et al., 2000; Ramananarivo, Godoy-Diana, & Thiria, 2011; Tang et al., 2010; Zheng et al., 2010), rigid body models (Van Den Bogert, Schamhardt, & Crowe, 1989) and video analysis (Kinugasa & Usami, 2016).

The posterior examination of the statistical relationships between the coefficients of the individual curves of movement and other animal attributes and traits with gait performance, made possible the identification of those variables that most largely influence this functional character. On the one hand, the kinematic parameters 'vertical velocity', 'total vertical displacement', 'horizontal velocity', 'vertical acceleration', 'acceleration', 'horizontal position', and 'horizontal acceleration', appeared to exert a significant effect on the good performance of camel's gaits. In addition to the benefits of good speed and acceleration for covering a specific distance in the shortest time possible (Barrey, 2013; Clayton & van Weeren, 2001), the 'vertical displacement' and the 'horizontal position' of certain body regions during locomotion play a fundamental role in the physical performance of these animals. The vertical displacement determines both the shape and magnitude of the impulse created (vertical jump), and weightlifting performance (Suchomel, Nimphius, & Stone, 2016; Whitmer et al., 2015). In regards of the horizontal position, this variable could be an indirect reliable measure of joint rotation and skeletal impairments, thus an indicator of stabilization, alignment and muscular force of the different body areas implicated in locomotion (Hrysomallis, 2011; Laudner, Sipes, & Wilson, 2008). Therefore, overall athletic performance in dromedary camels may be the result of the sum of joint powers and other different sport performance characteristics such as velocity, acceleration, jumping, and change of direction.

Such performance characteristics are known to be intrinsically modulated by linear and angular morphometric measurements, as well as animal physiology, in several vertebrate species (Biewener & Patek, 2018; Hans et al., 2014; Herrel et al., 2012; Ibáñez & Tambussi, 2012; Jackson, Segre, & Dial, 2009; Kristjansson et al., 2016; Ojanguren & Brana, 2003; Stefánsdóttir et al., 2021; Toro et al., 2003; Voss et al., 2011). Specifically, based on our results, a superior performance in camel gait is likely to be affected by the angle between the carpus and the fetlock on the fore limb ('angle 4'), the angle between the iliac crest and the greater trochanter of femur ('angle 5'), the angle between the stifle joint and the tarsus ('angle 7'), the proportion hump volume/body weight ('HV/BW'), the weight in cannon index, the chest height index, the body ratio, and the neutering status of the animals.

Similarly to other quadrupedal animals that are bred for sport activities such as horses and dogs, the skeletal structure and deviations of the vertical line of carpus/tarsus joint, either medially or laterally, cranially or caudally, would significantly predispose the camel to carpus/tarsus lameness and splints, thus negatively affect the gait score (Gillette & Angle, 2014; Mostafa & Elemmawy, 2020; Senna et al., 2015). Additionally, several authors confirmed the prominent role of fore and hind fetlock joint angles, stifle and hock joint angle, and pelvis inclination on weight absorption, energy of propulsion and storage of elastic strain in riding horses (Cano et al., 2001; Clayton et al., 2002; Hobbs & Clayton, 2022; Holmström, Fredricson, & Drevemo, 1994). Closely related to pelvis inclination, camels are known to be the only animal species that bend the thigh when moving (Villalobos, 2019). Besides, chest development ('chest height index') and tallness ('body ratio'), are reported to affect the static/dynamic balance and physical resistance in sport horses (Cervantes et al., 2009; do Pantanal et al., 2008; Sánchez et al., 2013; Signer-Hasler et al., 2012) and athletes (Granacher et al., 2013).

Furthermore, if the hump of a camel is mechanically compared to the size and position of a rider on a horse, it could be inferred that the relative weight and dimensions of the hump (relation HV/BW) have a significant effect on camel locomotion given its influence on body balance, force distribution and location of center of gravity, analogously to the effects that the rider-horse-saddle aggregation has on equine gait (Dyson et al., 2020). Moreover, the weight in cannon index is expected to have a prominent effect on camel locomotion as the study of the evolutionary history of these animal species has recently revealed. Through the analysis of the vertical ground reaction force with body mass in camelid species, Clemente et al. (2020) found that camels have large foot contact areas due to broad fat pads. This condition would be reducing loading rate and therefore peak locomotor foot pressures and musculoskeletal stresses along the limbs, and controlling for the disproportionalities at such forces as animals increase in body mass or move faster. These authors also encountered that dromedary camels load their forelimbs more than their hindlimbs, revealing the higher peak forces in forelimbs and thus their major functional relevance in this animal species locomotion. Hence, this adaptive trait may be correlated with the afore discussed prominent role of the alignment of the distal part of the fore limbs and the fore fetlock joint angle on the weight absorption and minimization of mechanic impact during camel locomotion.

In the last place, the correlation between physiology and function was revealed by the significant impact of neutering status of the camels in gait performance. In fact, different reports have discussed the advantages of castration in dromedary camels. Some authors highlight the larger effect of castration on body development in this species if carried out after the animals has reached sexual maturity (Faye, 1997; Payne & Wilson, 1999). Concretely, gelded camels are larger, more robust and more enduring (Pigière & Henrotay, 2012; Ucko & Dimbleby, 2007). In addition, Iglesias Pastrana et al. (2021) remarked an increased effect of neutering on camel organic development and behaviour if the animals are castrated not only when have reached their sexual maturity but have also been initiated in the training protocol for their functionality (e.g., leisure riding). Hence, apart from to the benefit in body growth and endurance, castration also has effects on camel behaviour, which ultimately constitutes a further criterion of notable interest for functional selection in working animals.

However, other morphometric, phaneroptic and performance-type variables such as the angle between the cranial side of the scapula and the shoulder joint ('angle 1'), the angle between the shoulder joint and the olecranon ('angle 2'), the angle between the olecranon and the carpus ('angle 3'), the angle between the greater trochanter of femur and the stifle joint ('angle 6'), the angle between the point of the hock (tarsus) and fetlock (metatarsophalangeal joint) on the hind limb ('angle 8'), body weight, hump volume, hump weight, density of fat, proportion hump weight/body weight, chest index, cefalic index, pelvic index, dactilothoracic index, conformation index, compactness index, pull force, load force, power, sex, age, coat colour and particularities, eye colour, owner, training regime, and type of gait, did not have a significant discriminatory effect on camel gait performance.

First, the aforementioned singular function of fore fetlock joint angles, stifle and hock joint angle, and pelvis inclination on weight absorption, energy of propulsion and storage of elastic strain in riding animals, could be explaining the lack of large impact of the remaining angular measurements evaluated for its potential implication in camel locomotion in the present study. Concerning the effects of body weight, hump volume and weight, and the proportional relationship between different body regions in camel gait performance, the absence of significant affectation of this functional trait by the mentioned factors partially resembles the results of de Oliveira Bussiman et al. (2018) for Brazilian horses. But contrasts with the results reported by Pratt-Phillips and Munjizun (2023) and Gómez et al. (2016). These authors support the effects of body mass index and body composition profile, and harmony of physical development, on exercise performance of sport horses, respectively, probably due to a combined effect between inflammation-type responses and the impacts of excessive weight carriage on limb health. Then, the contrasting results obtained for camels can be ascribed to different species-specific adaptive traits.

Fatty tissue in camels is mostly concentrated on the hump to improve heat removal via the skin, and hump size is related to the general reserve status (body condition score) of the animals (Adah, Ayo, & Adah, 2023). For this reason, the hump volume in relation to the body weight, and nor the volume and weight of the hump neither the body weight considered separately, significantly influences the locomotion of these animals, especially due to their interrelationship for maintaining the static/dynamic balance of the body. In addition, in the case of hump weight, this variable greatly depends on the specific fatty acid composition (Sbihi, Nehdi, & Al-Resayes, 2013), so a heavy hump does not necessarily mean a large volume hump. Apart from that, body balance is strongly controlled by the aforementioned functionality of the broad foot pads, which are responsible for solving the differential impact of the animal's weight and the speed of movement on the locomotor pressures that affect the musculoskeletal system forces. Lastly, in the case of the variables that relate different measurements corresponding to the dimensions of the trunk and extremities, their non-significant influence could also be explained by purely evolutionary reasons. Camels are provided with relatively narrow body, long legs, no flank fold that difficult the movement of hindlimbs, less rounded abdomen to allow the hind limbs freer motion, and limbs more closely to the midline to minimize oscillation between strides, as a result of natural selection for energy efficiency of movement (Fowler, 2011; Pfau et al., 2011). In close relationship with this last statement, from a pure evolutionary physiology background, pull force, load force, and power may have had a non-significant effect on camel gait performance.

Within the same phylogenetic background, sex, age, coat colour and particularities, eye colour, owner, training regime, and type of gait did not influence in a significant manner the physical performance of camels. At the time of walking, camels move their ipsilateral limbs in unison ('pacing gait', as referred to in the literature). Tracing back camel evolutive history, pacing gait is agreed to have been developed about 20 million years ago (Francis, 2019). Apart from the fact that the legs of camels can't collide at this pacing gait, the stride length, speed and kinematics efficiency are higher when compared to other gaits such as regular trot. However, pacing gait made the animal more prone to lateral instability. This way, camels have developed a broad foot pad and a digitigrade stance to abate such relative lack of instability, among other several osteomuscular (Janis et al., 2002; Villalobos, 2019). Contrary to horses, camels are known to be the only ungulate species that always use this pattern of leg movements, independently of speed (Janis et al., 2002). What's more, this is a highly conserved ancestral trait (Webb, 1972). Hence, the underlying genetic basis of camel gaits, that is elementally implicated in the sort of neural impulses from the spine to the extremities (Andersson et al., 2012) and presumably free of epistatic interactions from genes that control coat and eye colour associated traits, may be extrapolated to the whole range of physical activities that camels are feasible to perform. This last hypothesis could be confirmed in future approaches aimed at studying which genomic variants are statistically associated with an enhanced or decreased physical performance.

Then, these statements are contrary to the results presented by Al-Shorepy (2011) for racing camels, Entin (2007) for racehorses and Greyhound dogs, Vicente et al. (2014) for classical riding horses, and Navas González et al. (2018) for assisted-therapy donkeys, who reported a significant effect of sex and age on animal functional performance. But agreed with Senefeld et al. (2021), who support that large differences in athletic performance do not exist between sexes in animals. Regarding the association between coat and eye colour with different psychological constructs that are transcendental for animal trainability and safe interaction with, the molecular basis of these desirable traits have been identified mainly for dogs and horses (Finn et al., 2016; Jacobs et al., 2016; Kukekova, Trut, & Acland, 2013; van Rooy & Wade, 2019), and some inferences are discussed by Iglesias Pastrana et al. (2021) for dromedary camels.

Further, a non-negligible impact of rider fitness and interaction with the animal (Williams & Tabor, 2017), training regime (Holt, 2006; Inkilä et al., 2022), and type of gait (Ripollés-Lobo et al., 2022) on exercise performance, are also recognized in the literature for sport horses and dogs. Such controversy could be definitively ascribed to methodological issues (e.g., type and number of potential influencing factors considered, and statistical treatment of data), as well as to animal species and breed-mediated effects.

In summary, rather than the morphology of a specific region of the body, which is correlated with the weight of the animal (Iglesias Pastrana et al., 2022), or factors such as sex, age and phaneroptic, which have been presented to affect athletic performance in some animal species, a reduced number of angular morphometric measurements, definite body proportions that can affect the general balance of the body, the weight supported by structures with notable involvement in the damping of the mechanical forces produced during locomotion, post-neutering effects, and the particular mobility of specific joints, are the factors that should be considered when selecting dromedary camels for gait proficiency. More specifically, based on the data mining decision tree, the variables that serve to discriminate with greater accuracy between camels for gait performance are the neutering status, with advantage for neutering, and the kinematic behaviour of the scapula, shoulder, carpus, hip, and foot, anatomical structures of singular importance for propulsion, movement direction and limb support in quadrupeds, as cited above.

With special emphasis on kinematics, the horizontal position of scapula, the total vertical displacement of carpus, the horizontal velocity of shoulder, and the horizontal acceleration of hip in neutered animals; and the horizontal and vertical acceleration of scapula, and the total vertical displacement of foot in non-neutered animals, are the specific discriminating parameters among good and poor performance camels. It can be also appreciated that coefficient 2 is more relevant in castrated animals, while coefficients 1 and 3 are more discriminative among non-castrated animals. Based on the graphic behavior of cubic function, coefficients 1 and 3 for curves of movement could be related to the direction and force of the movement, while coefficient 2 would be with the amplitude of the movement, suspension duration and speed (Xue et al., 2012). From a viewpoint of athletic performance, these results may be indicative of a better dressage/beauty and endurance riding performance for intact and castrated animals, respectively. Anyway, the selection of the animals should be complemented by the use of behavior evaluation tools. Indeed, the common practice of castration in the camel breed studied in the present research consists on the neutering of the animals once they are initiated in the domestication protocol for leisure riding activities and are sexually mature. It is pursued that animals have reached proper general organic maturity by the mediation of plasma androgens (mainly brain structures) but avoiding harmful levels of these hormones from an ethological perspective (Iglesias Pastrana et al., 2021; Oliveira, 2009).

In respect of the quantitative evaluation of kinematic parameters, a better performance at gait in camels is achieved when the horizontal position of the scapula is greater than 0, the total vertical displacement of the carpus greater than -3.78, the horizontal velocity of the shoulder less than or equal to 2.25, and the horizontal acceleration of the hip greater than 5.74, for neutered animals; and when the acceleration of the scapula is less than or equal to 0, as well as the total vertical displacement of the foot greater than -2.24, for non-neutered animals. Elementally, the total vertical displacement of the carpus, as an anatomical structure significantly involved in forelimbs mechanical support and cushioning, would act as a corrector of the horizontal position of the scapula as well as of the horizontal velocity of the shoulder, thus achieving greater general stability and harmony and energy efficiency of the movement (Weishaupt et al., 2010). In the case of the horizontal acceleration of the hip, the higher its value, the greater the propulsion force and amplitude of the movement. Contrastingly, for intact camels, a lower acceleration of the scapula and a greater vertical displacement of the distal region of the hindlimbs determine a more harmonious and efficient movement. These values, being interpreted on the account of the relative significance of coefficients 1 and 3 for this animal subgroup, would be reflecting the relevance of the rear quarters to maintain the dynamic balance of the body, while limiting as far as possible a wide acceleration at the anterior third, in animals presumably more apt for riding/dressage activities. These functionalities make rear quarters to be broad, deep and heavy to support load carriage while moving in an efficient way (Lynghaug, 2009).

Ultimately, concerning the exploration of new potential functional niches, the results of the present study can assist the tasks of camel valorization and selection for their active participation in animal-assisted interventions, since those biomechanical and physiological traits of the animals that most influence locomotor performance, regardless of the type of gait, are identified. On the contrary, for equines, since the cadence of movement can vary between gaits, it may be necessary to look at different and varied selection criteria depending on the type of gait involved in each of the assisted activities in which these animals would be involved. Furthermore, camels are less flighty than horses (Larsson & Brothers, 2019) and the pelvic movement of a person when riding a camel is reported to be very similar to natural human pelvic movement during walking (Ni, 2020), thus therapeutic applications of camelback riding apart from mere leisure are clearly plausible.

Conclusions

Individual curve estimation regression analysis play a pivotal role in synthesizing complex datasets by constructing validated mathematical descriptions of locomotive behavior in camels. The posterior study of the relationships between morphology, physiology, phaneroptic and gait performance related traits made possible the identification of those factors that largely influence gait proficiency in dromedary camels, thus the criteria that should assist breeding decisions on camels dedicated to different athletic activities. Angularity and mechanical forces at distal fore and rear extremity areas, inclination of the pelvis, specific proportionalities affecting general balance of the body, neutering-mediated effects, and the velocity, acceleration, position, and displacement of particular body regions significantly affect the overall athletic performance in dromedary camels. More specifically, the kinematic behavior of the scapula, shoulder, carpus, hip, and foot, as these anatomical structures primarily control the take-off of the rear limbs and the impact forces of the front limbs, has a prominent impact in locomotor performance in dromedary camels. Other animal and environment-dependent variables do not influence camel gait performance, probably due to the mixed effect of different species-specific adaptive, inherited in response to desert environment demands such as the pacing gait, broad foot pads and energy efficiency of movement.

Author contributions: Conceptualization, C.I.P., F.J.N.G. and J.V.D.B.; Data curation, C.I.P., F.J.N.G. and C.M.N.; Formal analysis, C.I.P., F.J.N.G. and J.V.D.B.; Funding acquisition, E.C. and J.V.D.B.; Investigation, C.I.P. and F.J.N.G.; Methodology, C.I.P., F.J.N.G. and C.M.N.; Project administration, E.C. and J.V.D.B.; Resources, E.C. and J.V.D.B.; Software, C.I.P., F.J.N.G. and C.M.N.; Supervision, F.J.N.G., E.C. and J.V.D.B.; Validation, C.I.P., F.J.N.G. and C.M.N.; Visualization, E.C.; Writing—original draft, C.I.P. and F.J.N.G.; Writing—review & editing, F.J.N.G., E.C. and J.V.D.B. All authors have read and agreed to the published version of the manuscript.

Funding: The present research was carried out in the financing framework of the international project CA.RA.VA.N—'Toward a Camel Transnational Value Chain' (Reference APCIN-2016-00011-00-00) and during the covering period of a predoctoral contract (FPU Fellowship) funded by the Spanish Ministry of Science and Innovation and was developed under the context a Ramón y Cajal Post-Doctoral fellowship financially supported by MCIN/AEI/10.13039/501100011033 and European Union "NextGenerationEU"/PRTR" (Recovery, Transformation and Resilience Plan—Funded by the European Union—NextGenerationEU).

Data availability statement: The data presented in this study are available on request from the first author.

Acknowledgments: The authors would also like to thank 'Aires Africanos' Eco-tourism Company, Oasis Park Fuerteventura, and 'Camelus' Camellos de Almería, for their direct technical help and assistance.

Conflicts of interest: The authors declare no conflict of interest.

Ethics declaration statement: All farms included in the study followed specific codes of good practices and therefore, the animals received humane care in compliance with the national guide for the care and use of laboratory and farm animals in research. Written consent from the owners was obtained for their participation. The study was conducted in accordance with the Declaration of Helsinki. The Spanish Ministry of Economy and Competitivity through the Royal Decree Law 53/2013 and its credited entity, the Ethics Committee of Animal Experimentation from the University of Córdoba, permitted the application of the protocols present in this study as cited in the 5th section of its 2nd article, as the animals assessed were used for credited zootechnical use. This national Decree follows the European Union Directive 2010/63/UE, from the 22 September of 2010.

References

Abdo, M., Haddad, S. S., Aziz, E. K., Abdeen, A., & Sabek, A. (2019). Kinematics Biomechanical Analysis and Three Dimensional Reconstruction Diagnostic Technique of Carpal Joint during gait in One-Humped Camel (*Camelus dromedarius*). *Alexandria Journal for Veterinary Sciences*, 60(2).

Adah, A. S., Ayo, J. O., & Adah, D. A. (2023). Unique Physiological and Behavioural Adaptive Features of The One-Humped Camel (*Camelus dromedarius*) to Arid Environments. *Journal of Applied Veterinary Sciences*, 8(1), 57-64.

Al-Shorepy, S. S. (2011). Identification of environmental factors affecting the racing performance of race camels in the United Arab Emirates. *Emirates Journal of Food and Agriculture*, 424-430.

Alexander, R. M. (1991). Energy-saving mechanisms in walking and running. *Journal of experimental biology*, 160(1), 55-69.

Alexander, R. M., Maloiy, G., Ker, R., Jayes, A., & Warui, C. (1982). The role of tendon elasticity in the locomotion of the camel (*Camelus dromedarius*). *Journal of Zoology*, 198(3), 293-313.

Alsafy, M. A., El-Gendy, S. A., & Kamal, B. (2021). Computed tomographic and radiographic morphology of the pastern and coffin joints of One-Humped Camel (*Camelus dromedarius*). *Anatomia, histologia, embryologia*, 50(1), 108-113.

Andersson, L. S., Larhammar, M., Memic, F., Wootz, H., Schwochow, D., Rubin, C.-J., Patra, K., Arnason, T., Wellbring, L., Hjälm, G., Imsland, F., Petersen, J.L., McCue, M.E., Mickelson, J.R., Cothran, G., Ahituv, N., Roepstorff, L., Mikko, S., Vallstedt, A., Lindgren, G., Andersson, L., & Kullander, K. (2012). Mutations in DMRT3 affect locomotion in horses and spinal circuit function in mice. *Nature*, 488(7413), 642-646.

Badawy, A. M. (2011). Computed Tomographic anatomy of the fore foot in one-humped camel (*Camelus dromedrus*). *Global veterinaria*, 6(4), 417-423.

Barrey, E. (2013). Biomechanics of locomotion in the athletic horse. *Equine Sports Medicine and Surgery-Basic and Clinical Sciences of the Equine Athlete*, 189-211.

Bayraktaroglu, Z. Y., Butel, F., Pasqui, V., & Blazevic, P. (2000). Snake-like locomotion: Integration of geometry and kineto-statics. *Advanced Robotics*, 14(6), 447-458.

Bengoumi, M., Faulconnier, Y., Tabarani, A., Sghiri, A., Faye, B., & Chilliard, Y. (2005). Effects of feeding level on body weight, hump size, lipid content and adipocyte volume in the dromedary camel. *Animal Research*, 54(5), 383-393.

Biewener, A., & Patek, S. (2018). *Animal locomotion*: Oxford University Press.

Boujenane, I. (2019). Comparison of body weight estimation equations for camels (*Camelus dromedarius*). *Tropical animal health and production*, 51, 1003-1007.

Caicedo, A. L., Stinchcombe, J. R., Olsen, K. M., Schmitt, J., & Purugganan, M. D. (2004). Epistatic interaction between Arabidopsis FRI and FLC flowering time genes generates a latitudinal cline in a life history trait. *Proceedings of the National Academy of Sciences*, 101(44), 15670-15675.

Cano, M., Vivo, J., Miró, F., Morales, J., & Galisteo, A. (2001). Kinematic characteristics of Andalusian, Arabian and Anglo-Arabian horses: a comparative study. *Research in Veterinary Science*, 71(2), 147-153.

Cervantes, I., Baumung, R., Molina, A., Druml, T., Gutiérrez, J., Sölkner, J., & Valera, M. (2009). Size and shape analysis of morphofunctional traits in the Spanish Arab horse. *Livestock Science*, 125(1), 43-49.

Chan, Y. (2005). Biostatistics 303. Discriminant analysis. *Singapore medical journal*, 46(2), 54.

Clayton, H., Hoyt, D., Wickler, S., Cogger, E., & Lanovaz, J. (2002). Hindlimb net joint energies during swing phase as a function of trotting velocity. *Equine Veterinary Journal*, 34(S34), 363-367.

Clayton, H. M., & van Weeren, P. R. (2001). Performance in equestrian sports. *Equine locomotion*, 193-226.

Clemente, C. J., Dick, T. J., Glen, C. L., & Panagiotopoulou, O. (2020). Biomechanical insights into the role of foot pads during locomotion in camelid species. *Scientific reports*, 10(1), 3856.

Dagg, A. I. (1974). The locomotion of the camel (*Camelus dromedarius*). *Journal of Zoology*, 174(1), 67-78.

de Oliveira Bussiman, F., da Costa Perez, B., Ventura, R. V., e Silva, F. F., Peixoto, M. G. C. D., Vizoná, R. G.,Chicaroni Mattos, E., Sterman Ferraz, J.B., Pereira Eler, J., Abdallah Curi, R., & de Carvalho Balieiro, J.C. (2018). Genetic analysis of morphological and functional traits in Campolina horses using Bayesian multi-trait model. *Livestock Science*, 216, 119-129.

Delgado, J., Navas, F., Miranda, J., Miró, M., Arando, A., & Pizarro, M. (2014). Preliminary body weight estimation methodology and its application to the Andalusian donkey breed as an energetic producer. *Actas Iberoamericanas de Conservación Animal*, 4, 207-209.

do Pantanal, C., Biotecnologia, B.-D., Margaret, C., Santos, S. A., da Silva, J. A., Louvandini, H., & Bezerra, J. R. (2008). Body indices for the Pantaneiro horse. *Brazilian Journal of Veterinary Research and Animal Science*, 45(5), 362-370.

Dunbar, D. C., Macpherson, J. M., Simmons, R. W., & Zarcades, A. (2008). Stabilization and mobility of the head, neck and trunk in horses during overground locomotion: comparisons with humans and other primates. *Journal of experimental biology*, 211(24), 3889-3907.

Dyson, S., Ellis, A., Mackechnie-Guire, R., Douglas, J., Bondi, A., & Harris, P. (2020). The influence of rider: horse bodyweight ratio and rider-horse-saddle fit on equine gait and behaviour: A pilot study. *Equine Veterinary Education*, 32(10), 527-539.

El-Shafey, A., & Kassab, A. (2013). Computed Tomography and Cross-Sectional Anatomy of the Metatarsus and Digits of the One-humped Camel (*Camelus dromedarius*) and Buffalo (*Bos bubalis*). *Anatomia, histologia, embryologia*, 42(2), 130-137.

Entin, P. (2007). Do racehorses and Greyhound dogs exhibit a gender difference in running speed? *Equine and Comparative Exercise Physiology*, 4(3-4), 135-140.

Faye, B. (1997). *Guide de l'élevage du dromadaire*: Sanofi.

Fernández de Sierra, G., & Fabelo Marrero, F. J. (2017). *El camello canario*: Asociación de Criadores del Camello Canario.

Finn, J. L., Haase, B., Willet, C. E., van Rooy, D., Chew, T., Wade, C. M., Hamilton, C.M., & Velie, B. D. (2016). The relationship between coat colour phenotype and equine behaviour: A pilot study. *Applied Animal Behaviour Science*, 174, 66-69.

Fowler, M. (2011). *Medicine and surgery of camelids*: John Wiley & Sons.

Francis, R. C. (2019). *En manos humanas*: RBA Libros.

Gillette, R. L., & Angle, T. C. (2014). Canine locomotion analysis. *Canine rehabilitation and physical therapy*, 201-210.

Gómez, M., Gama, L., León, J., Fernández, J., Attalla, S., & Delgado, J. (2016). Genetic parameters for harmony and gaits in Hispano-Arabe horses estimated by Bayesian methods and restricted maximum likelihood. *Livestock Science*, 188, 159-165.

González Ariza, A., Arando Arbulu, A., Navas González, F. J., León Jurado, J. M., Delgado Bermejo, J. V., & Camacho Vallejo, M. E. (2022). Data mining-based discriminant analysis as a tool for the study of egg quality in native hen breeds. *Scientific Reports*, 12(1), 15873.

Granacher, U., Gollhofer, A., Hortobágyi, T., Kressig, R. W., & Muehlbauer, T. (2013). The importance of trunk muscle strength for balance, functional performance, and fall prevention in seniors: a systematic review. *Sports medicine*, 43, 627-641.

Hans, E. C., Zwarthoed, B., Seliski, J., Nemke, B., & Muir, P. (2014). Variance associated with subject velocity and trial repetition during force platform gait analysis in a heterogeneous population of clinically normal dogs. *The Veterinary Journal*, 202(3), 498-502.

Herrel, A., Gonwouo, L., Fokam, E., Ngundu, W., & Bonneaud, C. (2012). Intersexual differences in body shape and locomotor performance in the aquatic frog, *Xenopus tropicalis*. *Journal of Zoology*, 287(4), 311-316.

Hildebrand, M. (1977). Analysis of asymmetrical gaits. *Journal of Mammalogy*, 58(2), 131-156.

Hildebrand, M. (1980). The adaptive significance of tetrapod gait selection. *American Zoologist*, 20(1), 255-267.

Hobbs, S. J., & Clayton, H. M. (2022). The Olympic motto through the lens of equestrian sports. *Animal Frontiers*, 12(3), 45-53.

Holmström, M., Fredricson, I., & Drevemo, S. (1994). Biokinematic analysis of the Swedish Warmblood riding horse at trot. *Equine Veterinary Journal*, 26(3), 235-240.

Holt, K. M. (2006). *Performance Of The Flat Walking Tennessee Walking Horse Yearling Before And After A 60-Day Strength Training Regime*. Doctoral Thesis: Mississippi State University (USA).

Hrysomallis, C. (2011). Balance ability and athletic performance. *Sports medicine*, 41, 221-232.

Ibáñez, B., & Tambussi, C. P. (2012). Foot-propelled aquatic birds: pelvic morphology and locomotor performance. *Italian Journal of Zoology*, 79(3), 356-362.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S., & Bermejo, J. V. (2020). Biokinematics and applied thermography in the Canarian camel breed. *Archivos de zootecnia*, 69(265), 102-107.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Arando Arbulu, A., & Delgado Bermejo, J. V. (2021). The Youngest, the Heaviest and/or the Darkest? Selection Potentialities and Determinants of Leadership in Canarian Dromedary Camels. *Animals*, 11(10), 2886.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Camacho Vallejo, M. E., & Delgado Bermejo, J. V. (2022). Bayesian Linear Regression and Natural Logarithmic Correction for Digital Image-Based Extraction of Linear and Tridimensional Zoometrics in Dromedary Camels. *Mathematics*, 10(19), 3453.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Nogales Baena, S., & Delgado Bermejo, J. V. (2020). Camel Genetic Resources Conservation through Tourism: A Key Sociocultural Approach of Camelback Leisure Riding. *Animals*, 10(9), 1703.

Inkilä, L., Hyytiäinen, H. K., Hielm-Björkman, A., Junnila, J., Bergh, A., & Boström, A. (2022). Part I of finnish agility dog survey: training and management of competition-level agility dogs. *Animals*, 12(2), 212.

Jackson, B. E., Segre, P., & Dial, K. P. (2009). Precocial development of locomotor performance in a ground-dwelling bird (*Alectoris chukar*): negotiating a three-dimensional terrestrial environment. *Proceedings of the Royal Society B: Biological Sciences*, 276(1672), 3457-3466.

Jacobs, L. N., Staiger, E. A., Albright, J. D., & Brooks, S. A. (2016). The MC1R and ASIP coat color loci may impact behavior in the horse. *Journal of Heredity*, 107(3), 214-219.

Janis, C. M., Theodor, J. M., & Boisvert, B. (2002). Locomotor evolution in camels revisited: a quantitative analysis of pedal anatomy and the acquisition of the pacing gait. *Journal of vertebrate paleontology*, 22(1), 110-121.

Kinugasa, R., & Usami, Y. (2016). How Fast can a Human run?– Bipedal vs. Quadrupedal running. *Frontiers in Bioengineering and Biotechnology*, 4, 56.

Kristjansson, T., Bjornsdottir, S., Albertsdóttir, E., Sigurdsson, A., Pourcelot, P., Crevier-Denoix, N., & Arnason, T. (2016). Association of conformation and riding ability in Icelandic horses. *Livestock Science*, 189, 91-101.

Kukekova, A. V., Trut, L. N., & Acland, G. M. (2013). Genetics of domesticated behavior in dogs and foxes. In *Genetics and the behavior of domestic animals* (Chapter 10, pp. 275-323): Elsevier.

Larsson, M., & Brothers, D. (2019). Camels in animal-assisted interventions – survey of practical experiences with children, youth and adults. Proceedings of the International Society of Applied Ethology in Bergen (Norway).

Laudner, K. G., Sipes, R. C., & Wilson, J. T. (2008). The acute effects of sleeper stretches on shoulder range of motion. *Journal of athletic training*, 43(4), 359-363.

Lynghaug, F. (2009). *The official horse breeds standards guide: the complete guide to the standards of all North American equine breed associations*: Voyageur Press.

Mackay, T. F. (2014). Epistasis and quantitative traits: using model organisms to study gene–gene interactions. *Nature Reviews Genetics*, 15(1), 22-33.

Maloiy, G., Rugangazi, B., & Rowe, M. (2009). Energy expenditure during level locomotion in large desert ungulates: the one-humped camel and the domestic donkey. *Journal of Zoology*, 277(3), 248-255.

Moreno-Garcia, M., Pimenta, C. M., López Aldana, P. M., & Pajuelo Pando, A. (2007). The signature of a blacksmith on a dromedary bone from Islamic Seville (Spain). *Archaeofauna*, 16, 193-202.

Mostafa, M. B., & Elemmawy, Y. M. (2020). Relationships between morphometric measurements and musculoskeletal disorders in jumping Thoroughbred horses. *Journal of Equine Science*, 31(2), 23-27.

Navas González, F. J., Jordana Vidal, J., León Jurado, J. M., McLean, A. K., Pizarro Inostroza, G., & Delgado Bermejo, J. V. (2018). Genetic parameter estimation and implementation of the genetic evaluation for gaits in a breeding program for assisted-therapy in donkeys. *Veterinary research communications*, 42, 101-110.

Nelson, K., Bwala, D., & Nuhu, E. (2015). The dromedary camel; a review on the aspects of history, physical description, adaptations, behavior/lifecycle, diet, reproduction, uses, genetics and diseases. *Nigerian Veterinary Journal*, 36(4), 1299-1317.

Ni, B. B. (2020). *Human kinematic responses to walking and riding camels and horses*. Doctoral Thesis: Baylor University (Texas, USA).

Ojanguren, A., & Brana, F. (2003). Effects of size and morphology on swimming performance in juvenile brown trout (*Salmo trutta* L.). *Ecology of Freshwater Fish*, 12(4), 241-246.

Oliveira, R. F. (2009). Social behavior in context: hormonal modulation of behavioral plasticity and social competence. *Integrative and Comparative Biology*, 49(4), 423-440.

Park, J., Seeley, M. K., Francom, D., Reese, C. S., & Hopkins, J. T. (2017). Functional vs. traditional analysis in biomechanical gait data: an alternative statistical approach. *Journal of human kinetics*, 60(1), 39-49.

Payne, W. J. A., & Wilson, R. T. (1999). *An introduction to animal husbandry in the tropics*: Blackwell Science.

Pfau, T., Hinton, E., Whitehead, C., Wiktorowicz-Conroy, A., & Hutchinson, J. (2011). Temporal gait parameters in the alpaca and the evolution of pacing and trotting locomotion in the *Camelidae*. *Journal of Zoology*, 283(3), 193-202.

Pfau, T., Parsons, K., & Wilson, A. (2006). Mechanics of over-ground locomotion in the dromedary camel (*Camelus dromedarius*). *Journal of Biomechanics*(39), S359.

Pigière, F., & Henrotay, D. (2012). Camels in the northern provinces of the Roman Empire. *Journal of Archaeological Science*, 39(5), 1531-1539.

Pratt-Phillips, S., & Munjizun, A. (2023). Impacts of Adiposity on Exercise Performance in Horses. *Animals*, 13(4), 666.

Ramananarivo, S., Godoy-Diana, R., & Thiria, B. (2011). Rather than resonance, flapping wing flyers may play on aerodynamics to improve performance. *Proceedings of the National Academy of Sciences*, 108(15), 5964-5969.

Ripollés-Lobo, M., Perdomo-González, D., Sánchez-Guerrero, M., Bartolomé, E., & Valera, M. (2022). Genetic relationship between free movement and under rider gaits in young Pura Raza Española horses. *Livestock Science*, 263, 105031.

Saastamoinen, M. T., & Barrey, E. (2000). Genetics of conformation, locomotion and physiological traits. In *The genetics of the horse* (pp. 439-472): CAB International Wallingford UK.

Sánchez, M., Gómez, M., Molina, A., & Valera, M. (2013). Genetic analyses for linear conformation traits in Pura Raza Español horses. *Livestock Science*, 157(1), 57-64.

Sánchez, M. J., Gómez, M. D., Peña, F., Monterde, J. G., Morales, J. L., Molina, A., & Valera, M. (2013). Relationship between conformation traits and gait characteristics in Pura Raza Español horses. *Archiv Tierzucht*, 56(13), 137-148.

Sbihi, H. M., Nehdi, I. A., & Al-Resayes, S. I. (2013). Characterization of Hachi (*Camelus dromedarius*) fat extracted from the hump. *Food chemistry*, 139(1-4), 649-654.

Schulz, U. (2008). *El camello en Lanzarote*: Aderlan.

Senefeld, J. W., Shepherd, J. R., Baker, S. E., & Joyner, M. J. (2021). Sex-based limits to running speed in the human, horse and dog: The role of sexual dimorphisms. *FASEB journal: official publication of the Federation of American Societies for Experimental Biology*, 35(5), e21562.

Senna, N. A., Mostafa, M. B., Abu-Seida, A. M., & Elemmawy, Y. M. (2015). Evaluation of limb conformation in jumping thoroughbred horses. *Asian Journal of Animal Sciences*, 9(5), 208-216.

Signer-Hasler, H., Flury, C., Haase, B., Burger, D., Simianer, H., Leeb, T., & Rieder, S. (2012). A genome-wide association study reveals loci influencing height and other conformation traits in horses. *PloS one*, 7(5), e37282.

Stefánsdóttir, G., Jansson, A., Ragnarsson, S., & Gunnarsson, V. (2021). Speed of gaits in Icelandic horses and relationships to sex, age, conformation measurements and subjective judges' scores. *Comparative Exercise Physiology*, 17(2), 151-160.

Suchomel, T. J., Nimphius, S., & Stone, M. H. (2016). The importance of muscular strength in athletic performance. *Sports medicine*, 46, 1419-1449.

Susana Lopes, M., Azevedo, A. R., Mendonça, D., Rojer, H., Cabral, V., Ceraolo, F., Canto Brum, C., Mendes, B., & da Câmara Machado, A. (2023). Morphological and genetic characterization of the Graciosa donkey breed. *Journal of Applied Animal Research*, 51(1), 166-173.

Tang, C., Ma, S., Li, B., & Wang, Y. (2010). A cubic CPG model for snake-like robot to adapt to environment. Proceedings of the 2010 IEEE International Conference on Information and Automation.

Toro, E., Herrel, A., Vanhooydonck, B., & Irschick, D. J. (2003). A biomechanical analysis of intra-and interspecific scaling of jumping and morphology in Caribbean Anolis lizards. *Journal of Experimental Biology*, 206(15), 2641-2652.

Ucko, P. J., & Dimbleby, G. W. (2007). *The domestication and exploitation of plants and animals*: Transaction Publishers.

Van Den Bogert, A., Schamhardt, H., & Crowe, A. (1989). Simulation of quadrupedal locomotion using a rigid body model. *Journal of biomechanics*, 22(1), 33-41.

van Rooy, D., & Wade, C. M. (2019). Association between coat colour and the behaviour of Australian Labrador retrievers. *Canine genetics and epidemiology*, 6(1), 1-7.

Vicente, A., Carolino, N., Ralão-Duarte, J., & Gama, L. (2014). Selection for morphology, gaits and functional traits in Lusitano horses: II. Fixed effects, genetic trends and selection in retrospect. *Livestock Science*, 164, 13-25.

Villalobos, C. M. (2019). Simbolismo y astrología en los textos antiguos: el caso del camello. In *Studia classica et emblematica caro magistro Francisco J. Talauera Esteso dicata* (pp. 399-419): Libros Pórtico.

Voss, K., Wiestner, T., Galeandro, L., Hässig, M., & Montavon, P. (2011). Effect of dog breed and body conformation on vertical ground reaction forces, impulses, and stance times. *Veterinary and Comparative Orthopaedics and Traumatology*, 24(02), 106-112.

Webb, S. (1972). Locomotor evolution in camels. *Forma et functio. An international journal of functional biology*.

Weishaupt, M. A., Hogg, H., Auer, J., & Wiestner, T. (2010). Velocity-dependent changes of time, force and spatial parameters in Warmblood horses walking and trotting on a treadmill. *Equine Veterinary Journal*, 42, 530-537.

Whitmer, T. D., Fry, A. C., Forsythe, C. M., Andre, M. J., Lane, M. T., Hudy, A., & Honnold, D. E. (2015). Accuracy of a vertical jump contact mat for determining jump height and flight time. The *Journal of Strength & Conditioning Research*, 29(4), 877-881.

Williams, J., & Tabor, G. (2017). Rider impacts on equitation. *Applied Animal Behaviour Science*, 190, 28-42.

Xue, F., Chen, X., Liu, J., & Nardi, D. (2012). Real time biped walking gait pattern generator for a real robot. In *RoboCup 2011: Robot Soccer World Cup XV 15* (pp. 210-221): Springer Berlin Heidelberg.

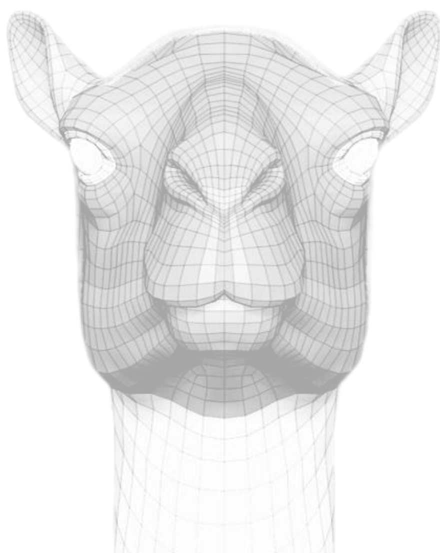
Zheng, L., Bi, S., Cai, Y., & Niu, C. (2010). Design and optimization of a robotic fish mimicking cow-nosed ray. Proceedings of the 2010 IEEE International Conference on Robotics and Biomimetics.

3.2 Thermographic ranges of dromedary camels undergoing physical exercise: applications for physical health/welfare monitoring and phenotypic selection

Carlos Iglesias Pastrana[1], Francisco Javier Navas González[1], Elena Ciani[2], Carmen Marín Navas[1] and Juan Vicente Delgado Bermejo[1]

[1]Department of Genetics, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain

[2]Department of Biosciences, Biotechnologies and Environment, Faculty of Veterinary Sciences, University of Bari 'Aldo Moro', 70121 Bari, Italy



Quality indicator information provided on the publication
***Latest information available (2022)*

Status of the manuscript: Submitted

Journal (year, volume, page(s)): *Frontiers in Veterinary Science*

International database in which it is indexed: Journal of Citation Reports (JCR)

Thematic area in the reference database: Veterinary Sciences

Impact index of the journal in the year of the article's publication: 3.2

Rank/number of thematic area journals: 12/143 (D1)

Abstract

Despite the empirical efforts to characterize the biomechanics of the camel, the immediate functional response that accompanies the execution of physical exercise remains unapproached. Hence, selective breeding programs are lacking from empirical basis to reach genetic improvement for physical stress tolerance traits and monitor camel welfare in this regard. Given the fact that physical exercise increases net heat production, infrared thermography (IRT) was selected to study the temperature changes at skin surface of different body areas in clinically normal dromedary camels mostly relegated to leisure activities. Such thermophysiological responses can be used as indirect measures of tissue activity in response to exercise, hence reliable indicators of animal tolerance to physical exercise-induced stress. Specifically, a lower dispersion at the individual level of the surface temperature at the withers, shoulder, and rump areas, as well as lower values for maximum temperature (T_{max}) and minimum temperature (T_{min}) at the region of the cornea, pectoral muscles, semimembranosus-semitendinosus muscles and hind fetlock after exercise, have to be remarked as breeding criteria for candidate selection. Sex, castration, age and iris pigmentation did also significantly impact thermophysiological response to exercise in the study sample, which can be attributed to hormone, general vigor and visual acuity-mediated effects.

Keywords

Thermophysiological response, exercise tolerance, camel welfare, camel phenotyping, genetic selection

Introduction

The socioeconomic interest in camel breeding fundamentally resides in the production of food (milk and meat) and other products and by-products such as wool, dung, skin and fat. Abundant literature does exist on the characterization of camel-based food products and subproducts, with special reference to the different animal- and management-related variables that potentially influence yield and thus economic benefits at these camel farming systems (Abdel-Rahman, Alzahrani, & Sulieman, 2020; Al-Hassan, 2020; Al Kanhal, 2010; Kadim et al., 2013; Li & Guo, 2013). However, several camel breeds are typically selected for their power and speed within a functional scenario of leisure, load carrying and traction works (Burger, Ciani, & Faye, 2019). Comparatively, little information is available for these specific tasks.

Elementary analyses of biomechanics of gait (Abdo et al., 2019; Dagg, 1974; Pfau, Parsons, & Wilson, 2006), the elastic extension of tendons (Alexander et al., 1982), the morphology of some parts of the distal skeleton (Abdo et al., 2019; Alsafy, El-Gendy, & Kamal, 2021; Badawy, 2011; El-Shafey & Kassab, 2013) and the pedal anatomy (Janis, Theodor, & Boisvert, 2002) in one-humped camels, shed lights on the normal movements, osteomuscular composition and locomotor adaptions of these animals to sandy terrains at desert ecosystems. More specifically, the repercussions that different exercise conditions have at a biochemical and hormonal level are relatively widely studied (El-Deeb & Abdelghani, 2022; Kumar et al., 2022; Maloiy, Rugangazi, & Rowe, 2009), highlighting the near-Newtonian behavior of camel blood as a response to endurance activities (Windberger et al., 2019). In regards of animal-dependent factors, Al-Shorepy (2011) conclude that age and sex have a significant effect on racing performance.

Notwithstanding this conglomerate of empirical knowledge on camel biomechanics, the basic physiology and function of the musculature in the working camel still remains unapproached. The knowledge of the immediate functional responses and organic adaptations that accompany the execution of a session of physical activity or exercise allows the accurate, early diagnosis of decreased levels of sport performance and the design of training/rehabilitation programs (Soroko, Jodkowska, & Dudek, 2015; Turner, Pansch, & Wilson, 2001). Since physical exercise has a remarkable direct effect on net heat production (Simon et al., 2006), infrared thermography (IRT) is the technique of choice to study the underlying physiological response of muscles and other organic tissues during and after exercise (Yarnell et al., 2014). This noninvasive imaging method is capable to detect temperature changes (thermogenesis) at skin surface that are an indirect measure of tissue activity (local blood flow and metabolism rate) in response to exercise (Eddy, Van Hoogmoed, & Snyder, 2001; Tunley & Henson, 2004).

In this context, the purpose of the present research is the thermographic examination of twenty-two body regions for their importance to monitor the impact of exercise in clinically normal dromedary camels, and the analysis of the relative influence of different animal-dependent factors on the thermophysiological responses at such body regions. The results obtained will serve to evaluate the potential of infrared thermography to be used as a tool for reliable assessment of camel physical fitness and thus welfare impacts when these animals participating at physically-demanding activities. The animal model used is the Canarian camel (*Camelus dromedarius*), an autochthonous endangered breed mainly relegated to leisure activities in which the physical health and performance of the animals have large significance (Iglesias et al., 2020).

Material and methods

Animal sample and data selection

A total of 130 Canarian dromedaries (72 males and 58 females; aged between 18 months and 35 years old) were included in this study. All dromedary camels had resided at the respective participating farm for at least one year prior to the study. Animals were checked before the evaluations to ensure they were in good health.

Study duration

The study was carried out over five consecutive days in January 2021. For the study of the thermophysiological response to exercise in leisure dromedaries, each dromedary camel participating in this study was exercised for 15 minutes by the same familiar handler. The exercise involved walking the animal for 15 minutes at a comfortable, active walking speed for each individual.

Thermal data collection

Thermal images for this study were captured using an Hti-Xintai HT-18 thermal imaging camera (220 x 160 IR resolution, 35200 pixels). The camera has a thermal sensitivity of <0.05 °C at temperatures of ≥30 °C, a temperature detection range between −20 °C and +120 °C, and an emissivity of 0.95.

To minimize the impact of environmental factors, thermographic evaluations were consistently conducted within an enclosed pen by the same technicians. Static thermal images were taken at a 90° angle from a distance of 1 m±50 cm from the animals, following recommendations from Yarnell et al. (2014).

Thermal images were captured at 22 body regions. Thermal images were taken at three separate sampling time points: pre-exercise, post-exercise 0 min, and post-exercise 5 min.

Evaluated areas and thermal quantitative variables

The software used for thermographic assessment was Batch Flir Image Converter (http://test.daves.cz/wrapper/wrapper.zip). Quantitative variables extracted from each thermal image included average temperature, maximum temperature, minimum temperature, and standard deviation, all measured in degrees Celsius.

The evaluated areas from which the aforementioned quantitative variables were sampled comprised Cornea, Withers, Shoulder, Pectoralis, Forearm, Carpus, Metacarpus, Front Fetlock, Front Digital flexor tendons, Front Coronary band, Front Navicular (distal sesamoid) cartilage, Front Heel bulbs, Lumbar region, Rump, Semimembranosus and semitendinosus muscles, Tarsus, Metatarsus, Rear Fetlock, Rear Digital flexor tendons, Rear Coronary band, Rear Navicular (distal sesamoid) cartilage, and Rear Heel bulbs.

The hump region was not evaluated due to its primarily fatty tissue composition, where fat thermogenesis primarily depends on the types of fatty acids present, which, in turn, are influenced by the animal's diet and other factors related to the animal's overall health status, factors that were not controlled in this study. Additionally, the knee region was not assessed due to the presence of a notable hard callus (active osteoblasts that mineralize the callus matrix) with significant dimensions (area and thickness) in this region, which functions to protect this area when the camel sits on hot sand.

For the front and rear limbs, the same image was used to extract the average and standard deviation temperatures for each individual region evaluated within each limb. This approach provided a more precise evaluation of the workload and physiological stress relative to each individual region compared to the overall limb (front or rear limb).

Statistical analysis

In line with the methodologies outlined in González Ariza et al. (2022), we initiated our analysis by employing discriminant canonical analysis. This allowed us to create a tool that assesses optimal linear combinations of unstandardized coefficients from cubic regression within and between different population clustering patterns.

Our dependent variables comprised average temperature, maximum temperature, minimum temperature, and standard deviation per evaluated region. Additional variables such as sex, age (months), coat color, coat particularities, eye colour, neutering status, and involvement in active or non-active desensitization protocols were included.

Results

A summary of the mean values for thermal information reported by all the variables considered across body regions sampled is reported in Figure 1.

Reliability of the Discriminant Canonical Analysis Model After conducting 49 rounds of multicollinearity analyses, the variables included in the discriminant canonical analysis are those outlined in Table 1.

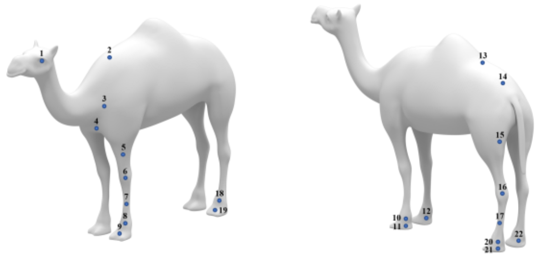
Pillai’s trace criterion reported a significant difference between pre and post exercise moments (Pillai’s trace criterion: 0.4434, F (Observed value): 1.9764, F (Critical value): 1.2695, df1: 98, df2: 680, p-value< 0,0001), confirming the validity of the discriminant canonical analysis.

Out of the two functions identified through discriminant analysis, one was found to be significant for their discriminant ability (Table 2). Among these, the F1 function exhibited the highest discriminatory power, with an eigenvalue of 0.5374, explaining 83.84% of the variance.

The various variables examined in this study were ranked based on their discriminative capacity. An evaluation of the equality of group means of the dependent variables involved in the discriminant canonical analysis is presented in Table 3. Higher

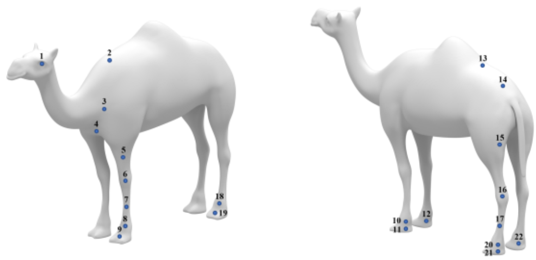
(A) Pre-exercise

Region	Mean	SD	T_{max}	T_{min}
1	22.95	14.39	39.30	14.23
2	23.24	14.31	41.87	19.95
3	21.05	15.00	41.87	19.95
4	20.28	16.82	39.30	23.73
5	20.86	10.25	41.87	19.95
6	21.47	8.80	41.87	19.95
7	21.59	8.90	41.87	19.95
8	23.11	6.90	41.87	19.95
9	23.04	10.74	41.87	19.95
10	23.27	7.71	41.87	19.95
11	23.36	9.60	41.87	19.95
12	22.97	11.36	41.87	19.95
13	22.64	15.55	41.92	20.28
14	22.17	19.64	39.67	24.02
15	18.11	16.36	39.67	23.97
16	22.45	9.05	41.92	20.28
17	23.59	8.61	41.92	20.28
18	23.58	6.76	41.92	20.28
19	22.64	10.85	41.92	20.28
20	23.36	7.61	41.92	20.28
21	23.05	9.65	41.92	20.28
22	23.82	11.31	41.92	20.28



(B) Post-exercise

Region	Mean	SD	T_{max}	T_{min}
1	22.30	15.67	39.30	16.02
2	22.76	14.49	41.38	19.56
3	21.46	15.43	41.38	19.56
4	17.78	16.39	40.51	24.06
5	21.28	9.37	41.38	19.56
6	21.56	7.79	41.38	19.56
7	24.38	7.28	41.38	19.56
8	24.71	5.19	41.38	19.56
9	24.59	8.83	41.38	19.56
10	24.60	5.58	41.38	19.56
11	24.71	7.83	41.38	19.56
12	24.94	9.34	41.38	19.56
13	22.72	15.25	41.53	19.67
14	21.58	19.86	42.92	23.22
15	17.99	16.00	42.94	23.31
16	21.81	8.16	41.53	19.67
17	24.42	8.23	41.53	19.67
18	25.22	5.94	41.53	19.67
19	24.92	8.46	41.53	19.67
20	25.37	6.40	41.53	19.67
21	25.19	8.14	41.53	19.67
22	25.09	9.08	41.53	19.67



1: Cornea; **2**: Withers; **3**: Shoulder; **4**: Pectoralis; **5**: Forearm; **6**: Carpus; **7**: Metacarpus; **8**: Front fetlock; **9**: Front coronary band; **10**: Front digital flexor tendons; **11**: Front navicular cartilage; **12**: Front heel bulbs; **13**: Lumbar; **14**: Rump; **15**: Semimembranous and semitendinous muscles; **16**: Tarsus; **17**: Metatarsus; **18**: Rear fetlock; **19**: Rear coronary band; **20**: Rear digital flexor tendons; **21**: Rear navicular cartilage; **22**: Rear heel bulbs

Figure 1. Average values for mean, standard deviation (SD), and maximum (T_{max}) and minimum (T_{min}) temperature per body region and evaluation state (pre and post-exercise 0 min). Data for post exercise 5 min was not presented due to the lack of differences with pre exercising, which suggest total thermal recovery of the animals after this time has passed.

Table 1. Summary of the value of tolerance and VIF after multicollinearity analysis of thermal information related variables in Canarian camel breed.

Statistic	Tolerance ($1-R^2$)	VIF (1/Tolerance)
Minimum Temperature-Cornea	0.6980	1.4326
Standard Deviation of Temperature-Metatarsus	0.6819	1.4666
Standard Deviation of Temperature-Withers	0.6514	1.5353
Standard Deviation of Temperature-Carpus	0.6406	1.5611
Standard Deviation of Temperature-Shoulder	0.6326	1.5808
Average Temperature-Semimembranous and semitendinous muscles	0.6234	1.6041
Standard Deviation of Temperature-Pectoralis	0.6149	1.6262
Standard Deviation of Temperature-Semimembranous and semitendinous muscles	0.6059	1.6504
Standard Deviation of Temperature-Metacarpus	0.6021	1.6609
Standard Deviation of Temperature-Cornea	0.5994	1.6683
Age (months)	0.5947	1.6814
Average Temperature-Pectoralis	0.5869	1.7040
Standard Deviation of Temperature-Lumbar	0.5792	1.7265
Average Temperature-Cornea	0.5763	1.7354
Standard Deviation of Temperature-Tarsus	0.5688	1.7580
Eye colour-Brownish with blue spots	0.5650	1.7700
Eye colour-Brownish	0.5507	1.8160
Standard Deviation of Temperature-Rump	0.5464	1.8301
Standard Deviation of Temperature-Forearm	0.5398	1.8524
Standard Deviation of Temperature-Rear fetlock	0.5164	1.9364
Standard Deviation of Temperature-Front fetlock	0.5020	1.9920
Average Temperature-Shoulder	0.4465	2.2395
Standard Deviation of Temperature-Front heel bulbs	0.4199	2.3813
Minimum Temperature-Rear fetlock	0.4156	2.4061
Average Temperature-Lumbar	0.4100	2.4389
Average Temperature-Withers	0.4068	2.4584
Standard Deviation of Temperature-Rear digital flexor tendons	0.3914	2.5548
Standard Deviation of Temperature-Rear heel bulbs	0.3687	2.7126
Standard Deviation of Temperature-Front digital flexor tendons	0.3640	2.7474
Average Temperature-Rump	0.3600	2.7781
Minimum Temperature-Pectoralis	0.3553	2.8149
Average Temperature-Tarsus	0.3539	2.8260
Average Temperature-Forearm	0.3374	2.9639
Standard Deviation of Temperature-Front navicular cartilage	0.3244	3.0829
Standard Deviation of Temperature-Rear coronary band	0.3233	3.0927
Average Temperature-Rear coronary band	0.3223	3.1026
Standard Deviation of Temperature-Front coronary band	0.3086	3.2402

Table 1. *Cont.*

Statistic	Tolerance (1-R^2)	VIF (1/Tolerance)
Minimum Temperature-Semimembranous and semitendinous muscles	0.2792	3.5811
Average Temperature-Carpus	0.2650	3.7735
Maximum Temperature-Cornea	0.2544	3.9306
Average Temperature-Metatarsus	0.2464	4.0586
Maximum Temperature-Semimembranous and semitendinous muscles	0.2436	4.1057
Sex-Male	0.2424	4.1246
Neutered-Yes	0.2313	4.3229
Standard Deviation of Temperature-Rear navicular cartilage	0.2225	4.4936
Average Temperature-Metacarpus	0.2181	4.5844
Maximum Temperature-Pectoralis	0.2149	4.6534
Average Temperature-Front fetlock	0.2097	4.7691
Average Temperature-Front coronary band	0.2047	4.8861

Interpretation thumb rule: VIF ≥ 5 (highly correlated); 1 < VIF < 5 (moderately correlated); VIF = 1 (not correlated).

Table 2. Canonical discriminant analysis efficiency parameters to determine the significance of each canonical discriminant function.

Test functions	Canonical Correlation	Eigenvalue	Variance discrimination(%)	Bartlett's statistic	P-value
1 through 2	0.5912	0.5374	83.8425	191.8897	0.0000
2	0.3063	0.1036	16.1575	35.7705	0.9038

values of F and lower values of Wilks' Lambda indicate greater discriminating power. The analysis revealed that Standard Deviation of Temperature-Metacarpus, Standard Deviation of Temperature-Front fetlock, Standard Deviation of Temperature-Front digital flexor tendons, Maximum Temperature-Semimembranous and semitendinous muscles, Standard Deviation of Temperature-Front navicular cartilage, Standard Deviation of Temperature-Front heel bulbs, Average Temperature-Pectoralis, Average Temperature-Rear coronary band, Standard Deviation of Temperature-Rear coronary band, Standard Deviation of Temperature-Rear heel bulbs, Standard Deviation of Temperature-Front coronary band, Standard Deviation of Temperature-Carpus, Standard Deviation of Temperature-Forearm, Average Temperature-Metacarpus, Standard Deviation of Temperature-Cornea, Maximum Temperature-Cornea, Standard Deviation of Temperature-Rear digital flexor tendons, Standard Deviation of Temperature-Tarsus, Maximum Temperature-Pectoralis, Average Temperature-Front coronary band made highly significant contributions ($P < 0.0001$) to the discriminant functions when qualitative gait evaluation levels were the clustering criteria.

Table 3. Results for the tests of equality of group means to test for difference in the means across sample groups once redundant variables have been removed.

Variable	Wilk's Lambda	F	P-value	Rank
Standard Deviation of Temperature-Metacarpus	0.9129	18.4583	< 0,0001	1
Standard Deviation of Temperature-Front fetlock	0.9173	17.4376	< 0,0001	2
Standard Deviation of Temperature-Front digital flexor tendons	0.9265	15.3445	< 0,0001	3
Maximum Temperature-Semimembranous and semitendinous muscles	0.9273	15.1775	< 0,0001	4
Standard Deviation of Temperature-Front navicular cartilage	0.9549	9.1459	0.001	5
Standard Deviation of Temperature-Front heel bulbs	0.9619	7.6602	0.001	6
Average Temperature-Pectoralis	0.9630	7.4278	0.001	7
Average Temperature-Rear coronary band	0.9649	7.0411	0.001	8
Standard Deviation of Temperature-Rear coronary band	0.9657	6.8670	0.001	9
Standard Deviation of Temperature-Rear heel bulbs	0.9689	6.2114	0.001	10
Standard Deviation of Temperature-Front coronary band	0.9693	6.1206	0.001	11
Standard Deviation of Temperature-Carpus	0.9744	5.0749	0.01	12
Standard Deviation of Temperature-Forearm	0.9771	4.5267	0.01	13
Average Temperature-Metacarpus	0.9792	4.1033	0.02	14
Standard Deviation of Temperature-Cornea	0.9822	3.5162	0.03	15
Maximum Temperature-Cornea	0.9839	3.1698	0.04	16
Standard Deviation of Temperature-Rear digital flexor tendons	0.9842	3.1018	0.05	17
Standard Deviation of Temperature-Tarsus	0.9843	3.0787	0.05	18
Maximum Temperature-Pectoralis	0.9849	2.9664	0.05	19
Average Temperature-Front coronary band	0.9851	2.9274	0.05	20
Standard Deviation of Temperature-Shoulder	0.9865	2.6566	0.0715	
Standard Deviation of Temperature-Rump	0.9877	2.4128	0.0909	
Standard Deviation of Temperature-Pectoralis	0.9877	2.4110	0.0911	

Table 3. *Cont.*

Variable	Wilk's Lambda	F	P-value	Rank
Standard Deviation of Temperature-Rear navicular cartilage	0.9882	2.3194	0.0997	
Minimum Temperature-Cornea	0.9890	2.1567	0.1171	
Standard Deviation of Temperature-Rear fetlock	0.9896	2.0414	0.1312	
Standard Deviation of Temperature-Lumbar	0.9911	1.7433	0.1763	
Average Temperature-Front fetlock	0.9920	1.5569	0.2121	
Average Temperature-Shoulder	0.9934	1.2780	0.2798	
Average Temperature-Metatarsus	0.9940	1.1634	0.3135	
Average Temperature-Carpus	0.9951	0.9574	0.3848	
Average Temperature-Rump	0.9952	0.9322	0.3946	
Standard Deviation of Temperature-Metatarsus	0.9955	0.8716	0.4191	
Minimum Temperature-Semimembranous and semitendinous muscles	0.9956	0.8524	0.4272	
Average Temperature-Withers	0.9957	0.8292	0.4372	
Average Temperature-Lumbar	0.9961	0.7582	0.4692	
Average Temperature-Tarsus	0.9968	0.6136	0.5419	
Average Temperature-Semimembranous and semitendinous muscles	0.9981	0.3670	0.6930	
Standard Deviation of Temperature-Semimembranous and semitendinous muscles	0.9983	0.3372	0.7140	
Average Temperature-Cornea	0.9984	0.3154	0.7297	
Standard Deviation of Temperature-Withers	0.9984	0.3121	0.7321	
Minimum Temperature-Rear fetlock	0.9986	0.2762	0.7588	
Minimum Temperature-Pectoralis	0.9992	0.1578	0.8541	
Average Temperature-Forearm	0.9993	0.1396	0.8697	
Age (months)	1.0000	0.0000	1.0000	
Sex-Male	1.0000	0.0000	1.0000	
Eye colour-Brownish with blue spots	1.0000	0.0000	1.0000	
Eye colour-Bluish	1.0000	0.0000	1.0000	
Neutered-Yes	1.0000	0.0000	1.0000	

df1=2;df2=387

Standardized discriminant coefficients were used to assess the relative weight of each dependent variable across the two significantly established discriminant functions (Supplementary Table S1).

A Press' Q value of 51.80 (n = 390; n' = 197; K = 3) was computed for thermal information across exercise moment levels (Pre and Post, o and 5 min), indicating that predictions can be considered better than chance at a 95% confidence level (Chan, 2005).

Calculation of centroids for different moments of exercise (pre and Post, 0 and 5 min) was conducted. The relative positions of each centroid were determined by substituting the mean values for the observations represented in each of the two detected discriminant functions (F1 and F2). The results for the functions at the centroids are presented in Table 4.

Table 4. Functions at the centroids for the two discriminant functions detected in this study.

Function/Moment of exercise	Post exercise 0 min	Post exercise 5 min	Pre exercise
F1	-1.0064	0.7037	0.3027
F2	0.1017	0.3318	-0.4334

Subsequently, we computed squared Mahalanobis distances to measure dissimilarities between pre exercise moments and post exercise (0 and 5 min) moments. These squared Mahalanobis distances were determined using the following formula:

$$D_{ij}^2 = (\bar{Y}_i - \bar{Y}_j)\ COV^{-1}(\bar{Y}_i - \bar{Y}_j)$$

where D_{ij}^2 is the distance between population i and j; $\bar{Y}_i$ and $\bar{Y}_j$ are the means of the variable x in the ith and jth populations, respectively; and COV^{-1} is the inverse of the covariance matrix of measured variable x.

We employed the squared Mahalanobis distance to visually illustrate the clustering patterns arising from variations in thermal information among the different exercise times (Pre and Post, 0 and 5 min) considered in this study. To achieve this, we constructed a dendrogram representing the potential exercise moment categories (Figure 2). This dendrogram was created using the underweighted pair-group method arithmetic averages (UPGMA) from Universität Rovira i Virgili (URV), Tarragona, Spain, and the Phylogeny procedure of MEGA X 10.0.5 (Institute of Molecular Evolutionary Genetics, The Pennsylvania State University, State College, PA, USA).

The absence of differences between Pre and Post exercise thermal information 5 min after exercise may be explained by the fact that camels are energy-efficient animals, hence it takes for them less than 5 min to completely recover at a thermophysiological level (Alexander, 1991; Janis et al., 2002; Maloiy et al., 2009).

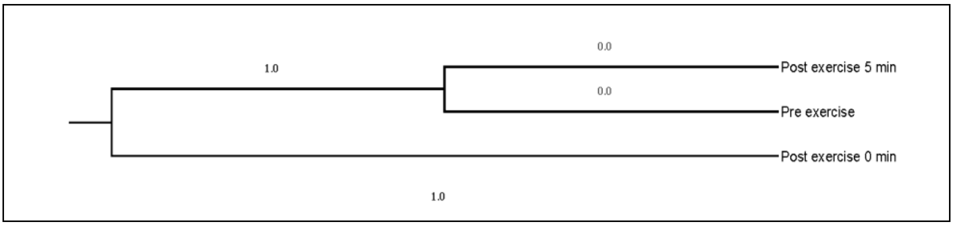


Figure 2. Dendrogram constructed from Mahalanobis distances across exercise moments (Pre and Post (0 and 5 min)).

Discussion

The thermophysiological response to physical exercise was evaluated through infrared thermography at twenty-two body regions of clinically normal dromedary camels. The mean temperature is generally higher after exercise in almost all the body regions evaluated, while the opposite trend can be observed for the values of standard deviation, maximum temperature (T_{max}) and minimum temperature (T_{min}). As T_{max} and T_{min} do not decrease by approximately the same amount between evaluated time periods, the standard deviation is expected to decrease and the mean to move up, and vice versa (Delmas & Liu, 2005). From a pure physiological viewpoint, the mean temperature of the body regions can be anticipated to be increased after physical exercise due to the near-immediate local rise at blood flow, nutrient supply and metabolic rate, but also the temperature to be more or less homogeneous along each local body area depending on their specific functional repercussion in locomotion. Besides, considering the natural selection for energy efficiency of movement and optimization at extreme environments in camelids (Fowler, 2011), a low temperature dispersion should appear.

At the individual level, a more irregular regional temperature dispersion could be indicative of local functional alteration (e.g., microcirculation failures or inflammation) that might compromise animal physical health and thus performance (Kirimtat et al., 2020). On the other hand, a higher regional temperature dispersion at the group level, might be indicative of substantial interindividual variability for the thermophysiological local response, that could be attributed to the effects of different animal- and environment-related factors, and therefore plausible to be used as a reliable measure of individual tolerance to physical exercise-induced stress. But this could also be reflecting the higher latency of thermophysiological response signals to exercise at these body areas, which then indicates that thermographic evaluation of these areas should be prioritized to accurately examine tolerance to physical exercise.

This last particular thermophysiological behavior is indeed patent for some of the examined body regions. For the cornea, withers, pectoral muscles, rump, and semimembranosus-semitendinosus muscles, the mean temperature is lower, and the mean standard deviation and/or T_{max} and T_{min} are higher, after exercise. Only at shoulder area, the mean temperature and the mean standard deviation are higher, and/or T_{max} and T_{min} are lower, after exercise. First, during exercise, as a potential stress-inducing activity, eyelid contractions and sensory inputs from the visual, vestibular, and somatosensory systems for the visual-motor coordination to maintain postural balance are enhanced (Merkies et al., 2019; Ogard, 2011), which might be manifested in an increase in local temperature. Such visual-motor coordination and thus the level of stress with which the animal has to deal is in turn governed by different influencing factors related to the anatomy and general biomechanics of each individual. Moreover, such idiosyncrasy will be reflected on the variability at thermophysiological response at withers, shoulder and rump areas, which are largely implicated on the attenuation of impact forces from the feet to the head and back during quadrupedal locomotion (Dunbar et al., 2008).

In regards of the generally higher mean maximum and minimum temperatures at the cornea, pectoral muscles, rump, and semimembranosus-semitendinosus muscles after exercise, the mean maximum temperature of the cornea hardly varies between the resting state and after exercise, which could be attributed to the existence of a local critical temperature due to the greater risk of heat damage at the tissues of the eye and adjacent brain structures for their elevated sensitivity to the effects of heating (Yarmolenko et al., 2011). Further, a higher mean T_{max} and/or T_{min} at the pectoral muscles, rump and semimembranosus-semitendinosus muscles after exercise would be explained by the potential role of such areas as external projection windows for cardiac work and blood flow at the level of the brachial plexus (Kozlov & Son'kin, 2019), and for the work of the caudal region of the musculature at posterior third in the flexion-extension of the hip and knee and the propulsive forces (Yarnell et al., 2014), respectively.

However, for the specific case of the tarsal region, the mean temperature, standard deviation, T_{max} and T_{min} are lower in the post-exercise state. Such finding is revealing the importance of early physiological recovery of this area to maintain good mechanical performance (Khumsap, Lanovaz, & Clayton, 2004), hence it can be used as a reliable indicator of physical health in these animal species. In the animal sample studied, as they are functionally relegated to riding activities, the mechanics of the rear limbs is crucial for a good performance and maintenance of a good health status. This peculiar thermal behavior could be also suggesting the potential existence of an extraordinary blood vessel circulation involved in heat dissipation at this local body region, and that should be specifically approached in future applied studies.

In summary, the quantitative trends discussed, together with the discriminant potential between the resting and post-exercise states of the standard deviation values for surface temperature in practically all the regions evaluated, and to a lesser extent the mean temperature values and the mean edge values of the range, serve to construct a non-invasive protocol for the monitoring of the impact of physical exercise and welfare status in dromedary camels subjected to physical exercise. Such statement is additionally reinforced with the percentages of correct classification of individuals based on discriminant analysis, from which a significant number of camels in resting state are classified by the discriminant analysis as if they would have performed physical exercise. Following the same logic, those camels that are classified as a resting state after have performed exercise, would be the individuals to be selected for breeding purposes since they are able to physiologically recover quickly after physical effort.

Specifically, the greater the variability in surface temperature values at the discriminating regions after exercise, the induced stress will presumably be greater or, what it's the same, the individual tolerance to exercise and physical fitness will be lesser. At the pragmatic level, such variability would be observed in the thermographic camera as a relatively heterogeneous map of colours and tones in the pertinent region(s). The T_{max} and the T_{min} at the region of the cornea, pectoral muscles, semimembranosus-semitendinosus muscles, and rear fetlock, have also discriminant potential between the resting and post-exercise states' surface temperatures. For the specific case of the cornea, additional evidence is thus provided to the existing literature for other animal species, which reports that eye temperature is one of the most accurate, non-invasive tools to study animal welfare (Ijichi et al., 2020). For pectoralis region, its discriminating potential reinforces the abovementioned significance of its role as a window of external projection for cardiac work and brachial plexus blood flow. Concerning the semimembranosus-semitendinosus muscles and rear fetlock, these structures have a prominent implication in the coordination of movement and effectiveness of locomotion, mainly due to the control that they exert at the propulsive forces and their support of body weight in the animal model used (riding camels) (Schulz, 2008). Although the T_{min} at rear fetlock is the same as the other structures evaluated at rear limbs for methodological reasons, its discriminating potential derives from the statistical relationships that exist between the thermophysiological behavior at this body area and the pertinent for the remaining regions evaluated at the population level.

Then, the detection at these discriminating areas of thermophysiological responses contrary to the indicated, specific trend, or exceptional extreme values, could be interpreted as the incidence of a functional alteration, probably subclinical, with local (e.g., osteomuscular alteration in rear limbs) or systemic (e.g., cardiac pathology) repercussion. Notwithstanding, the determination of the possible deviation from the thermophysiological behavior in a single individual and their preference to be included in the breeding schemes should be carefully implemented with the consideration of the effects of other qualitative and quantitative factors such as sex, age, neutering status and eye colour. Males, neutered and young (sexually immature) animals, and camels with brownish and relatively spotted blue iris, display greater variability in the thermophysiological response to physical exercise. Contrastingly, ambient temperature, breed and training level, but neither gender nor age, have significant effects on skin temperature in other sport animal species such as racehorses (Soroko et al., 2017).

The impact of sex and neutering status on individual physiological recovery capacity after exercise in camels would be basically explained by hormonal mechanisms (e.g., androgen-mediated effects) (Wood, 2004) and the higher body corpulence after castration (Pigière & Henrotay, 2012), as well as on the differences between sexes for cell composition and skin structure in dromedaries (Hamdi et al., 2022). In relation to age, the lower general vigour and functional maturity of the thermoregulatory system in early stages of development would be determining a relative greater variability at the individual thermoregulatory abilities (Dreiss et al., 2016). Lastly, the higher the heterogeneity in iris pigmentation, the lower the visual acuity may be (Frank et al., 2000), which may cause further stress when visual effort to maintain proprioception during a physical exercise needs to be consistent.

Contrastingly, coat colour and particularities, and training regime did not significantly affect the body surface temperature in the study sample. The camel hair medulla, independently of their colour and the possible influence of colour on light reflection capacity, provides animals with a notable thermoregulatory capacity (Hasi, Amu, & Zhang, 2020). These results are in accordance with those reported by Abdoun et al. (2013), who found a non-significant effect of coat colour on thermophysiological responses and heat tolerance in Saudi dromedaries. Such outcome would also explain why it do exist camels of very different colours, even dark, at desert-like environments. Finally, the non-meaningful influence of training regimen on thermophysiological response in camels could be derived from the above cited physiological adaptations of these animals to energy optimization in arid and semi-arid environments.

Future applied thermography studies should focus on the overcome of some current limitations such as the measurement of rectal temperature and the analysis of biochemistry data so that correlations between thermographic and physiological parameters can be established. Additionally, if we would include age as a covariate to this information set, we could estimate the life span of sport dromedaries. With this aim, it would be taken as a reference that, when significantly higher values of surface temperature and levels of stress-related biomarkers are detected for the same physical effort among animals of different ages, tolerance to physical exercise would be lower and, therefore, greater probability of negative impact on individual well-being.

Conclusions

The lesser the regional dispersion at the thermophysiological response after physical exercise, the more likely to discard potential local functional alterations with possible systemic impact. Moreover, a greater individual tolerance to physical exercise-induced stress and thus lesser negative impact on animal welfare can be assumed. Specifically, a lower dispersion of the surface temperature at the withers, shoulder, and rump areas, should be preferably used to select dromedary camels for traits related to tolerance to physical exercise-related stress, given that larger overall data variability was detected at these body regions within the study population. In addition, the edge values of the temperature range at the local level for cornea, pectoral muscles, semimembranosus-semitendinosus muscles and hind fetlock, have a discriminating effect in this regard, and camels with lower values for T_{max} and T_{min} at these areas after exercise have to be prioritized for selection with genetic improvement purposes. Sex, castration, age and iris pigmentation also significantly affect thermophysiological response to exercise in dromedaries, which can be related to variations at stress levels because of hormone, general vigor and visual acuity-mediated effects. Future applied studies are encouraged to correlate thermographic measurements with other physiological data, as well as to estimate life span of sport dromedaries by including the age as covariate in the combined monitoring (non-invasive and invasive techniques) of tolerance to physical exercise.

Author contributions: Conceptualization, C.I.P., F.J.N.G. and J.V.D.B.; Data curation, C.I.P., F.J.N.G. and C.M.N.; Formal analysis, C.I.P., F.J.N.G. and J.V.D.B.; Funding acquisition, E.C. and J.V.D.B.; Investigation, C.I.P. and F.J.N.G.; Methodology, C.I.P., F.J.N.G. and C.M.N.; Project administration, E.C. and J.V.D.B.; Resources, E.C. and J.V.D.B.; Software, C.I.P., F.J.N.G. and C.M.N.; Supervision, F.J.N.G., E.C. and J.V.D.B.; Validation, C.I.P., F.J.N.G. and C.M.N.; Visualization, E.C.; Writing—original draft, C.I.P. and F.J.N.G.; Writing—review & editing, F.J.N.G., E.C. and J.V.D.B. All authors have read and agreed to the published version of the manuscript.

Funding: The present research was carried out in the financing framework of the international project CA.RA.VA.N—'Toward a Camel Transnational Value Chain' (Reference APCIN-2016-00011-00-00) and during the covering period of a predoctoral contract (FPU Fellowship) funded by the Spanish Ministry of Science and Innovation and was developed under the context a Ramón y Cajal Post-Doctoral fellowship financially supported by MCIN/AEI/10.13039/501100011033 and European Union "NextGenerationEU"/PRTR" (Recovery, Transformation and Resilience Plan—Funded by the European Union—NextGenerationEU).

Data availability statement: The data presented in this study are available on request from the first author.

Acknowledgments: The authors would also like to thank 'Aires Africanos' Eco-tourism Company, Oasis Park Fuerteventura, and 'Camelus' Camellos de Almería, for their direct technical help and assistance.

Conflicts of interest: The authors declare no conflict of interest.

Ethics declaration statement: All farms included in the study followed specific codes of good practices and therefore, the animals received humane care in compliance with the national guide for the care and use of laboratory and farm animals in research. Written consent from the owners was obtained for their participation. The study was conducted in accordance with the Declaration of Helsinki. The Spanish Ministry of Economy and Competitivity through the Royal Decree Law 53/2013 and its credited entity, the Ethics Committee of Animal Experimentation from the University of Córdoba, permitted the application of the protocols present in this study as cited in the 5th section of its 2nd article, as the animals assessed were used for credited zootechnical use. This national Decree follows the European Union Directive 2010/63/UE, from the 22 September of 2010.

References

Abdel-Rahman, E. H., Alzahrani, F. S., & Sulieman, A. M. E. H. (2020). Potential of camel dung as promising organic manure in Saudi Arabia. *Advancements in Life Sciences*, 7(4), 202-207.

Abdo, M., Haddad, S. S., Aziz, E. K., Abdeen, A., & Sabek, A. (2019). Kinematics Biomechanical Analysis and Three Dimensional Reconstruction Diagnostic Technique of Carpal Joint during gait in One-Humped Camel (*Camelus dromedarius*). *Alexandria Journal for Veterinary Sciences*, 60(2).

Abdoun, K., Samara, E., Okab, A., & Al-Haidary, A. (2013). The relationship between coat colour and thermoregulation in dromedary camels (*Camelus dromedarius*). *Journal of Camel Practice and Research*, 20(2), 251-255.

Al-Hassan, A. (2020). Gelatin from camel skins: Extraction and characterizations. *Food Hydrocolloids*, 101, 105457.

Al-Shorepy, S. S. (2011). Identification of environmental factors affecting the racing performance of race camels in the United Arab Emirates. *Emirates Journal of Food and Agriculture*, 424-430.

Al Kanhal, H. A. (2010). Compositional, technological and nutritional aspects of dromedary camel milk. *International Dairy Journal*, 20(12), 811-821.

Alexander, R. M. (1991). Energy-saving mechanisms in walking and running. *Journal of experimental biology*, 160(1), 55-69.

Alexander, R. M., Maloiy, G., Ker, R., Jayes, A., & Warui, C. (1982). The role of tendon elasticity in the locomotion of the camel (*Camelus dromedarius*). *Journal of Zoology*, 198(3), 293-313.

Alsafy, M. A., El-Gendy, S. A., & Kamal, B. (2021). Computed tomographic and radiographic morphology of the pastern and coffin joints of One-Humped Camel (*Camelus dromedarius*). *Anatomia, histologia, embryologia*, 50(1), 108-113.

Badawy, A. M. (2011). Computed Tomographic anatomy of the fore foot in one-humped camel (*Camelus dromedarius*). *Global veterinaria*, 6(4), 417-423.

Burger, P. A., Ciani, E., & Faye, B. (2019). Old World camels in a modern world–a balancing act between conservation and genetic improvement. *Animal Genetics*, 50(6), 598-612.

Chan, Y. (2005). Biostatistics 303. Discriminant analysis. *Singapore medical journal*, 46(2), 54.

Dagg, A. I. (1974). The locomotion of the camel (*Camelus dromedarius*). *Journal of Zoology*, 174(1), 67-78.

Delmas, R., & Liu, Y. (2005). Exploring students' conceptions of the standard deviation. *Statistics Education Research Journal*, 4(1), 55-82.

Dreiss, A. N., Séchaud, R., Béziers, P., Villain, N., Genoud, M., Almasi, B., Jenni, L., & Roulin, A. (2016). Social huddling and physiological thermoregulation are related to melanism in the nocturnal barn owl. *Oecologia*, 180, 371-381.

Dunbar, D. C., Macpherson, J. M., Simmons, R. W., & Zarcades, A. (2008). Stabilization and mobility of the head, neck and trunk in horses during overground locomotion: comparisons with humans and other primates. *Journal of Experimental Biology*, 211(24), 3889-3907.

Eddy, A., Van Hoogmoed, L., & Snyder, J. (2001). The role of thermography in the management of equine lameness. *The veterinary journal*, 162(3), 172-181.

El-Deeb, W., & Abdelghani, M. A. (2022). Investigation of Lameness in Racing Dromedary Camels (*Camelus Dromedarius*) and Associated Oxidative Stress Biomarkers. *Indian Journal of Animal Science*, 29(2), 215-222.

El-Shafey, A., & Kassab, A. (2013). Computed Tomography and Cross-Sectional Anatomy of the Metatarsus and Digits of the One-humped Camel (*Camelus dromedarius*) and Buffalo (*Bos bubalis*). *Anatomia, histologia, embryologia*, 42(2), 130-137.

Fowler, M. (2011). *Medicine and surgery of camelids*: John Wiley & Sons.

Frank, R. N., Puklin, J. E., Stock, C., & Canter, L. A. (2000). Race, iris color, and age-related macular degeneration. *Transactions of the American Ophthalmological Society*, 98, 109.

González Ariza, A., Arando Arbulu, A., Navas González, F. J., León Jurado, J. M., Delgado Bermejo, J. V., & Camacho Vallejo, M. E. (2022). Data mining-based discriminant analysis as a tool for the study of egg quality in native hen breeds. *Scientific Reports*, 12(1), 15873.

Hamdi, I., Benaissa, A., Babelhadj, B., Bedda, H., Aboub, S., & Loubaki, R. (2022). Composition and structure of the skin of dromedary (*Camelus dromedarius*, L. 1758) from two Algerian populations. *Journal of Animal Behaviour and Biometeorology*, 10(2), 0-0.

Hasi, S., Amu, G., & Zhang, W. (2020). Camel hair structure, properties, and commercial products. In *Handbook of research on health and environmental benefits of camel products* (pp. 328-347): IGI Global.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S., & Bermejo, J. V. (2020). Biokinematics and applied thermography in the Canarian camel breed. *Archivos de zootecnia*, 69(265), 102-107.

Ijichi, C., Evans, L., Woods, H., & Yarnell, K. (2020). The Right Angle: Validating a standardised protocol for the use of infra-red thermography of eye temperature as a welfare indicator. *Animal Welfare*, 29(2), 123-131.

Janis, C. M., Theodor, J. M., & Boisvert, B. (2002). Locomotor evolution in camels revisited: a quantitative analysis of pedal anatomy and the acquisition of the pacing gait. *Journal of vertebrate paleontology*, 22(1), 110-121.

Kadim, I. T., Mahgoub, O., Faye, B., & Farouk, M. M. (2013). *Camel meat and meat products*: CABI Books.

Khumsap, S., Lanovaz, J., & Clayton, H. (2004). Three-dimensional kinematic analysis of horses with induced tarsal synovitis. *Equine Veterinary Journal*, 36(8), 659-663.

Kirimtat, A., Krejcar, O., Selamat, A., & Herrera-Viedma, E. (2020). FLIR vs SEEK thermal cameras in biomedicine: comparative diagnosis through infrared thermography. *BMC bioinformatics*, 21(2), 1-10.

Kozlov, A., & Son'kin, V. (2019). Infrared Thermography Diagnostics of Subcutaneous Thermogenerators of Non-Shivering Thermogenesis. *Human Physiology*, 45(6), 658-672.

Kumar, S., Lamo, D., Gahlawat, G., Bharti, V. K., & Kumar, K. (2022). Effect of endurance load exercise on physio-biochemical and hormonal parameters of single-humped camels (*Camelus dromedarius*) at high altitude. *Indian Journal of Animal Sciences*, 92(7), 837-842.

Li, H. J., & Guo, K. K. (2013). Research on structure and properties of camel wool. *Advanced Materials Research*, 750, 2313-2316.

Maloiy, G., Rugangazi, B., & Rowe, M. (2009). Energy expenditure during level locomotion in large desert ungulates: the one-humped camel and the domestic donkey. *Journal of Zoology*, 277(3), 248-255.

Merkies, K., Ready, C., Farkas, L., & Hodder, A. (2019). Eye blink rates and eyelid twitches as a non-invasive measure of stress in the domestic horse. *Animals*, 9(8), 562.

Ogard, W. K. (2011). Proprioception in sports medicine and athletic conditioning. *Strength & Conditioning Journal*, 33(3), 111-118.

Pfau, T., Parsons, K., & Wilson, A. (2006). Mechanics of over-ground locomotion in the dromedary camel (*Camelus dromedarius*). *Journal of Biomechanics*(39), S359.

Pigière, F., & Henrotay, D. (2012). Camels in the northern provinces of the Roman Empire. *Journal of Archaeological Science*, 39(5), 1531-1539.

Schulz, U. (2008). *El camello en Lanzarote*: Aderlan.

Simon, E. L., Gaughan, E. M., Epp, T., & Spire, M. (2006). Influence of exercise on thermographically determined surface temperatures of thoracic and pelvic limbs in horses. *Journal of the American Veterinary Medical Association*, 229(12), 1940-1944.

Soroko, M., Howell, K., Dudek, K., Henklewski, R., & Zielińska, P. (2017). The influence of breed, age, gender, training level and ambient temperature on forelimb and back temperature in racehorses. *Animal Science Journal*, 88(2), 347-355.

Soroko, M., Jodkowska, E., & Dudek, K. (2015). Thermography diagnosis in monitoring the annual training cycle of racehorses. *Medycyna Weterynaryjna*, 71(1), 52-58.

Tunley, B., & Henson, F. (2004). Reliability and repeatability of thermographic examination and the normal thermographic image of the thoracolumbar region in the horse. *Equine veterinary journal*, 36(4), 306-312.

Turner, T. A., Pansch, J., & Wilson, J. H. (2001). Thermographic assessment of racing Thoroughbreds. *Proceedings of the American Association of Equine Practitioners* , 47, 344-346.

Windberger, U., Auer, R., Seltenhammer, M., Mach, G., & Skidmore, J. A. (2019). Near-Newtonian Blood Behavior–Is It Good to Be a Camel? *Frontiers in Physiology*, 10, 906.

Wood, R. I. (2004). Reinforcing aspects of androgens. *Physiology & behavior*, 83(2), 279-289.

Yarmolenko, P. S., Moon, E. J., Landon, C., Manzoor, A., Hochman, D. W., Viglianti, B. L., & Dewhirst, M. W. (2011). Thresholds for thermal damage to normal tissues: an update. *International Journal of Hyperthermia*, 27(4), 320-343.

Yarnell, K., Fleming, J., Stratton, T. D., & Brassington, R. (2014). Monitoring changes in skin temperature associated with exercise in horses on a water treadmill by use of infrared thermography. *Journal of Thermal Biology*, 45, 110-116

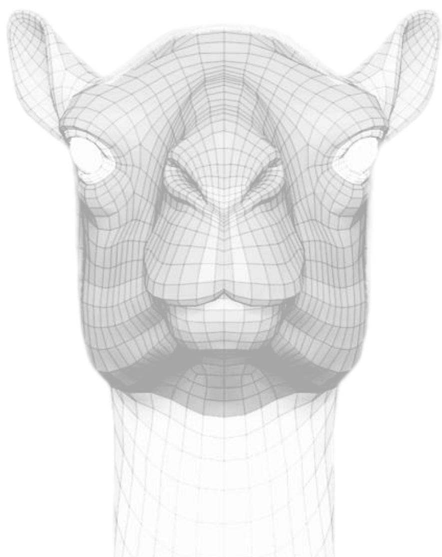
CHAPTER 4
ETHOLOGICAL CHARACTERIZATION OF 'CANARIAN CAMEL' BREED

4.1 Lunar cycle, climate, and onset of parturition in domestic dromedary camels: implications of species-specific metabolic economy and social ecology

Carlos Iglesias Pastrana[1], Francisco Javier Navas González[1], Juan Vicente Delgado Bermejo[1] and Elena Ciani[2]

[1]Department of Genetics, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain

[2]Department of Biosciences, Biotechnologies and Biopharmaceutics, Faculty of Veterinary Sciences, University of Bari 'Aldo Moro', 70121 Bari, Italy



Quality indicator information provided on the publication
Latest information available (2022)

Status of the manuscript: Published

Journal (year, volume, page(s)): *Biology* 2023, *12*, 607

International database in which it is indexed: Journal of Citation Reports (JCR)

Thematic area in the reference database: Biology

Impact index of the journal in the year of the article's publication: 4.2

Rank/number of thematic area journals: 25/92 (Q2)

Abstract

Given energy costs for gestating and caring for male offspring are higher than those of female newborns, external environmental conditions might be regarded as likely to affect the timing of delivery processes differentially depending on the sex of the newborn calf to be delivered. The aim of the present paper is to evaluate the association between environmental stressors such as the moon phase and weather-related factors and the onset of labor in female dromedaries. A binary logistic regression model was developed to find the most parsimonious set of variables that are most effective in predicting the probability for a gravid female dromedary to give birth to a male or a female calf, assuming that higher gestational costs and longer labor times are ascribed to the production of a male offspring. Although the differences in the quantitative distribution of spontaneous onset of labor across lunar phases and the mean climate per onset event along the whole study period were deemed nonsignificant ($p > 0.05$), a non-negligible prediction effect of a new moon, mean wind speed and maximum wind gust was present. At slightly brighter nights and lower mean wind speeds, a calf is more likely to be male. This microevolutionary response to the external environment may have been driven by physiological and behavioral adaptation of metabolic economy and social ecology to give birth to cooperative groups with the best possible reduction of thermoregulatory demands. Model performance indexes then highlighted the heterothermic character of camels to greatly minimize the impact of the external environment. The overall results will also enrich the general knowledge of the interplay between homeostasis and arid and semi-arid environments.

Keywords

Labor onset, lunar phase, weather factors, offspring sex, social communication, heterothermia, epigenetic control

Introduction

Circadian rhythm, or the physiological functions and behavioral responses that are regulated in a 24-h day-night cycle, have been widely investigated in an attempt to understand its adaptive role, evolution, and relative significance (Patke, Young, & Axelrod, 2020; Vaze & Sharma, 2013). Photoperiod is indeed the most cited factor within the theoretical background and analyses of the environmental cues responsible for oscillations on circadian timing (Benstaali et al., 2001; López-Olmeda, Madrid, & Sánchez-Vázquez, 2006; Prokkola & Nikinmaa, 2018). The secretion of the hormone melatonin, being inversely related to day length, provides organisms with the signal to measure time physiologically and thus maximize the investment of energy differentially among competing processes, ranging from subcellular metabolism to more complex traits such as thermoregulation and behavior (Walton, Weil, & Nelson, 2011). In the last case, although many behaviors affected by photoperiod are associated with reproduction seasonality, some affective responses, cognitive outputs, and migratory states are also controlled by environmental light independently of circulating gonadal steroids (Reppert, 2006; Weil, Bowers, & Nelson, 2007; Workman, Bowers, & Nelson, 2009).

The exploration of the effects of the lunar cycle on animal behavior and physiology represents the most striking example of how not only hormonal but also immunological and neural pathways that underlie complex phenotypic traits are modulated by the amount of light and darkness in a daily cycle. Being the putative molecular mechanisms that are still undetermined, moonlight intensity, geomagnetism, and gravity are argued to be more likely the primary causes of the periodic deviation in frequency or intensity for specific brain and body functions. Specifically, defense behavior and spacing, predator-prey dynamics (Grant, Halliday, & Chadwick, 2013; Kronfeld-Schor et al., 2013), and systematic variations in birth rate, fertility, ovulation, and locomotor activity, are reported to be lunar-synchronized events in different species and that have particular adaptive values depending on the ecological niche of each aggrupation of organisms (Abecia, Arrébola, & Palacios, 2017; Fernández-Duque, De La Iglesia, & Erkert, 2010; Palacios & Abecia, 2014; Palmer et al., 2017; Yonezawa et al., 2016) .

In spite of the fact that the light–darkness cycle may be the primary environmental cue used by living organisms to synchronize physiological processes with regular exogenous fluctuations, this temporal rhythm is also sensible to varying weather, so the circadian clock has evolved to shape both the dynamics of the light–darkness cycle and climatic signals (Pfeuty et al., 2012; Troein et al., 2009). Warm, dry, and calm conditions are linked to the advancement of the timing of reproduction and the date of termination of hibernation and a decrease in growth rate and semen quantity and quality variables in some animal species (Boutin & Lane, 2014; Chinchilla-Vargas, Kerns, & Rothschild, 2018; Linton & Macdonald, 2018). Similarly, significant associations between weather variables such as temperature, humidity, precipitation, or wind patterns and adverse pregnancy outcomes in humans (Beltran, Wu, & Laurent, 2014) and cows (Sasaki et al., 2019) have been found. Moreover, changes in atmospheric pressure have been reported to influence the occurrence of the spontaneous onset of labor in term pregnancies and the birth rate (Ammann et al., 2016; Noller, Resseguie, & Vossb, 1996). However, the significance of the effects of the moon phase and weather conditions on physiology is a subject that arouses controversy within the scientific community, given the disparity of the results found. Several studies that have been carried out with regard to this applied field have concluded the effects were not statistically significant or the modeled size of the effect was not consistent enough so as for a clinical implication to be determined (Aguilar, Cuervo-Arango, & Santa Juliana, 2015; Alberghina et al., 2021).

Among the most criticized errors of the aforementioned studies is the common preference for birth rate rather than the onset of labor as the variable to be correlated with the moon phase or meteorological conditions. Stern, Glazer, and Sanduleak (1988) stated that if the moon phase influences the birth rate, it could be only a final consequence of the effects of the satellite on the time of the onset of labor ending in the birth itself. Among the principal factors, particularly endocrine, involved in the process of animal parturition are the changes in hormonal levels of estrogen, progesterone, prostaglandins, oxytocin, corticotrophin-releasing hormone, and cortisol (Reyes-Lagos et al., 2019). Although different environmental stressors are reported to interfere with the endocrinology of reproductive function (Bova et al., 2014; Pankhurst & King, 2010; Parraguez & Gonzalez-Bulnes, 2020), the exact effects of the moon cycle and climate-related factors on the mechanisms and mediation of endocrine but also nervous (e.g., allostatic load) (Palagini et al., 2014) and immune systems (e.g., cytokines and surfactant proteins) (Mendelson & Condon, 2005) that lead to the initiation of parturition, are hardly elucidated for several species.

Additionally, the methods, when used, of determining individual exposure to the moon and weather effects may generate bias in the power of statistical tests to detect significant relationships (Alderman et al., 1988). Apart from that, from a meta-analytical viewpoint, the disparity of results might be a reflection of the gene variation of the circadian clock across large geographical areas, hence the latitudinal clines discovered in its gene frequencies (Kyriacou et al., 2008). Lastly, and strongly related to the previous argument, the inclusion of non-native organisms into the study sample could derive from the lack of strong association between local environmental conditions and the body functioning of inhabiting beings, especially if the history of adaptation dates recently and the heritability of adaptive traits remains low (Heckwolf et al., 2021).

Canarian dromedaries are an endangered, unique breed with a historical record of local adaptation and evolution for six centuries but which lacks a rigorous estimation and control of its reproductive timing for management and conservation purposes (Pastrana et al., 2021). Although an increasing tendency for intensification of camel farming systems is patent, these animals are mostly reared in traditional extensive forms (Faye, 2020), thus being relatively exposed to environmental stressors (climatic, chemical, wildfire, physical, and biological stressors). In these regards, environmental-based epigenetic modifications can occur in embryonic tissues and cells via mother-fetus communication through the placenta (Record, 2014; Walton et al., 2011). Furthermore, higher gestational costs and longer labor times are ascribed to the production of male offspring in comparison with female offspring (Dama, 2012; Dwyer, 2003). Moreover, metabolic maturity, general vigor, and the ability to thermoregulate female offspring are expected to be reached sooner than the respective for male offspring (Plush, 2014). In this scenario, dromedaries are well known to have developed exceptional physiological and biochemical adaptations to extreme arid environments and limitation of resources, in addition to the seasonal nature of their reproduction, that allow them to optimize both the utilization and storage of energy and water with a central role of thermoregulatory mechanisms (Hoter, Rizk, & Naim, 2019). Among such adaptations, female dromedaries have been reported to modulate pregnancy length in response to some environmental stresses (Nagy & Juhász, 2019; Tibary & El Allali, 2020).

Therefore, considering that parturition is a highly energy-demanding process (Tokach et al., 2019) and gravid dromedary females would seek to maintain homeostasis, different impacts of environmental factors in the onset of labor depending on the sex of offspring could be expected given the abovementioned differential sex-mediated energy costs. That is an adaptive allocation of energy to maximize the constancy of the internal environment and general fitness. In this context, the present research aims to study the effects of the lunar cycle and weather conditions on the spontaneous onset of labor, depending on the sex of the offspring, in Canarian dromedary camels.

To the best of our knowledge, this is the first approach to the potential prediction of the spontaneous onset of labor based on a large dataset of environmental cues in dromedary camels, which includes additional weather factors different from temperature, relative humidity, and length of daylight. From the perspective of clinicians and breeders, in the absence of dedicated algorithms and machine-learning technologies for calving prediction in this animal species, these results would be of help in a meaningful manner to know which factors impact the most on the onset of parturition and, thus, plan adapted perinatal assistance to favor the establishment of the mother-calf bond in the best conditions, which is crucial to stimulate milk let-down in these animals (Dioli, 2022). In addition, the research community will be provided with a deeper empirical exploration of phenotypic plasticity in dromedaries and boosted for the examination of both the existence and extent of latitudinal clines in circadian clock gene frequencies in these animals, in view of the fact that their historical range of habitat is relatively restricted (Burger & Ciani, 2022). Altogether, such outcoming pieces of knowledge will assist in filling knowledge gaps on physiological ecology and ecological genetics in camels (Iglesias Pastrana et al., 2020).

Material and methods

Animal sample: candidate selection

The data used for the present retrospective study resulted from the registries of the date and hour of initiation of 415 spontaneous onsets of labor at term over the period of time between January 1992 and March 2022, both inclusive, in Canarian she-dromedaries reared at Fuerteventura (Canary Islands, Spain; 28°25′57″ N–14°00′11″ W). Concerning the sex of the resultant offspring, the study sample comprised 208 male and

207 female newborns. Each calving event registered concerned a single different gravid primiparous female; hence no subsequent parturitions of the same gravid she-dromedary existed in the database. This way, the reproductive phenology across the lunar cycle and weather in the study population can be evaluated under the scope of epigenetics, that is, inherited modifications linked to the exposure to environmental factors and that are not patent in DNA sequence (Cavalli & Heard, 2019).

Initially, gravid she-dromedaries were pre-selected based on a clinical examination to ensure the proper health status of the pair dam-fetus at the final stage (last month) of the normal gestation period. Then, the clinical signs that were subjected to observation in the pre-selected gravid females as indicators of the spontaneous initiation of labor were the following: relative isolation from the main herd, restlessness with the alternate of lying down and standing up, increase in urination frequency, and swelling of the vulva, udder, and teats (Khanvilkar, Samant, & Ambore, 2009). When at least three of these symptoms were observed simultaneously in a gravid female, the date and hour of the observation were annotated as the spontaneous onset of labor. The reliability of these clinical signs to advance the time of parturition was confirmed with the appearance of the first water bag at the vulva within the next few minutes. Once the calf was upright with all four legs fully extended for the first time, the sex of the newborn (response variable) was recorded. All the episodes of the spontaneous onset of parturition recorded for this study were those that ended in the successful survival of the offspring.

All calving events used for this investigation were produced at the same facilities, without any prominent variation in housing conditions during the study period to reduce the magnitude to which the effects of environmental variables on the onset of parturition could be masked by other factors both on an individual camel and herd level.

Farming environment: a historical background

The study site (Fuerteventura, Canary Islands, Spain) is the most representative emplacement where Canarian dromedaries, the only camel breed along Europe and cataloged in danger of extinction by the Spanish Ministry of Agriculture, Food, and Environment since 2012 (Order AAA/251/2012), have been and still are bred and used for the exportation of live animals. For utilitarian and managerial reasons, Canarian dromedaries are reared in single-sex groups with the best procured homogeneous distribution of age structure (Iglesias Pastrana et al., 2021).

Since their arrival to the archipelago from the nearest African coast circa 1405, dromedaries in the Canary Islands mainly served as service animals for rural laborers and were immersed in family farming production regimes in which a lack of rigorous genealogical records was routinely practiced (Schulz, 2008). However, the mechanization of these activities from the last third of the twentieth century led to a decrease in the census and obligated the local breeders to seek new functional niches for their animals. Fortunately, the relatively rapid conversion of dromedaries into a far-iconic attractiveness within the touristic and recreational industry in the archipelago around the 1990s resulted in a population recovery (Wilson & Gutierrez, 2015). Thenceforth, Canarian dromedaries were progressively allocated at higher stocking densities in more controlled environments to carefully manage populations for their reproductive and genetic health (Schulz, 2008).

The housing environment of the study population consisted of square-shaped fenced corrals with a shelter creating a shaded area in the middle of the pen that had enough extension so that the total number of dromedary camels kept in the same pen could lie on it. Both the feeding and drinking points were placed along one of the lateral sides of the facility.

Moon phase and weather variables: data collection

In addition to the response variable (sex of the calf), the records were completed with the moon phase and the average value for weather variables during the 24 h previous to the registered hour of onset of parturition for each gravid female. This timeframe is reported to be the most reliable temporal period to detect signals that are significantly related to the date of delivery (Ricci et al., 2018).

Moon phase information was retrieved from lunar calendars. The number of days since the previous full moon was calculated for each onset of labor date, following the methodology of Grant, Halliday and Chadwick (2013). Eight moon phases were analyzed: full moon to waning gibbous (Lunar phase 1), waning gibbous to the third quarter (Lunar phase 2), third quarter to a waning crescent (Lunar phase 3), waning crescent to new moon (Lunar phase 4), new moon to waxing crescent (Lunar phase 5), waxing crescent to the first quarter (Lunar phase 6), first quarter to waxing gibbous (Lunar phase 7), and waxing gibbous to full moon (Lunar phase 8).

The weather parameters were obtained from two different data repositories. The respective values for the variables 'Mean temperature' (°C), 'Minimum temperature' (°C), 'Maximum temperature' (°C), 'Precipitation' (L/m^2), 'Mean wind speed' (m/s), 'Maximum wind gust' (m/s), 'Direction of the maximum wind gust' (tens of degrees), 'Hours of sunshine' (h), 'Mean atmospheric pressure' (hPa), 'Minimum atmospheric pressure' (hPa), and 'Maximum atmospheric pressure' (hPa) were acquired from the official, historical data repository of the meteorological station located near to the study site (https://datosclima.es/ accessed on 2 December 2022; ID of the weather station: C249I; Coordinates: 28°26′41″ N– 13°51′47″ W). 'Relative humidity' (%) and 'Mean visibility' (km) were computed from an additional free repository for the same weather local station (https://www.tutiempo.net/ accessed on 2 December 2022).

Statistical analyses

First, we tested for significant differences in (1) annual variation in proportions of spontaneous onset of parturition across lunar phases, (2) the total number of male and female calves that were born in each lunar phase along the whole study period, (3) annual mean values per weather variable considering all the spontaneous onsets of labor produced in a year, and (4) mean values for each weather variable at the onset of labor depending on the sex of offspring during the whole study period, in order to have a general view of the reproductive phenology across the lunar cycle and weather on the studied population. Since all the data sets violated the normality assumption (Shapiro–Wilk test, $p < 0.05$), non-parametric Mann–Whitney U tests (Mann & Whitney, 1947) were performed to investigate whether there were statistically significant differences in the median between associated subgroups values.

Afterward, a binary logistic regression model was developed to find the most parsimonious set of predictors that are most effective in predicting the probability for a gravid she-dromedary to give birth to a male or a female calf (dependent, binary variable) (Harrell, 2015). To ensure the independence of the regressors, a preliminary test of multicollinearity was run. The thumb rules used for the interpretation of the existence of multicollinearity were values of tolerance lesser than 0.10 and/or a variance inflation factor (VIF) greater than 5 (Midi, Sarkar, & Rana, 2010).

Hence, the probability of giving birth to a male or a female calf was modeled according to the equation: Logit (P) = ln (P / (1-P)) = f, where P is the probability of the response variable to be modeled, and f is defined by the following function $f = b_0 + b_1 F_1 + b_2 F_2 + \ldots + b_n F_n + b_{12} F_1 F_2 + \ldots + b_{n-1,n} F_{n-1} F_n$; in which b refers parameters to be fitted, and F_n represents the used finally as predictors in the model after the multicollinearity analysis. For the particular case of the independent predictor variable 'Lunar phase', since it is a categorical variable, the statistical procedure recoded it automatically.

The 'Enter' method was selected to include the predictive factors in the model. Several predictive performance indexes and the goodness of fit of the statistical model were computed: (i) omnibus test, (ii) coefficient of determination Nagelkerke R^2, and (iii) Hosmer- Lemeshow (HL) statistic.

All the statistical procedures described were fitted in IBM® SPSS® Statistics 25.0 software (IBM SPSS, Inc., Chicago, IL, USA), with a confidence interval and level of significance of 95% and $p < 0.05$, respectively.

Results

Quantitative distribution of spontaneous onset of labor across lunar phases

No statistically significant differences ($p > 0.05$) were found neither for the annual proportions of spontaneous onset of parturition across lunar phases between years nor for the total number of male and female calves that were born in each lunar phase along the whole study period.

Figure 1 depicts the relative frequency of the spontaneous onset of labor in each lunar phase per year. An incipient change in the relative distribution of the onset of parturition across lunar phases per year can be truly appreciated more remarkably since 2004; from the concentration of most of the annual deliveries in a reduced number of lunar phases (Lunar phases 4, 5, and 6) during the first decade, the initiation of parturition in Canarian dromedaries has become an event that is distributed in a relatively homogeneous proportion between lunar phases but still with a comparatively superior predominance of the same lunar phases.

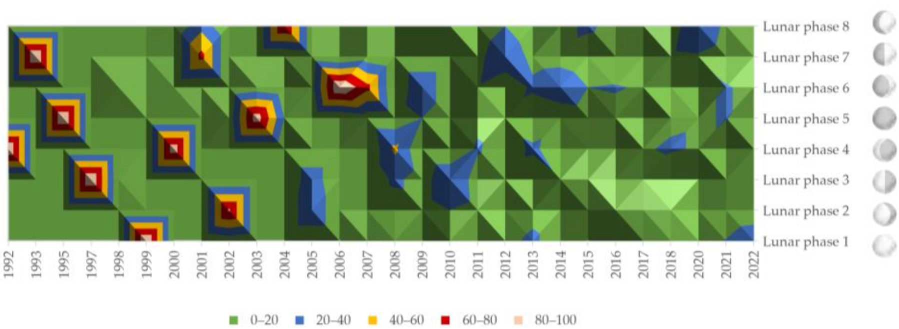


Figure 1. Relative frequency (percentage, %) of spontaneous onset of labor in each lunar phase per year. The relative frequency of spontaneous onset of parturition is defined as the number of births in each lunar phase in relation to all episodes of spontaneous onset of labor recorded in a specific year.

The total number of male and female calves that were born per lunar phase during the study period is represented in Figure 2. For newborn male calves, the onset of labor is most likely to be produced during the lunar phases 4 or 6 (decreasing and increasing moonlight intensity, respectively), while the lunar phase 5 (lowest moonlight intensity) is the time of the lunar calendar at which the probability of a female calf to be born is higher.

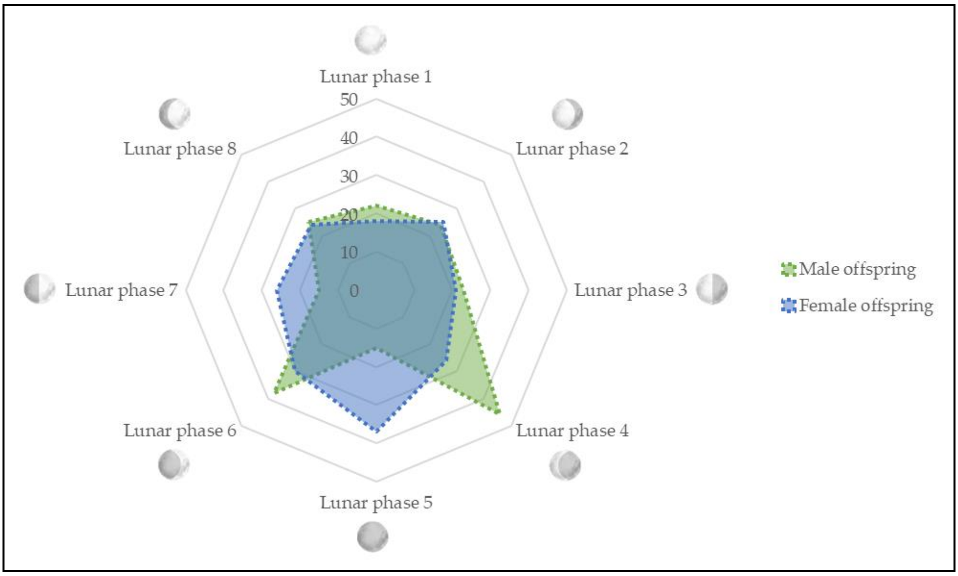


Figure 2. Total number of male and female calves that were born in each lunar phase throughout the whole study period.

Mean climate per spontaneous onset of parturition

The interannual variation in the mean values for weather variables at the onsets of parturition registered each year is graphically displayed in Figure 3. Although no statistically significant differences ($p > 0.05$) were found between annual mean values per weather variable considering all the spontaneous onsets of labor produced in a year, particular trends of variation can be observed for some variables. Those weather conditions directly related to temperature ('Mean temperature', 'Minimum temperature', and 'Maximum temperature') and ambient air ('Mean wind speed', 'Maximum wind gust', and 'Direction of the maximum wind gust') have experimented with a progressive increase over the study period. The inverse tendency can be observed for those weather variables that refer to atmospheric pressure ('Mean atmospheric pressure', 'Minimum atmospheric pressure', 'Maximum atmospheric pressure'), relative humidity, and mean visibility. The remaining studied variables ('Precipitation' and 'Hours of sunshine') showed relatively constant variation across years.

When considering the mean values for weather variables at the onsets of parturition depending on the sex of offspring through the whole study period, the differences were not statistically significant ($p > 0.05$). Slight differences did exist for the variables related to precipitation, ambient air, and humidity (Figure 4).

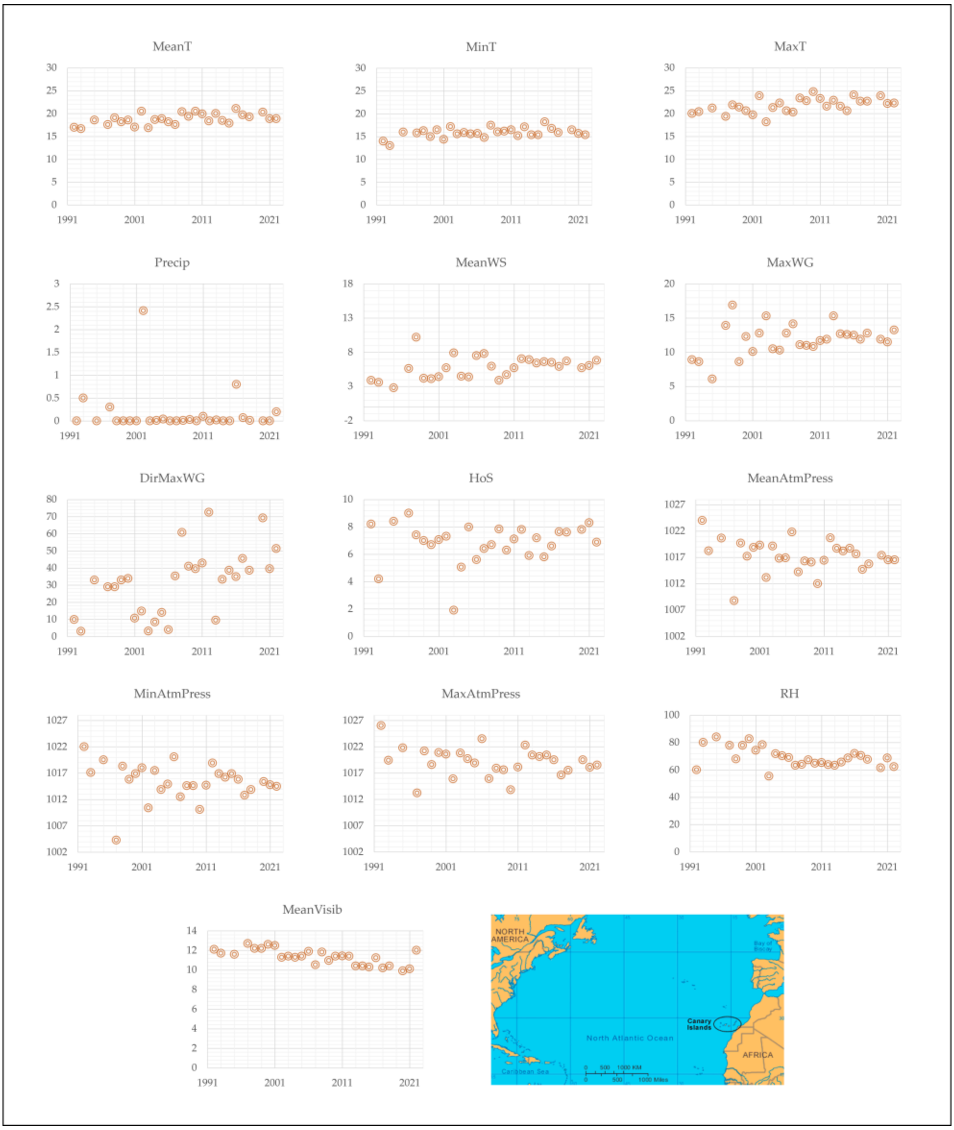


Figure 3. Interannual variation in the mean values for weather variables at the onsets of parturition registered each year. A map with the geographical location of the study area (black circle) is included at the bottom right of the figure. MeanT: Mean temperature, MinT: Minimum temperature, MaxT: Maximum temperature, Precip: Precipitation, MeanWS: Mean wind speed, MaxWG: Maximum wind gust, DirMaxWG: Direction of the maximum wind gust, HoS: Hours of sunshine, MeanAtmPress: Mean atmospheric pressure, MinAtmPress: Minimum atmospheric pressure, MaxAtmPress: Maximum atmospheric pressure, RH: Relative humidity, MeanVisib: Mean visibility.

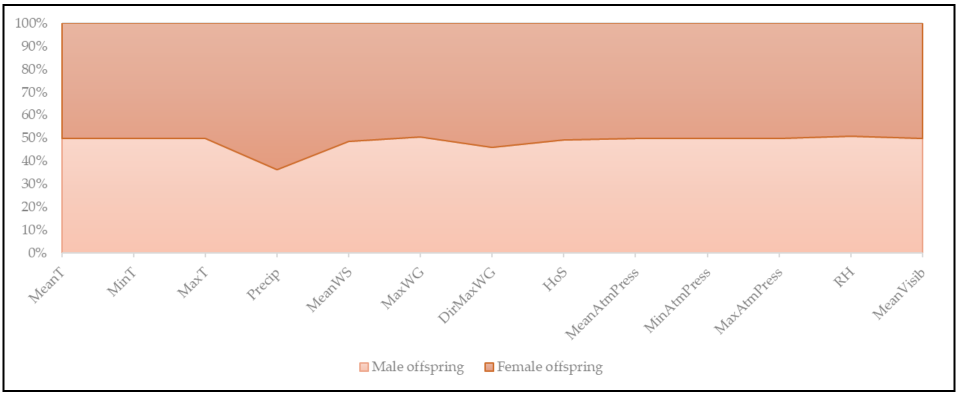


Figure 4. One hundred percent stacked area graph for the comparison of mean values for weather variables at the onsets of parturition depending on the sex of offspring over the study period. MeanT: Mean temperature, MinT: Minimum temperature, MaxT: Maximum temperature, Precip: Precipitation, MeanWS: Mean wind speed, MaxWG: Maximum wind gust, DirMaxWG: Direction of the maximum wind gust, HoS: Hours of sunshine, MeanAtmPress: Mean atmospheric pressure, MinAtmPress: Minimum atmospheric pressure, MaxAtmPress: Maximum atmospheric pressure, RH: Relative humidity, MeanVisib: Mean visibility.

Prediction of spontaneous onset of parturition based on environmental variables

Multicollinearity analysis

After multicollinearity analyses, only the variables of 'Lunar phase', 'Precipitation', 'Mean wind speed', 'Maximum wind gust', 'Direction of the maximum wind gust', 'Hours of sunshine', 'Relative humidity', and 'Mean visibility' were retained in the binary logistic regression model (tolerance values > 0.10 and VIF values < 5; Table 1).

Model performance

Table 2 summarizes the evaluation of the performance of the model and the regression coefficients, Wald values, statistical significances, and odds ratio (OR) for each variable that contributes to the model. Note that the reference or baseline category for the categorical predictor 'Lunar phase' that is used to compare one situation to another against the dependent variable is the last phase ('Lunar phase 8'). Since all odds ratios will be a comparison to the reference category, it means the OR for the reference category is equal to 1 (Tripepi et al., 2008).

Table 1. Multicollinearity analysis of lunar phase and weather-related variables to discard redundant factors.

Variable	Tolerance (1-R^2)	VIF (1/Tolerance)
Lunar phase	0.931	1.074
Mean temperature	0.000	4575.800
Minimum temperature	0.001	1132.490
Maximum temperature	0.001	1697.666
Precipitation	0.879	1.138
Mean wind speed	0.289	3.463
Maximum wind gust	0.314	3.182
Direction of the maximum wind gust	0.846	1.183
Hours of sunshine	0.691	1.448
Mean atmospheric pressure	0.060	16.239
Minimum atmospheric pressure	0.059	16.820
Maximum atmospheric pressure	0.063	15.838
Relative humidity	0.731	1.368
Mean visibility	0.888	1.126

Table 2. Model goodness-of-fit summary statistics and coefficient values for each independent factor in the equation.

Omnibus test	Nagelkerke R^2	HL Goodness-of-Fit test	Prediction Accuracy Rate (%)	Variable	Coefficient (*B*)	Standard error of *B*	Wald Statistic	Statistical significance	Estimated Odds Ratio (exp(*B*))
0.000	0.125	0.025	59.3	Lunar phase 8 (reference category)			17.860	0.013	1
				Lunar phase 1	−0.404	0.451	0.802	0.370	0.668
				Lunar phase 2	0.093	0.425	0.048	0.827	1.097
				Lunar phase 3	0.013	0.434	0.001	0.977	1.013
				Lunar phase 4	−0.526	0.405	1.685	0.194	0.591
				Lunar phase 5	1.024	0.439	5.430	0.020	2.783
				Lunar phase 6	−0.277	0.396	0.329	0.566	0.797
				Lunar phase 7	0.394	0.455	0.749	0.387	1.482
				Precipitation	0.156	0.106	2.149	0.143	1.168
				Mean wind speed	0.265	0.075	12.574	0.000	1.303
				Maximum wind gust	−0.177	0.056	10.123	0.001	0.838
				Direction of the maximum wind gust	0.002	0.003	0.454	0.500	1.002
				Hours of sunshine	0.051	0.043	1.371	0.242	1.052
				Relative humidity	−0.012	0.011	1.212	0.271	0.988
				Mean visibility	0.145	0.104	1.959	0.162	1.156
				Constant	−0.654	1.627	0.162	0.687	0.520

Discussion

The genus *Camelus* is widely recognized to have experimented with particular adaptations in its anatomic structure, physiological functioning, and ecological niche in order to survive harsh extreme environmental conditions while maintaining the energy reserves and structural integrity considerably well balanced (Warda et al., 2014). For a deeper understanding of the interplay between homeostasis and arid and semi-arid environments, it is useful to inquire into the particular influence of the external environment on high-energy demanding and challenging processes such as parturition and offspring care. Both the biochemical and endocrinological preparation for parturition and the posterior implication of parents to care for their offspring are subject to variation because of species-specific evolved responses to environmental selection pressures (Mitchell, Wolf, & Martin, 2022). In the present study, the effects of the lunar cycle and meteorological conditions on the spontaneous onset of labor, with special attention to the sex distribution of the resulting offspring, in dromedary camels have been examined for the first time.

Although no significant variation was encountered for the temporal distribution of the onset of parturition across lunar phases and weather conditions over the years, quantitative differences can be effectively observed (Figures 1–4). This suggests a progressive and successful adaptation of dromedaries to avoid important energy unbalance and thus minimize potential early undesirable adaptation processes that may have occurred (Rosenberger et al., 2019).

Additionally, the variability explained by the statistical model tested is not very high (Nagelkerke R^2; Table 2), which may lay on the fact that the impact of the environmental variables considered on the study population is not high or may rather involve a greater variety of factors nor has it been significant over time.

These findings highlight the ability of camels to switch their thermoregulation from endothermic homeothermy to becoming heterothermic and effectively minimize the impact of the external environment (Tibary & El Allali, 2020). From the viewpoint of animal welfare, an applied topic that is growing in a contemporaneous scene but still remains limited for camels (Iglesias Pastrana et al., 2020), it could be inferred the relatively higher importance of animal and herd-level indicators to rely on when designing camel rearing and handling protocols. That is, substantial attention should be paid to animal and herd-based measures so that the general fitness of the animals is the best possible to ensure good adaptive plasticity by putting into action their intrinsic mechanisms of adaptation to heterogeneous external environments.

Despite the moderate performance of the regression model, some of the potential predictors included did have a non-negligible effect (Table 2). Concretely, the variables that would significantly serve to predict, with a moderate accuracy rate (≈60%), the probability for a gravid she-camel to give birth to a male or a female calf were those related to the lunar phase (new moon) and ambient air (mean wind speed and maximum wind gust) (Table 2). That is, the local variation in these environmental features would have driven the adaptation of the time of delivery depending on the sex of the offspring. The phase of the new moon had the greatest influence on the model response variable (OR = 2.783; Table 2), with an OR value of 1.303 and 0.838 for the mean wind speed and maximum wind gust, respectively.

From an animal functional perspective, the underlying components of this adaptive strategy can be categorized into the differential energy costs of gestating a male or a female calf and the benefits of social cohabitation and interaction. Further, on the basis that camels have been involved in migration activities since their early domestication, these animals can be anticipated to have developed patterns of recognition of some celestial indicators. In these regards, some authors agree that the evolution of strategies to best adapt reproduction timing in dynamic environments will result in the benefit of offspring fitness both at the moment of birth and at subsequent life stages (Buckles & Hungerman, 2013; Isen, Rossin-Slater, & Walker, 2017; Shima et al., 2020). Similarly, Havenith (2002) stated that behavioral modulation is the most powerful thermoregulatory effector, a condition of paramount importance in desert-living animals.

In a transnational scenario, if we replicate the methodology for other camel populations, different values for the regression model performance as well as various weather conditions with predictive potential, would be revealed. Such variance might be ascribed to the phenotypic plasticity that exists between populations due to the particularities of the socio-geographical context in which they develop (evolutionary history) (Murren et al., 2015), and that may be determining the latitudinal clines in gene frequencies of the circadian clocks in these species which are imprinting an evolutionary response. In any case, the sample size needs to be carefully considered when interpreting and comparing the statistical results since some locally adapted camel populations are reared in a restricted habitat and have a reduced effective population size (Björklund & Bergek, 2009). However, it can be hypothesized that this between-population differentiation is not large and statistically significant given the already mentioned low genomic variability that is intrinsic to this animal species (genetic history), as well as the relatively limited eco-geographic distribution range of dromedary camels (Burger, Ciani, & Faye, 2019).

Low moonlight increases affiliative behavior and territorial defense

The relative frequency of the spontaneous onset of labor across lunar phases over the study period did experiment with a change in its quantitative trend (Figure 1). During the first decade, most of the annual deliveries were concentrated in the lunar phases of waning crescent to new moon (Lunar phase 4), new moon to waxing crescent (Lunar phase 5), and waxing crescent to the first quarter (Lunar phase 6). However, a relatively homogeneous proportion of the onset of labor events between lunar phases from the beginning of the 2000s until the present can be noticed. However, a comparatively superior predominance of the aforementioned lunar phases is still patent.

This finding could be indicative of a progressive adaptation of the animals to an environment with more controlled conditions, thus with a reduced impact of potential external stressors. Furthermore, in line with the social character of camels, the increase in the effective census of the population in recent years (Schulz, 2008) may promote the positive evolution of spatial cohesivity and cooperation among congeners towards the group defense and benefit. In addition, the fact that births continue to be numerically more probable under certain environmental lighting conditions, even though camels are in more controlled housing conditions, could reflect the existence of a phenotypic trait with an inheritable molecular signature in these animals.

In this paradigm, Goswami, et al. (2022) underlined the reasons that are responsible for the major variation in the timing and tempo of evolutionary change in mammals. Among the factors that best predicted the response of mammalian species to rapid changes in their environment were habitat, social behavior, diet, parental care, and patterns of locomotor activity. Concretely, social skills, diet, and locomotion are the most influential factors, as they are the main drivers of the morpho-functional evolution of brain size and cognitive abilities. Hence, social species, which can generally be differentiated by the development of characteristic morphological features that serve them for fighting and social display, evolve much faster than solitary species. Likewise, herbivores evolve faster than carnivores, probably because they follow changes in plants and the environment more closely than carnivores. On the other hand, species with a strict activity pattern, whether diurnal or nocturnal, would evolve more slowly than animals without fixed habits of activity.

Within this contextualization and specifically concerning the specific influence of environmental light on social behavior, an increase in the social communication and/or interaction between congeners in dim light conditions for some mammal and bird species is reported (Bender, Bayne, & Brigham, 1996; Kurvers & Hoelker, 2015; Penteriani & Delgado, 2017; Pérez-Granados, Schuchmann, & Marques, 2022; York, Young, & Radford, 2014). This, in turn, might enforce social cohesion both at a horizontal and vertical level. Similarly, the activity in mammals (Gutman et al., 2011; Krief et al., 2014; Penteriani et al., 2013; Sábato et al., 2006), birds (Pyle et al., 1993; Rodríguez et al., 2016), reptiles (Clarke, Chopko, & Mackessy, 1996; Seligmann et al., 2007), urodeles (Grant, Chadwick, & Halliday, 2009), and invertebrates (Gebresilassie et al., 2015; Ray & Chakraverty, 1934; Souza et al., 2005) is positively correlated with decreasing moonlight. During a full moon, animals' visual skills may be better and move at lesser proportions since they can identify both surrounding resources and potential threats more easily, but they are also more exposed to predators in these bright light conditions. On the other hand, during dark nights, visibility is worse, and they would need to move more to access resources but are more aggregated and in continuous communication with their congeners to feel guarded or safe.

Spawning behavior in marine organisms (Chakraborty, 2020; Shima et al., 2020) and amphibians (Vignoli & Luiselli, 2013) and spontaneous birth in cattle (Aguirre et al., 2021; Ammann et al., 2016; Yonezawa et al., 2016) are also generally more prevalent around the new moon. The most common hypothesis is that offspring born near the new moon tended to have a stronger fitness through to adulthood, and also as an anti-predation strategy since an increase in predation risk is patent when the full moon's light is particularly bright (Griffin et al., 2005). In fact, in ewes, the incidence of parturition reached its peak at the full moon, but the mortality rate of offspring was also the highest at this lunar phase (El-Darawany, El-Tarabany, & Teama, 2014).

In these regards, a recent study provided insight into the neuroendocrine basis of mammalian aggression by revealing the role of melatonin, which is synthesized during ambient darkness, in the reduction of neurosteroid levels and the elevation of aggressive behavior (Munley et al., 2021). Strongly linked to this, the blood circulation levels of a neurohormone such as melatonin are expected to be higher when the Earth's electromagnetic intensity decreases from the third quarter (Lunar phase 3) to the first quarter (Lunar phase 7) (Bevington, 2015; Burch, Reif, & Yost, 2008).

Therefore, the social character of camels (Iglesias Pastrana et al., 2021) could be responsible for female dromedaries' advantage of increased social cohesion during low moonlight conditions, mediated both by hormonal signals and compensatory mechanisms, to give birth in a safe and cooperative environment. This way, not only the group performance in the struggle against external agents will be improved, but also the fact of being born into groups of cooperative and vigilant mothers could increase the altruistic behavior of females to nurse a non-filial offspring (allonursing) and reduce the thermoregulatory demands (Walton et al., 2011). That is, camels may adapt the time of delivery to make long-term survival probability increase by sharing resources with conspecifics so that physiological resources are liberated for other processes.

Regarding the proportion of newborns of each sex that were born in a certain lunar phase throughout the entire study period, male offspring are usually born under lighter conditions (Lunar phases 4 and 6) than female calves (Lunar phase 5). This observation would be explained based on specific strategies of female dromedaries for the promotion of the survival of the offspring based on their sex, taking into consideration that survival, growth, immunity, and organ development in mammals species are higher for female newborns than their male counterparts at neonatal stages (Bæk et al., 2021; Zisk et al., 2011).

Then, neonatal intensive care procedures are particularly decisive for compromised newborns of the male sex, but also, they are more vulnerable to variation in parental condition since males require higher nutritional investment due to their generally larger body size (Dama, 2012). Experimental research on this topic has concluded that such sex-specific differences in newborn animals can be attributed to variations in hormonal signaling and stress responses, partially due to maternal influences at organizational effects on offspring development (Elsmén, Steen, & Hellström-Westas, 2004; McGhee et al., 2012).

Specifically, Hammadi, et al. (2021) studied maternal and neonatal behaviors in dromedaries and concluded that male newborns took more time to raise their heads, stand up, and suckle their mothers. Hence, the ambient light when male calves are born, although minimal to avoid potential external threats and benefit from the greater social communication, slightly higher than the lunar phase in which the birth of female offspring is concentrated, benefits the mothers to be able to better interact visually with the immature male newborn in the first stages of its extra-uterine life. In fact, a male-biased maternal investment is reported for camels (Brandlová, Bartoš, & Haberová, 2013), as well as for other desert-living species such as the Dorcas gazelle (Fiialkovskyi et al., 2022) and some other ungulates (Berube, Festa-Bianchet, & Jorgenson, 1996; Birgersoon, Tillbom, & Ekvall, 1998; Cassinello, 2001; Clutton-Brock, Albon, & Guinness, 1981; Gloneková, Brandlová, & Pluháček, 2020; Hejcmanová et al., 2011).

Dissimilar but complementary effects of air velocity on thermal comfort and olfactory maternal behavior

Patterns of genetic selection consistent with the adaptation of camels to desert conditions have been identified. They include tolerance to extreme temperature, dehydration, and sandy terrains (Fitak et al., 2020). Regardless of this widespread knowledge of the interaction between camels and these environmental variables, the variables related to temperature were deemed redundant in the present study (Table 1), which could be explained on the basis that local dromedaries have evolved in a relatively uniform climate due to the geographical situation of the Canary Islands (Rancel Rodriguez, 2016). Contrastingly, those climatic variables related to air velocity would serve to explain a local adaptive mechanism of Canarian dromedaries, as their interannual variation in the study area is recognized to be of notable magnitude (Azorin-Molina et al., 2018).

Existing literature dealing with other animal species suggests that the variation in temperature and barometric pressure is related to the rate of birth in cows (Ammann et al., 2016) but negatively associated with the occurrence of preterm calving in the same livestock species (Sasaki et al., 2019). Other authors found that warm, dry, and calm conditions lead to earlier parturition dates and advanced juvenile development, whilst cold, wet, and windy weather delays birth timing and juvenile growth in bats (Linton & Macdonald, 2018). Changes in breeding phenology and reproductive performance in response to temperature and rainfall are also reported in wild deer (Moyes et al., 2011; Sims et al., 2007) and seabirds (Frederiksen et al., 2004).

The potential of the mean wind speed and a maximum wind gust to predict the onset of parturition in Canarian dromedaries depending on the sex of offspring (Table 2) may reveal the specific influence of these weather conditions on the thermal comfort and metabolic economy of the gravid she-camels, which are expected to be more energetically compromised when the offspring that they are expecting is a male.

According to Virens and Cree (2022), the heat transfer between an animal and its environment and, thus, the individual energy budget is predominantly modulated by the wind. Specifically, thermal comfort decreases as air velocity does (Veselý & Zeiler, 2014), resulting in an increase in the rate of water loss that provides no cooling (Foster et al., 2022).

Under this theoretical prospect, pregnant females would initiate the delivery of their male offspring to avoid major imbalances which could put their health and that of their offspring at risk. Furthermore, a comparatively superior energy-demanding process when the velocity of ambient air is lower, and its transient increase (gust) is higher (Figure 4). Under these conditions, the temperature regulation by regulatory changes in metabolic heat production and/or evaporative heat loss is consistent; hence the metabolic economy and general organic status are compromised. These results contrast those reported by Roche, Lee, and Berry (2006), who described that a calf is more likely to be male than to be a female if it is born following periods of high air temperature and or high evaporation in dairy cattle. Species-specific metabolic and behavioral responses to environmental cues may explain such contrasting results.

Parallelly, according to literature, wind effects on the success at the establishment of the mother-calf bond could be expected, considering that olfactory stimuli (sniffing) are of special interest to favor mother–young interaction and fast winds impede proper olfaction (Togunov, Derocher, & Lunn, 2017). Canarian she-dromedaries may be rather prone to deliver male newborns on days with decreasing wind speed given the more precocious stage of development and, thus, the need for paternal care/recognition of male neonates in comparison to female calves. In fact, the multisensory recognition through vocal and chemical communication between mother and young from parturition to weaning is reported to be more practiced towards newborns of the male sex in camels (Hammadi et al., 2021), beef cattle (Stěhulová et al., 2013), and rodents (Lévy, Keller, & Poindron, 2004), when compared to females.

In the context of climate change, and in view of the increasing trend of variables related to wind in the study area, future applied studies should evaluate the possible effects of this specific interannual variability on maternal rejection rates as well as abortions, preterm births, and other adverse pregnancy outcomes. The study of animal–environment interaction in local domestic scenarios will also aid in the optimum definition of handling protocols for the effective and safe management of animals.

Conclusions

New moon and ambient air have a non-negligible effect on the prediction of the onset of spontaneous parturition depending on the sex of offspring in dromedaries. These lunar and weather phenologies can be interpreted as a manifestation of phenotypic adaptation that involves species-specific social ecology and body-fluid balance features to maximize parent fitness and offspring survival. To give birth during low moonlight conditions means a safer and more cooperative environment due to the increased social cohesion between congeners, mostly regulated through hormonal pathways. Male offspring are usually born under lighter conditions than their female counterparts, which may be explained on the basis that slightly higher moonlight may benefit the mothers to be able to better interact visually with the immature male newborn in the first stages of its extra-uterine life. Pregnant she-camels would have adapted the time of delivery according to the velocity of ambient air and the intensity of its transient increases, a trade-off mediated by the influence of wind in the ability of camels to maintain a thermal balance state and minimizes metabolic use, condition of paramount importance for survival at arid and semi-arid habitats. When the mean wind speed is low, and the wind gust is high, a calf is more likely to be male. At these specific climatic conditions, the thermal comfort is negatively affected so that the gravid female would initiate the parturition to avoid major organic imbalances that could limit its posterior performance and survival, but also to interact through olfactory stimuli with the immature male newborn more accurately.

Author contributions: Conceptualization, C.I.P. and F.J.N.G.; Data curation, C.I.P. and F.J.N.G.; Formal analysis, C.I.P. and F.J.N.G.; Funding acquisition, J.V.D.B.; Investigation, C.I.P. and F.J.N.G.; Methodology, C.I.P. and F.J.N.G.; Project administration, E.C. and J.V.D.B.; Resources, F.J.N.G. and J.V.D.B.; Software, C.I.P. and F.J.N.G.; Supervision, F.J.N.G., E.C. and J.V.D.B.; Validation, C.I.P., F.J.N.G., E.C. and J.V.D.B.; Visualization, C.I.P., F.J.N.G., E.C. and J.V.D.B.; Writing—original draft, C.I.P., F.J.N.G. and E.C.; Writing—review & editing, C.I.P., F.J.N.G., E.C. and J.V.D.B. All authors have read and agreed to the published version of the manuscript.

Funding: The present research was carried out in the financing framework of the international project CA.RA.VA.N—'Toward a Camel Transnational Value Chain' (Reference APCIN-2016-00011-00-00) and during the covering period of a predoctoral contract (FPU Fellowship) funded by the Spanish Ministry of Science and Innovation and was developed under the context a Ramón y Cajal Post-Doctoral fellowship financially supported by MCIN/AEI/10.13039/501100011033 and European

Union "NextGenerationEU"/PRTR" (Recovery, Transformation and Resilience Plan—Funded by the European Union—NextGenerationEU).

Data availability statement: Data will be made available from first author upon reasonable request.

Acknowledgments: Thanks to the staff at Oasis Park in Fuerteventura for their attention and support.

Conflicts of interest: The authors declare no conflict of interest.

References

Abecia, J.-A., Arrébola, F., & Palacios, C. (2017). Offspring sex ratio in sheep, cattle, goats and pigs: influence of season and lunar phase at conception. *Biological Rhythm Research*, 48(3), 417-424.

Aguilar, J., Cuervo-Arango, J., & Santa Juliana, L. (2015). Lunar cycles at mating do not influence sex ratio at birth in horses. *Chronobiology International*, 32(1), 43-47.

Aguirre, A. A., Palomares, R. A., De Ondiz, A. D., Soto, E. R., Perea, M. S., Hernández-Fonseca, H. J., & Perea, F. P. (2021). Lunar cycle influences reproductive performance of crossbred Brahman cows under tropical conditions. *Journal of Biological Rhythms*, 36(2), 160-168.

Alberghina, D., Gioè, M., Quartuccio, M., & Liotta, L. (2021). The influence of lunar cycle at the time of conception on sex offspring distribution in dogs. *Chronobiology International*, 38(11), 1517-1521.

Alderman, B. W., Boyko, E. J., Loy, G. L., Jones, R. H., Keane, E. M., & Daling, J. R. (1988). Weather and occurrence of eclampsia. *International journal of epidemiology*, 17(3), 582-588.

Ammann, T., Hässig, M., Rüegg, S., & Bleul, U. (2016). Effects of meteorological factors and the lunar cycle on onset of parturition in cows. *Preventive veterinary medicine*, 126, 11-18.

Azorin-Molina, C., Menendez, M., McVicar, T. R., Acevedo, A., Vicente-Serrano, S. M., Cuevas, E., Minola, L., & Chen, D. (2018). Wind speed variability over the Canary Islands, 1948–2014: focusing on trend differences at the land–ocean interface and below–above the trade-wind inversion layer. *Climate Dynamics*, 50(11), 4061-4081.

Bæk, O., Cilieborg, M. S., Nguyen, D. N., Bering, S. B., Thymann, T., & Sangild, P. T. (2021). Sex-specific survival, growth, immunity and organ development in preterm pigs as models for immature newborns. *Frontiers in pediatrics*, 9, 626101.

Beltran, A. J., Wu, J., & Laurent, O. (2014). Associations of meteorology with adverse pregnancy outcomes: a systematic review of preeclampsia, preterm birth and birth weight. *International journal of environmental research and public health*, 11(1), 91-172.

Bender, D. J., Bayne, E. M., & Brigham, R. M. (1996). Lunar condition influences coyote (*Canis latrans*) howling. *American Midland Naturalist*, 413-417.

Benstaali, C., Mailloux, A., Bogdan, A., Auzeby, A., & Touitou, Y. (2001). Circadian rhythms of body temperature and motor activity in rodents: their relationships with the light-dark cycle. *Life sciences*, 68(24), 2645-2656.

Berube, C. H., Festa-Bianchet, M., & Jorgenson, J. T. (1996). Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. *Behavioral Ecology*, 7(1), 60-68.

Bevington, M. (2015). Lunar biological effects and the magnetosphere. *Pathophysiology*, 22(4), 211-222.

Birgersoon, B., Tillbom, M., & Ekvall, K. (1998). Male-biased investment in fallow deer: an experimental study. *Animal Behaviour*, 56(2), 301-307.

Björklund, M., & Bergek, S. (2009). On the relationship between population differentiation and sampling effort: is more always better? *Oikos*, 118(8), 1127-1129.

Boutin, S., & Lane, J. E. (2014). Climate change and mammals: evolutionary versus plastic responses. *Evolutionary Applications*, 7(1), 29-41.

Bova, T. L., Chiavaccini, L., Cline, G. F., Hart, C. G., Matheny, K., Muth, A. M., Voelz, B.E., Kesler, D., & Memili, E. (2014). Environmental stressors influencing hormones and systems physiology in cattle. *Reproductive Biology and Endocrinology*, 12(1), 1-5.

Brandlová, K., Bartoš, L., & Haberová, T. (2013). Camel calves as opportunistic milk thefts? The first description of allosuckling in domestic bactrian camel (*Camelus bactrianus*). *PLoS One*, 8(1), e53052.

Buckles, K. S., & Hungerman, D. M. (2013). Season of birth and later outcomes: Old questions, new answers. *Review of Economics and Statistics*, 95(3), 711-724.

Burch, J. B., Reif, J. S., & Yost, M. G. (2008). Geomagnetic activity and human melatonin metabolite excretion. *Neuroscience Letters*, 438(1), 76-79.

Burger, P. A., & Ciani, E. (2022). Structural and functional genomics in Old World camels—where do we stand and where to go. *Animal Frontiers*, 12(4), 30-34.

Burger, P. A., Ciani, E., & Faye, B. (2019). Old World camels in a modern world–a balancing act between conservation and genetic improvement. *Animal Genetics*, 50(6), 598-612.

Cassinello, J. (2001). Offspring grazing and suckling rates in a sexually dimorphic ungulate with biased maternal investment (*Ammotragus lervia*). *Ethology*, 107(2), 173-182.

Cavalli, G., & Heard, E. (2019). Advances in epigenetics link genetics to the environment and disease. *Nature*, 571(7766), 489-499.

Chakraborty, U. (2020). Effects of different phases of the lunar month on living organisms. *Biological Rhythm Research*, 51(2), 254-282.

Chinchilla-Vargas, J., Kerns, K., & Rothschild, M. F. (2018). Lunar and climatic effects on boar ejaculate traits. *Animal reproduction science*, 193, 117-125.

Clarke, J. A., Chopko, J. T., & Mackessy, S. P. (1996). The effect of moonlight on activity patterns of adult and juvenile prairie rattlesnakes (*Crotalus viridis viridis*). *Journal of Herpetology*, 192-197.

Clutton-Brock, T. H., Albon, S., & Guinness, F. (1981). Parental investment in male and female offspring in polygynous mammals. *Nature*, 289(5797), 487-489.

Dama, M. S. (2012). Parasite stress predicts offspring sex ratio. *PLoS ONE,* 7(9), e46169.

Dioli, M. (2022). Observation on dromedary (Camelus dromedarius) welfare and husbandry practices among nomadic pastoralists. *Pastoralism*, 12(1), 1-23.

Dwyer, C. (2003). Behavioural development in the neonatal lamb: effect of maternal and birth-related factors. *Theriogenology*, 59(3-4), 1027-1050.

El-Darawany, A., El-Tarabany, A., & Teama, F. (2014). Circalunar Rhythms Induced Changes in the Body Functions and Reproductive Performance in Pregnant Ewes. *Arab Journal of Nuclear Sciences and Applications*, 47(2), 181-188.

Elsmén, E., Steen, M., & Hellström-Westas, L. (2004). Sex and gender differences in newborn infants: why are boys at increased risk? *Journal of Men's Health and Gender*, 1(4), 303-311.

Faye, B. (2020). How many large camelids in the world? A synthetic analysis of the world camel demographic changes. *Pastoralism*, 10(1), 1-20.

Fernández-Duque, E., De La Iglesia, H., & Erkert, H. G. (2010). Moonstruck primates: owl monkeys (*Aotus*) need moonlight for nocturnal activity in their natural environment. *PLoS One*, 5(9), e12572.

Fiialkovskyi, P., Cassinello, J., Brandlová, K., & Ceacero, F. (2022). Evidence of three distinct lactation stages in nursing gazelles: implications on maternal behaviour assessment. *Applied Animal Behaviour Science*, 105814.

Fitak, R. R., Mohandesan, E., Corander, J., Yadamsuren, A., Chuluunbat, B., Abdelhadi, O., Raziq, A., Nagy, P., Walzer, C., Faye, B., & Burger, P. (2020). Genomic signatures of domestication in Old World camels. *Communications biology*, 3(1), 1-10.

Foster, J., Smallcombe, J. W., Hodder, S., Jay, O., Flouris, A. D., & Havenith, G. (2022). Quantifying the impact of heat on human physical work capacity; part II: the observed interaction of air velocity with temperature, humidity, sweat rate, and clothing is not captured by most heat stress indices. *International journal of biometeorology*, 66(3), 507-520.

Frederiksen, M., Harris, M. P., Daunt, F., Rothery, P., & Wanless, S. (2004). Scale-dependent climate signals drive breeding phenology of three seabird species. *Global Change Biology*, 10(7), 1214-1221.

Gebresilassie, A., Yared, S., Aklilu, E., Kirstein, O. D., Moncaz, A., Tekie, H., Balkew, M., Warburg, A., Hailu, A., & Gebre-Michael, T. (2015). The influence of moonlight and lunar periodicity on the efficacy of CDC light trap in sampling *Phlebotomus* (*Larroussius*) *orientalis* Parrot, 1936 and other *Phlebotomus* sandflies (*Diptera*: *Psychodidae*) in Ethiopia. *Parasites & vectors*, 8(1), 1-7.

Gloneková, M., Brandlová, K., & Pluháček, J. (2020). Higher maternal care and tolerance in more experienced giraffe mothers. *Acta ethologica*, 23(1), 1-7.

Goswami, A., Noirault, E., Coombs, E. J., Clavel, J., Fabre, A.-C., Halliday, T. J., Churchill, M., Curtis, A., Watanabe, A., Simmons, N.B., Beatty, B.L., Geisler, J.H., Fox, D.L., & Felice, R. N. (2022). Attenuated evolution of mammals through the Cenozoic. *Science*, 378(6618), 377-383.

Grant, R., Halliday, T., & Chadwick, E. (2013). Amphibians' response to the lunar synodic cycle—a review of current knowledge, recommendations, and implications for conservation. *Behavioral Ecology*, 24(1), 53-62.

Grant, R. A., Chadwick, E. A., & Halliday, T. (2009). The lunar cycle: a cue for amphibian reproductive phenology? *Animal Behaviour*, 78(2), 349-357.

Griffin, P. C., Griffin, S. C., Waroquiers, C., & Mills, L. S. (2005). Mortality by moonlight: predation risk and the snowshoe hare. *Behavioral Ecology*, 16(5), 938-944.

Gutman, R., Dayan, T., Levy, O., Schubert, I., & Kronfeld-Schor, N. (2011). The effect of the lunar cycle on fecal cortisol metabolite levels and foraging ecology of nocturnally and diurnally active spiny mice. *PLoS One*, 6(8), e23446.

Hammadi, I., Chniter, M., Atigui, M., Brahmi, M., Seddik, M., Salem, W., Levy, F., Nowak, R., & Hammadi, M. (2021). Dam parity and calf sex affect maternal and neonatal behaviors during the first week postpartum in stabled Maghrebi dairy camels. *Animal*, 15(3), 100149.

Harrell, F. E. (2015). Binary logistic regression. In *Regression modeling strategies* (pp. 219-274): Springer.

Havenith, G. (2002). Interaction of clothing and thermoregulation. *Exogenous Dermatology*, 1(5), 221-230.

Heckwolf, M. J., Morim, T., Riccioli, F., & Baltazar-Soares, M. (2021). Fresh start after rough rides: understanding patterns of genetic differentiation upon human-mediated translocations. *Biological Invasions*, 23(12), 3625-3639.

Hejcmanová, P., Vymyslická, P., Koláčková, K., Antonínová, M., Havlíková, B., Stejskalová, M., Policht, R., & Hejcman, M. (2011). Suckling behavior of eland antelopes (*Taurotragus* spp.) under semi-captive and farm conditions. *Journal of ethology*, 29(1), 161-168.

Hoter, A., Rizk, S., & Naim, H. Y. (2019). Cellular and molecular adaptation of Arabian camel to heat stress. *Frontiers in Genetics*, 10, 588.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Arando Arbulu, A., & Delgado Bermejo, J. V. (2021). The Youngest, the Heaviest and/or the Darkest? Selection Potentialities and Determinants of Leadership in Canarian Dromedary Camels. *Animals*, 11(10), 2886.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Barba Capote, C. J., & Delgado Bermejo, J. V. (2020). Effect of research impact on emerging camel husbandry, welfare and social-related awareness. *Animals*, 10(5), 780.

Isen, A., Rossin-Slater, M., & Walker, R. (2017). Relationship between season of birth, temperature exposure, and later life wellbeing. *Proceedings of the National Academy of Sciences*, 114(51), 13447-13452.

Khanvilkar, A., Samant, S., & Ambore, B. (2009). Reproduction in camel. *Veterinary World*, 2(2), 72.

Krief, S., Cibot, M., Bortolamiol, S., Seguya, A., Krief, J.-M., & Masi, S. (2014). Wild chimpanzees on the edge: nocturnal activities in croplands. *PLoS One*, 9(10), e109925.

Kronfeld-Schor, N., Dominoni, D., De la Iglesia, H., Levy, O., Herzog, E. D., Dayan, T., & Helfrich-Forster, C. (2013). Chronobiology by moonlight. *Proceedings of the Royal Society B: Biological Sciences*, 280(1765), 20123088.

Kurvers, R. H., & Hoelker, F. (2015). Bright nights and social interactions: a neglected issue. *Behavioral Ecology*, 26(2), 334-339.

Kyriacou, C. P., Peixoto, A. A., Sandrelli, F., Costa, R., & Tauber, E. (2008). Clines in clock genes: fine-tuning circadian rhythms to the environment. *Trends in Genetics*, 24(3), 124-132.

Lévy, F., Keller, M., & Poindron, P. (2004). Olfactory regulation of maternal behavior in mammals. *Hormones and behavior*, 46(3), 284-302.

Linton, D. M., & Macdonald, D. W. (2018). Spring weather conditions influence breeding phenology and reproductive success in sympatric bat populations. *Journal of Animal Ecology*, 87(4), 1080-1090.

López-Olmeda, J. F., Madrid, J. A., & Sánchez-Vázquez, F. J. (2006). Light and temperature cycles as zeitgebers of zebrafish (*Danio rerio*) circadian activity rhythms. *Chronobiology International*, 23(3), 537-550.

Mann, H. B., & Whitney, D. R. (1947). On a test of whether one of two random variables is stochastically larger than the other. *The annals of mathematical statistics*, 50-60.

McGhee, K. E., Pintor, L. M., Suhr, E. L., & Bell, A. M. (2012). Maternal exposure to predation risk decreases offspring antipredator behaviour and survival in threespined stickleback. *Functional Ecology*, 26(4), 932-940.

Mendelson, C. R., & Condon, J. C. (2005). New insights into the molecular endocrinology of parturition. *Journal of steroid biochemistry and molecular biology*, 93(2-5), 113-119.

Midi, H., Sarkar, S. K., & Rana, S. (2010). Collinearity diagnostics of binary logistic regression model. *Journal of interdisciplinary mathematics*, 13(3), 253-267.

Mitchell, A. E., Wolf, B. O., & Martin, T. E. (2022). Proximate and evolutionary sources of variation in offspring energy expenditure in songbirds. *Global Ecology and Biogeography*, 31(4), 765-775.

Moyes, K., Nussey, D. H., Clements, M. N., Guinness, F. E., Morris, A., Morris, S., Pemberton, J.M., Kruuk, L.E.B., & Clutton-Brock, T. H. (2011). Advancing breeding phenology in response to environmental change in a wild red deer population. *Global Change Biology*, 17(7), 2455-2469.

Munley, K. M., Trinidad, J. C., Deyoe, J. E., Adaniya, C. H., Nowakowski, A. M., Ren, C. C., Murphy, G.V., Reinhart, J.M., & Demas, G. E. (2021). Melatonin-dependent changes in neurosteroids are associated with increased aggression in a seasonally breeding rodent. *Journal of Neuroendocrinology*, 33(3), e12940.

Murren, C. J., Auld, J. R., Callahan, H., Ghalambor, C. K., Handelsman, C. A., Heskel, M. A., Kingsolver, J.G., Maclean, H.J., Masel, J., Maughan, H., Pfennig, D.W., Relyea, R.A., Seiter, S., Snell-Rood, E., Steiner, U.K., & Schlichting, C.D. (2015). Constraints on the evolution of phenotypic plasticity: limits and costs of phenotype and plasticity. *Heredity*, 115(4), 293-301.

Nagy, P., & Juhász, J. (2019). Pregnancy and parturition in dromedary camels I. Factors affecting gestation length, calf birth weight and timing of delivery. *Theriogenology*, 134, 24-33.

Noller, K. L., Resseguie, L. J., & Vossb, V. (1996). The effect of changes in atmospheric pressure on the occurrence of the spontaneous onset of labor in term pregnancies. *American journal of obstetrics and gynecology*, 174(4), 1192-1199.

Palacios, C., & Abecia, J. (2014). Does lunar cycle affect lamb production after artificial insemination in sheep? *Biological Rhythm Research*, 45(6), 869-873.

Palagini, L., Gemignani, A., Banti, S., Manconi, M., Mauri, M., & Riemann, D. (2014). Chronic sleep loss during pregnancy as a determinant of stress: impact on pregnancy outcome. *Sleep medicine*, 15(8), 853-859.

Palmer, M. S., Fieberg, J., Swanson, A., Kosmala, M., & Packer, C. (2017). A 'dynamic'landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. *Ecology letters*, 20(11), 1364-1373.

Pankhurst, N., & King, H. (2010). Temperature and salmonid reproduction: implications for aquaculture. *Journal of Fish Biology*, 76(1), 69-85.

Parraguez, V. H., & Gonzalez-Bulnes, A. (2020). Endocrinology of reproductive function and pregnancy at high altitudes. *Current Opinion in Endocrine and Metabolic Research*, 11, 27-32.

Pastrana, C. I., González, F. J. N., Ciani, E., Ariza, A. G., & Bermejo, J. V. D. (2021). A tool for functional selection of leisure camels: Behaviour breeding criteria may ensure long-term sustainability of a European unique breed. *Research in Veterinary Science*, 140, 142-152.

Patke, A., Young, M. W., & Axelrod, S. (2020). Molecular mechanisms and physiological importance of circadian rhythms. *Nature reviews Molecular cell biology*, 21(2), 67-84.

Penteriani, V., & Delgado, M. d. M. (2017). Living in the dark does not mean a blind life: bird and mammal visual communication in dim light. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1717), 20160064.

Penteriani, V., Kuparinen, A., del Mar Delgado, M., Palomares, F., López-Bao, J. V., Fedriani, J. M., Calzada, J., Moreno, S., Villafuerte, R., Campioni, L., & Lourenço, R. (2013). Responses of a top and a meso predator and their prey to moon phases. *Oecologia*, 173(3), 753-766.

Pérez-Granados, C., Schuchmann, K.-L., & Marques, M. I. (2022). Addicted to the moon: vocal output and diel pattern of vocal activity in two Neotropical nightjars is related to moon phase. *Ethology Ecology & Evolution*, 34(1), 66-81.

Pfeuty, B., Thommen, Q., Corellou, F., Djouani-Tahri, E. B., Bouget, F. Y., & Lefranc, M. (2012). Circadian clocks in changing weather and seasons: lessons from the picoalga Ostreococcus tauri. *BioEssays*, 34(9), 781-790.

Plush, K. J. (2014). *Metabolic maturity and vigour in neonatal lambs, and subsequent impacts on thermoregulation and survival*. Doctoral Thesis: University of Adelaide (Adelaide, Australia).

Prokkola, J. M., & Nikinmaa, M. (2018). Circadian rhythms and environmental disturbances–underexplored interactions. *Journal of Experimental Biology*, 221(16), jeb179267.

Pyle, P., Nur, N., Henderson, R. P., & DeSante, D. F. (1993). The effects of weather and lunar cycle on nocturnal migration of landbirds at southeast Farallon Island, California. *The Condor*, 95(2), 343-361.

Rancel Rodriguez, N. M. (2016). *Biodiversity of epiphyllous, heterocyst-forming cyanobacteria in the laurel forest of the Canary Islands*. Doctoral Thesis: Universität zu Köln (Köln, Germany).

Ray, H., & Chakraverty, M. (1934). Lunar periodicity in the conjugation of *Conchophthirius lamellidens* Ghosh. *Nature*, 134(3391), 663-664.

Record, M. (2014). Intercellular communication by exosomes in placenta: a possible role in cell fusion? *Placenta*, 35(5), 297-302.

Reppert, S. M. (2006). A colorful model of the circadian clock. *Cell*, 124(2), 233-236.

Reyes-Lagos, J. J., Ledesma-Ramírez, C. I., Pliego-Carrillo, A. C., Peña-Castillo, M. Á., Echeverría, J. C., Becerril-Villanueva, E., Pavón, L., & Pacheco-López, G. (2019). Neuroautonomic activity evidences parturition as a complex and integrated neuro–immune–endocrine process. *Annals of the New York Academy of Sciences*, 1437(1), 22-30.

Ricci, A., Racioppi, V., Iotti, B., Bertero, A., Reed, K., Pascottini, O., & Vincenti, L. (2018). Assessment of the temperature cut-off point by a commercial intravaginal device to predict parturition in Piedmontese beef cows. *Theriogenology*, 113, 27-33.

Roche, J., Lee, J., & Berry, D. (2006). Climatic factors and secondary sex ratio in dairy cows. *Journal of Dairy Science*, 89(8), 3221-3227.

Rodríguez, A., Chiaradia, A., Wasiak, P., Renwick, L., & Dann, P. (2016). Waddling on the dark side: Ambient light affects attendance behavior of little penguins. *Journal of Biological Rhythms*, 31(2), 194-204.

Rosenberger, A., Beijer, Å., Schoenau, E., Mester, J., Rittweger, J., & Zange, J. (2019). Changes in motor unit activity and respiratory oxygen uptake during 6 weeks of progressive whole-body vibration combined with progressive, high intensity resistance training. Journal of *Musculoskeletal & Neuronal Interactions*, 19(2), 159.

Sábato, M. A. L., de Melo, L. F. B., Magni, E. M. V., Young, R. J., & Coelho, C. M. (2006). A note on the effect of the full moon on the activity of wild maned wolves, *Chrysocyon brachyurus*. *Behavioural processes*, 73(2), 228-230.

Sasaki, Y., Kitai, N., Uematsu, M., Kitahara, G., & Osawa, T. (2019). Daily calving frequency and preterm calving is not associated with lunar cycle but preterm calving is associated with weather conditions in Japanese Black cows. *PLoS One*, 14(7), e0220255.

Schulz, U. (2008). *El camello en Lanzarote*: Aderlan.

Seligmann, H., Anderson, S. C., Autumn, K., Bouskila, A., Saf, R., Tuniyev, B. S., & Werner, Y. L. (2007). Analysis of the locomotor activity of a nocturnal desert lizard (Reptilia: *Gekkonidae*: *Teratoscincus scincus*) under varying moonlight. *Zoology*, 110(2), 104-117.

Shima, J. S., Osenberg, C. W., Alonzo, S. H., Noonburg, E. G., Mitterwallner, P., & Swearer, S. E. (2020). Reproductive phenology across the lunar cycle: parental decisions, offspring responses, and consequences for reef fish. *Ecology*, 101(8), e03086.

Sims, M., Elston, D. A., Larkham, A., Nussey, D. H., & Albon, S. D. (2007). Identifying when weather influences life-history traits of grazing herbivores. *Journal of Animal Ecology*, 761-770.

Souza, N. A., Andrade-Coelho, C. A., Silva, V. C., Peixoto, A. A., & Rangel, E. F. (2005). Moonlight and blood-feeding behaviour of Lutzomyia intermedia and Lutzomyia whitmani (*Diptera*: *Psychodidae*: *Phlebotominae*), vectors of American cutaneous leishmaniasis in Brazil. *Memórias do Instituto Oswaldo Cruz*, 100, 39-42.

Stěhulová, I., Špinka, M., Šárová, R., Máchová, L., Kněz, R., & Firla, P. (2013). Maternal behaviour in beef cows is individually consistent and sensitive to cow body condition, calf sex and weight. *Applied Animal Behaviour Science*, 144(3-4), 89-97.

Stern, E. W., Glazer, G. L., & Sanduleak, N. (1988). Influence of the full and new moon on onset of labor and spontaneous rupture of membranes. *Journal of Nurse-Midwifery*, 33(2), 57-61.

Tibary, A., & El Allali, K. (2020). Dromedary camel: A model of heat resistant livestock animal. *Theriogenology*, 154, 203-211.

Togunov, R. R., Derocher, A. E., & Lunn, N. J. (2017). Windscapes and olfactory foraging in a large carnivore. *Scientific Reports*, 7(1), 1-10.

Tokach, M., Menegat, M., Gourley, K., & Goodband, R. (2019). Nutrient requirements of the modern high-producing lactating sow, with an emphasis on amino acid requirements. *Animal*, 13(12), 2967-2977.

Tripepi, G., Jager, K., Dekker, F., & Zoccali, C. (2008). Linear and logistic regression analysis. *Kidney international*, 73(7), 806-810.

Troein, C., Locke, J. C., Turner, M. S., & Millar, A. J. (2009). Weather and seasons together demand complex biological clocks. *Current Biology*, 19(22), 1961-1964.

Vaze, K. M., & Sharma, V. K. (2013). On the adaptive significance of circadian clocks for their owners. *Chronobiology International*, 30(4), 413-433.

Veselý, M., & Zeiler, W. (2014). Personalized conditioning and its impact on thermal comfort and energy performance–A review. *Renewable and Sustainable Energy Reviews*, 34, 401-408.

Vignoli, L., & Luiselli, L. (2013). Better in the dark: two Mediterranean amphibians synchronize reproduction with moonlit nights. *Web Ecology*, 13(1), 1-11.

Virens, E., & Cree, A. (2022). Wind of change: A diurnal skink thermoregulates between cooler set-points and for an increased amount of time in the presence of wind. *Journal of Experimental Biology*, 225(6), jeb244038.

Walton, J. C., Weil, Z. M., & Nelson, R. J. (2011). Influence of photoperiod on hormones, behavior, and immune function. *Frontiers in neuroendocrinology*, 32(3), 303-319.

Warda, M., Prince, A., Kim, H. K., Khafaga, N., Scholkamy, T., Linhardt, R. J., & Jin, H. (2014). Proteomics of old world camelid (*Camelus dromedarius*): Better understanding the interplay between homeostasis and desert environment. *Journal of advanced research*, 5(2), 219-242.

Weil, Z. M., Bowers, S. L., & Nelson, R. J. (2007). Photoperiod alters affective responses in collared lemmings. *Behavioural brain research*, 179(2), 305-309.

Wilson, R., & Gutierrez, C. (2015). The one-humped camel in the Canary Islands: History and present status. *Tropicultura*, 33(4).

Workman, J. L., Bowers, S. L., & Nelson, R. J. (2009). Enrichment and photoperiod interact to affect spatial learning and hippocampal dendritic morphology in white-footed mice (*Peromyscus leucopus*). *European Journal of Neuroscience*, 29(1), 161-170.

Yonezawa, T., Uchida, M., Tomioka, M., & Matsuki, N. (2016). Lunar cycle influences spontaneous delivery in cows. *PLoS One*, 11(8), e0161735.

York, J. E., Young, A. J., & Radford, A. N. (2014). Singing in the moonlight: dawn song performance of a diurnal bird varies with lunar phase. *Biology letters*, 10(1), 20130970.

Zisk, J. L., Genen, L. H., Kirkby, S., Webb, D., Greenspan, J., & Dysart, K. (2011). Do premature female infants really do better than their male counterparts? *American journal of perinatology*, 28(03), 241-246.

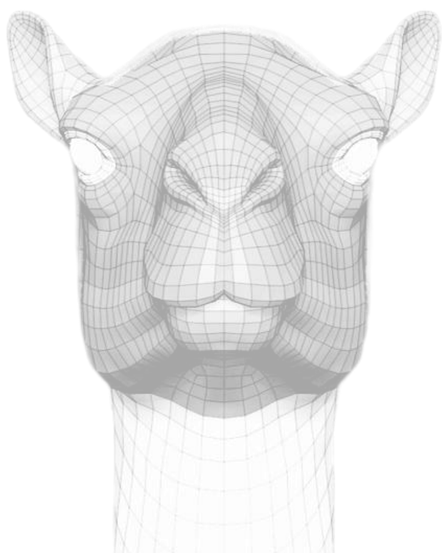
4.2 Behavioural-type coping strategies in leisure dromedary camels: factors determining reactive vs. proactive responses

Carlos Iglesias Pastrana[1], Francisco Javier Navas González[1], Elena Ciani[2], Amy Katherine McLean[3] and Juan Vicente Delgado Bermejo[1]

[1]Department of Genetics, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain

[2]Department of Biosciences, Biotechnologies and Environment, Faculty of Veterinary Sciences, University of Bari 'Aldo Moro', 70121 Bari, Italy

[3]Department of Animal Science, University of California Davis, 95616 California, USA



Quality indicator information provided on the publication
***Latest information available (2022)**

Status of the manuscript: Submitted

Journal (year, volume, page(s)): *Applied Animal Behaviour Science*

International database in which it is indexed: Journal of Citation Reports (JCR)

Thematic area in the reference database: Veterinary Sciences

Impact index of the journal in the year of the article's publication: 2.3

Rank/number of thematic area journals: 35/143 (Q1)

Abstract

Domestic animals use a varied set of strategies (behavioural- and physiological-type) to cope with aversive situations at rearing systems. Camels, although widely used as an animal model for the study of strategies to cope with environmental stress in desert-type natural habitats, remain disregarded for their coping styles at man-made environments, in which they are progressively gaining presence for their sustainability traits. In this scenario, the present paper has explored the concept of coping from a behavioral perspective in leisure dromedary camels. By means of a multivariate statistical analysis, the influence of different animal-dependent factors on the type of behavioural-type coping styles has been quantified. Negative reinforcement strategies, together with the use of a combination of visual and auditory stimuli, favor the proactivity in leisure dromedaries. On behalf of their condition as social species, the presence of congeners also promotes proactive coping behaviour. Sexual hormones and selection make male dromedaries more proactive as age increases, whereas this condition enhances reactivity coping responses in females. Hence, training protocols are recommended to be initiated at the earliest ages possible in order to reduce the probability of undesired reactivity as the animal grows and to encourage proactive attitudes as quickly as possible in females and males, respectively. However, the castration of the animals once sexual maturity is reached and domestication protocols for their functional aptitude are initiated, will stimulate not only general organic development but also proactive behaviour. With reference to body language signals, the more backward the ears are, the greater the proactivity of the camel is expected. The present results will make possible the tailoring of training protocols for leisure camels to improve the safety of human-camel interaction, valorize camels for new potential niches (i.e., assisted therapy), and enhance the list of breeding criteria for reactivity traits in these animals.

Keywords

Stress response, human-controlled environment, human-camel interaction, training protocol, negative reinforcement, selective breeding

Introduction

Within the field of animal behaviour, coping or coping strategies are those conscious efforts or specific tactics, with adaptive meaning, that an individual draws upon in order to reduce, eliminate, or master stressors. They are the result of the interplay between innate and adaptive environmental and social species-specific factors (Zozulya et al., 2008) and include both behavioural and physiological response patterns. Although Benus, Bohus, Koolhaas, and Van Oortmerssen (1991) initially proposed the classification of the animals into 'passive' or 'active' subjects according to their stress responses, Koolhaas et al. (1999) argued that such a qualitative distinction did not consider the impact of the environment on animal coping behavior and then suggested using the terms ‘reactive’ and ‘proactive’ coping. From a behavioural viewpoint, proactive individuals are usually bolder, more aggressive, and dominant, and show less flexibility to environmental cues than reactive animals (Koolhaas et al., 2010). Physiologically, the formers show lower activity at the level of the hypothalamic-pituitary–adrenal (HPA) axis as well as decreased brain serotonergic and higher dopaminergic activity (Vindas et al., 2017).

Stress physiology and behavior have been broadly investigated in different animal species (Barreto & Volpato, 2011; Bolhuis et al,, 2005; Budzyńska, 2014; Çakmakçı, Karaca, & María, 2021; Correa et al., 2019; Ferrari et al., 2013; González et al., 2018; Martins et al., 2011; Øverli et al., 2004; Wechsler, 1995; Zidar et al., 2017). In spite of the fact that the majority of the academic work has been performed on farm animals, emerging livestock species such as dromedary camels (*Camelus dromedarius*) are disregarded for their coping styles at man-made environments. By contrast, dromedaries are extensively used as an animal model for the study of physiological and behavioural strategies to cope with environmental stress in desert-type natural habitats. Behavioral coping strategies in dromedaries involve activities such as seeking shade, water, and food and adjusting their activity patterns to avoid the hottest parts of the day, thus reducing their energy expenditure and water loss (Wilson, 2012). On the other hand, key physiological coping strategies such as the reduction of urine output, reabsorption of water from feces (Al-Jassim & Sejian, 2015) and a unique red blood cell structure (Windberger et al., 2019), allow these animals to greatly tolerate dehydration and maintain blood flow to vital organs. Moreover, dromedary camels have a large nasal cavity and a carotid rete that help to cool and humidify the air they breathe and keep the brain’s temperature within a safe range (Abdullah, Said, & Ossen, 2019; Shahda, Abd Elhafeez, & El Mokadem, 2018), and they can regulate their body temperature by increasing respiratory rate (Gaughan, 2011) and reducing metabolic rate (Bouâouda et al., 2014).

Under the evidence of an increase in socio-economic interests for camel rearing and production (Iglesias Pastrana et al., 2020a), the present research aims to study behavioural-type coping styles in dromedary camels so that breeders and owners are given empirical knowledge to predict the behavior of animals when facing challenging situations. Hence, training protocols and housing systems will be tailored and designed to meet the animal’s needs, improve the safety of human-camel interaction, and valorize camels for new potential functional destinations (i.e., assisted therapy). In addition, understanding the influence of different animal-dependent factors on coping strategies would enhance the list of selection criteria for leisure camels.

The unique camel breed along Europe, the Canarian camel, has been used as a model within this research approach given the fact that its main functionality is leisure riding. That is, close interaction with humans is seeked to be as safe and enjoyable as possible, with a particular focus on camel behaviour during the interactive experience. Given the fact that this camel breed is officially cataloged as endangered autochthonous livestock, the results of the present study would aid in developing selection strategies for its genetic improvement and conservation (Iglesias Pastrana et al., 2020b; Pastrana et al., 2021).

Material and methods

Animal sample and study context

The collection of coping styles data occurred from September 2019 to January 2021 and involved 130 individuals belonging to the Canarian camel breed, comprising 58 females and 72 males. These camels were situated in three representative breeding locations across Spain: Huelva (Doñana National Park, coordinates 36.972330, −6.427498), Almería (coordinates 36.902180, −2.429520), and Fuerteventura (coordinates 28.186777, −14.158361). To ensure the suitability of the animals for the study, comprehensive clinical examinations were conducted to assess their well-being and eligibility. Both age and live weight did not conform to a normal distribution ($p < 0.05$). Live weight was calculated using the formula (Equation 1) proposed by Boujenane (2019):

$$\text{Live Weight} = 6.46 \times 10^{-7} (HW + ChG + HG)^{3.17}$$

where HW represents height at the withers, ChG denotes chest girth, and HG signifies hump girth.

The age of female Canarian dromedary camels in the study ranged from 40 to 423 months, while male Canarian dromedary camels spanned from 18 to 385 months in age. The broad age range was chosen to accommodate all animals included in the study, as the stimulus battery used for assessing coping styles/reactivity was suitable for all age groups. This was particularly important as we were evaluating an endangered breed, and individual information was indispensable.

Regarding live weight, female Canarian dromedary camels exhibited weights ranging from 327.03 to 687.13 Kg, while their male counterparts weighed between 342.72 and 777.56 Kg.

Behavioural tests, scales, and phenotyping

Data were collected during annual behavior assessment sessions conducted randomly over five days between September 2019 to January 2021 at three different farms across Southern Spain.

Each recorded entry included three scores for every animal, describing the coping strategies exhibited when they encountered twelve consecutive stimuli that combined different elements, including people, animals, and objects. These elements could be either unknown (unfamiliar to the animal) or known (already familiar to the animal), and they could be visual (perceptible by sight, such as all stimuli) or visual and acoustic (perceptible by sight and sound, including a horn and a red speaker that played a car engine sound). These stimuli were presented to the dromedary camels from various positions, either from the front or from a rear position, consistently at a distance of 2 meters from the animals.

Coping strategies or styles referred to the progressively aversive responses exhibited by the Canarian dromedary camels as they approached or avoided the potential threats represented by each of the twelve stimuli. Three scores were recorded for each animal, characterizing their coping strategies in three distinct traits: mood/emotion when facing the stimuli, response type toward the stimuli, and the intensity of such responses. Mood/emotion denoted the emotional/psychological state of the dromedary camel, which could last for varying durations and typically resulted from external stimuli, such as those presented in our test. The mood/emotion scale was developed considering the definitions provided by Navas González et al. (2018a), Navas González et al. (2018b) and Navas González et al. (2020) (Table 1).

We designed the scale to assess response type based on the study by Budzyńska (2014), categorizing animals according to the coping strategy they employed. This involved whether the dromedary camels paid no attention to the presented stimulus, adopted a reactive approach, or demonstrated a proactive response to it. The response intensity scale measured the degree to which emotional/psychological states, as indicated in the first scale, were expressed, following the methodologies outlined in studies by Berger et al. (2013) and Geuens and De Pelsmacker (2002).

The behavioral test was conducted in an open area that the dromedary camels were already familiar with, as it was part of their daily activity area. It comprised two phases involving two different approaches: an operant conditioning test and a single-stimulus presentation test (Phase I and II), as outlined in Navas González et al. (2018a), Navas González et al. (2018b) and Navas González et al. (2020).

In Phase I (operant conditioning test, first group of stimuli from stimulus 1 to 6), the dromedary camels were guided to cross a 200 × 200 cm oilcloth with a wooden print on it, utilizing increasingly aversive techniques (stimuli 1 to 6). Phase I commenced when handler B raised and positioned the oilcloth on the floor, 2 m in front of the dromedary camels. Handler A led the dromedary camels using a leading rope (stimuli 1 to 4 and 6). For stimulus 5, an additional handler (handler B) and leading rope were employed to guide the dromedary camels over the oilcloth. In stimuli 1 and 2, only handler A

Table 1. Scale translation and description for the three coping style/reactivity related traits assessed in Canarian Dromedary Camels. Response type (reactive, neutral and proactive), mood/emotion (1–12) and degree/intensity of response (1–5).

Mood/Attitude Scale	Mood/Attitude	Response type scale	Response type	Attitude towards the stimulus presented (Extinction/Learning)	Response intensity
1	Distracted	1	Reactive	Pays attention[a] and moves towards other stimuli around, without paying attention to the stimulus presented in the test.	Low, mid-low, mid, mid-high, high (1 to 5).
2	Dejected/Depressed	1	Reactive	Overall, the body posture displays a lowered head and neck, rounding of the spine, and a tucked tail. The animal does not pay attention to any stimuli around.	
3	Indifferent/ Nonresponsive	1	Reactive	Maintains a normal posture. Pays no attention to the stimulus presented but is not distracted by other stimuli around.	
4	Calm	2	Neutral	Does not get startled. Stands still. Pays attention to other stimuli around while also paying attention to the stimulus presented.	
5	Awaiting	2	Neutral	Does not get startled. Stands still. Solely focuses on the stimulus presented.	
6	Curious	2	Neutral	Does not get startled. Stands still. Solely focuses on the stimulus presented. Moves its head towards the stimulus presented.	
7	Cautious	2	Neutral	Does not get startled. Pays attention and moves slightly towards the stimulus (less than 1 m).	

Table 1. *Cont.*

Mood/Attitude Scale	Mood/Attitude	Response type scale	Response type	Attitude towards the stimulus presented (Extinction/Learning)	Response intensity
8	Mistrustful	2	Neutral	Does not get startled. Pays attention to and moves towards the stimulus until approaching it completely.	Low, mid-low, mid, mid-high, high (1 to 5).
9	Surprised	3	Proactive	Solely focused on the stimulus being presented. Gets startled but moves towards the stimulus.	
10	Nervous	3	Proactive	Solely focused on the stimulus being presented. Gets startled and attempts to move away from the stimulus presented initially. Able to move towards the stimulus presented if guided by the operator.	
11	Fearful	3	Proactive	Gets startled. Solely focused on the stimulus being presented. Attempts to move away from the stimulus presented. Unable to move towards the stimulus presented if led by the operator.	
12	Rejection	3	Proactive	Solely focused on the stimulus being presented. Gets startled and moves away from the stimulus presented noticeably. Pulls away from the leading rope when the operator tries to move towards the stimulus presented.	

[a] Pay attention to the stimuli means that the animal held direct visual contact with and/or directed its ear/s towards it.

interacted with the dromedary camel to guide it across the oilcloth. From stimulus 3 to 6, handler B introduced progressively aversive methods from a distance of 2 m (methods detailed in Navas et al. (2017) and Iglesias et al. (2020)) to encourage the dromedary camels to cross the oilcloth. No pressure was applied to the rope during stimulus 1, but from stimulus 2 to 6, pressure was exerted on the rope (two ropes in stimulus 5) until the animal complied or the allotted time expired. A third person (cameraman) stood at a distance of two meters from the side of the oilcloth to record the proceedings, ensuring accuracy in scoring during later analysis. Phase I did not have any breaks and lasted for a total of 450 s (75 s per stimulus).

In Phase II (single-stimulus presentation test, second group of stimuli from stimulus 7 to 12), the dromedary camels were exposed to six additional external stimuli presented by handler B from a distance of one meter while handler A held the dromedary camel using the same leading rope as before. The same third person (cameraman) was stationed at a distance of two meters alongside the animal to record the events. Phase II also lasted for a total of 450 s (75 s per stimulus).

All stimuli were presented to every dromedary camel, and whether an animal completely crossed the oilcloth or not during stimuli 1 to 6 did not affect the presentation of subsequent stimuli. During Phase I, if a dromedary camel had crossed the oilcloth during stimulus 1, it was led back to cross it again for stimuli 2 to 6. Stimuli 7 to 12 were consecutively presented, regardless of the dromedary camel's response to any of them. All stimuli were standardized and presented equally to the dromedary camels, except for stimulus 12, where the choice of animal species depended on the species cohabiting the farm with the dromedary camels being tested.

The dromedary camels were not given additional time to complete the experiences. Once the allocated 75 s for each stimulus passed, the next stimulus was presented in ascending order from 1 to 12, with no pauses in between. The test commenced with the dromedary camel crossing the oilcloth for stimulus 1 and concluded with the assessment of their reaction to other animals in stimulus 12, spanning a total duration of 900 s.

While an animal can shift its attention multiple times within 75 s, this study focused on evaluating the coping styles/reactivity of the animals based on their immediate responses to each stimulus. Any subsequent reactions during the test after the presentation of stimuli were not considered. The study did not emphasize whether the animals crossed the oilcloth entirely, but rather their response and coping strategies when each stimulus was presented. Each dromedary camel received three scores, one for each of the three traits, to describe its coping strategy for each of the 12 stimuli: one for response type, one for mood/emotion, and one for response intensity. These scores were based on different scales. The recorded scores represented the initial coping strategy exhibited by each animal when facing each stimulus from 1 to 12. These scores exclusively captured the animal's response during the test to the stimulus presented, without accounting for its attention to other elements in the testing environment. The dromedary camels had been previously familiarized with the test area, as they were already present in the area during their daily activities. This familiarization aimed to prevent the presence of any new elements from affecting the animal's response to the presented stimuli.

The evaluation of the dromedary camels' responses involved three scales to assess mood/emotion, response type, and response intensity. The mood/emotion scale, with its detailed levels outlined in Table 1, characterized the emotional state of the dromedary camel during stimulus encounters. The second scale, reliant on the mood/emotion scale, classified the type of response exhibited by the animals in response to stimuli 1 to 3. A score of 1 indicated a reactive response (corresponding to mood/emotion scores 1 to 3 in the first scale), 2 represented a neutral response (reflecting mood/emotion scores 4 to 8 in the first scale), and 3 indicated a proactive response (associated with mood/emotion scores 9 to 12 in the first scale). This classification followed the principles set forth by Budzyńska (2014), with reactive dromedary camels showing no attention to the presented stimulus, neutral responders fitting the reactive or passive copers category described by Budzyńska (2014), and hyperreactive dromedary camels classified as active or proactive copers, all of which align with the definitions presented in Table 1.

The final scale scored animals from 1 to 5 based on the intensity of their responses, regardless of the displayed mood/emotion (refer to Table 1). Our response intensity scale incorporated elements from the research by Berger et al. (2013) and adapted the affect intensity scale outlined by Geuens and De Pelsmacker (2002). This scale combined the time it took for the dromedary camels to react to the stimulus (latency) with the scale from Geuens and De Pelsmacker (2002) to measure response intensity. The levels defined for the response intensity scale were as follows: 1 represented dromedary camels that did not startle more than 60 s after the stimulus presentation, indicating low-intensity or negative startle responses; 2 covered dromedary camels that startled between 40 and 60 s after the stimulus presentation, denoting middle-low intensity or mild negative startle responses; 3 encompassed dromedary camels that startled between 20 and 40 s after the stimulus presentation, reflecting middle intensity or serenity responses; 4 included dromedary camels that startled between 10 and 20 s after the stimulus presentation, indicating middle-high intensity or mild positive startle responses; and 5 accounted for dromedary camels that startled in less than 10 s after the stimulus presentation, signifying high intensity, positive intensity, or strong startle responses.

Given that each animal received a single score, opposing behaviors were not scored concurrently within the same animal. For instance, a very calm animal was not simultaneously assessed as slightly nervous, as an animal cannot exhibit both nervousness and calmness simultaneously, regardless of the intensity level of their mood/emotion. The translation and relationships between the scales for the three traits are illustrated in Table 1. Detailed descriptions and the development of the tests and scales employed in the study can be found in Iglesias et al. (2020) and Navas et al. (2017).

The scores for each individual were recorded consistently by the same three trained judge for all stimuli and animals. No intra-observer discrepancies were observed, as all on-field scores matched those obtained from tape reviews. A preliminary analysis involving Cohen's κ test was conducted during the initial stages of the study (Iglesias et al., 2020) to assess intra-observer reliability and ascertain agreement among the judgments by each of the assessors for 30 individuals (23.1% of the total sample) across the categorical variables of response type, mood, and response intensity.

Cohen's κ was used to determine whether the model's repeatability was sufficient to eliminate the intra observer effect, which may enable collection of a single measure per observer, in line with the guidelines from Landis and Koch (1977).

Subsequently, 95% confidence intervals (95% kappa IC) were computed as 95% kappa IC = κ ±1.96 SEκ, where SEκ = [(po(1-po)/n(1-pe)2]0.5, employing the Crosstabs procedure of SPSS Statistics for Windows, Version 24.0, IBM Corp. (2016). This preliminary analysis aimed to assess the reliability of the scoring system, and it demonstrated high reliability, with statistically significant perfect agreement among the observations by the same assessors' judgments for response type and response intensity across all 12 stimuli. When evaluating mood/emotion, highly statistically significant perfect agreement was observed among the observations by the same raters for all traits and stimuli.

Once, intraobserver effect had been discarded, as recommended by Bunting et al. (2019), we used the Intraclass Correlation Coefficient (ICC) as a reference method to assess the reproducibility and reliability of numeric measurements as three different trained operators had measured the same variable across all the animals involved in the study (interobserver reliability).

There are no fixed standards for acceptable ICC reliability values. A low ICC may indicate poor agreement among raters or measurements and may also be linked to limited subject variability, a small sample size, or a small number of raters involved. As a general guideline, we recommend using at least 30 diverse samples and involving a minimum of 3 raters when conducting a reliability study. Under these conditions, ICC values can be interpreted as follows: less than 0.5 indicates poor reliability, 0.5 to 0.75 suggests moderate reliability, 0.75 to 0.9 signifies good reliability, and values above 0.90 indicate excellent reliability (Koo & Li, 2016).

Following the criteria set by Fleiss and Cohen (1973), we interpreted ICC values as follows: less than 0.4 (low), 0.4 to 0.59 (reasonable), 0.6 to 0.74 (good), and 0.75 to 1.0 (excellent) to determine if we achieved sufficient reproducibility and repeatability. We used the "Two-Way Random" model, as recommended by Koo and Li (2016), and calculated 95% confidence intervals using the formula 95% kappa Confidence Interval (95%CI) = κ ± 1.96 SEκ, utilizing the reliability analysis routine in SPSS Statistics for Windows, Version 25.0, IBM Corp. (2017).

This analysis aimed to assess the reliability of the scoring system, and it demonstrated high reliability, with statistically significant perfect agreement among the three assessors' judgments for response type and response intensity across all 12 stimuli as shown in Table 2.

Table 2. Results for the interobserver reliability analysis.

Raters combinations		**Rater 1 vs Rater 2**		**Rater 1 vs Rater 3**		**Rater 2 vs Rater 3**	
Measures		Single	Average	Single	Average	Single	Average
Intraclass Correlation		0.871	0.931	0.902	0.949	0.886	0.939
95% Confidence Interval	**Lower Bound**	0.858	0.923	0.892	0.943	0.874	0.933
	Upper Bound	0.883	0.938	0.912	0.954	0.896	0.945
F Test with True Value 0	**Value**	14.498	14.498	19.512	19.512	16.492	16.492
	df1	1429	1429	1429	1429	1429	1429
	df2	1429	1429	1429	1429	1429	1429
	Sig.	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Parallelly, body language of dromedary camels was registered through the evaluation of frontal and lateral view of the ears. The ethogram for two-dimensional ear movements (frontal and lateral) is presented in Table 3. This table provides descriptions of three levels of ear positions, specifically focusing on both lateral and frontal orientations as suggested in Fowler (2011). A unified score was assigned to each position.

Table 3. Lateral and frontal ear position category description.

Frontal view	**Lateral view**
Ears forward	Ears sideward and forward
Ears erected	Ears sideward
Ears backward	Ears sideward and backward

Statistical analysis

In accordance with the methodologies presented by González Ariza et al. (2021), our initial approach involved conducting a discriminant canonical analysis. The primary objective was to develop a tool capable of assessing the most optimal linear combinations of coping style related traits, weight and age as well as phaneroptics (eye and coat colour and particularities), sex, and neutering status, but also owner, training plan and in regards the type of test and stimulus presented to the animals method used, stimulus nature (visual or visual/acoustic), type of reinforcement (positive or negative), familiarity towards stimulus (known or unknown) and ear position (frontal/lateral view). Response intensity levels (scored from one to five as presented in Table 1) formed the basis for population clustering patterns in this study and they served as independent variables in our analytical framework.

For the classification, prediction, interpretation, and manipulation of observations associated with the aforementioned dependent variables, we employed the Chi-squared automatic interaction detection (CHAID) decision tree method. This method allowed for a discrete analysis of the independent variables and the relationships that it describes with Response intensity levels (scored from one to five as presented in Table 1).

To assess the reliability of the CHAID decision tree model, we conducted cross-validation. This involved evaluating the model's predictive performance when applied to new data samples, comparing it to the training sample. Cross-validation provided valuable insights into how effectively the model could generalize to unseen data. To validate the CHAID decision tree and determine whether the selected predictors effectively explained differences across response intensity levels (scored from one to five as presented in Table 1), we employed a ten-fold cross-validation approach.

Results

Discriminant canonical analysis model reliability

Following 6 rounds of multicollinearity analyses, the variables included in the discriminant canonical analyses are detailed in Table 4.

Pillai's trace criterion reported a significant difference across Response intensity levels (scored from one to five as presented in Table 1) (Pillai's trace criterion: 0.6441, F (Observed value): 40.9662, F (Critical value): 1.2744, df1: 80, df2: 17076, p-value< 0,0001), confirming the validity of the discriminant canonical analysis.

Four out of the four functions identified through the discriminant analysis demonstrated significant discriminant ability (Table 5). Among these functions, F1 displayed the highest discriminatory power (eigenvalue of 0.6419, respectively; Table 5), explaining a significant 69.18% of the variance. Consequently, F1 through F4 collectively explained 100% of the variability.

Canonical coefficients and loading interpretation

The variables investigated in this study were ranked based on their discriminative capacity. A test comparing group means of the dependent variables involved in the discriminant canonical analysis was performed, as shown in Table 6. Higher F-values and lower values of Wilks' Lambda indicate greater discriminatory power.

Table 4. Summary of the value of tolerance and VIF after multicollinearity analysis of behavioural-type coping strategies in Canarian camel breed.

Statistic	Tolerance (1-R^2)	VIF (1/Tolerance)
Age (months)	0.7574	1.3204
Eye colour-Brownish with blue spots	0.6933	1.4425
Eye colour-Brownish	0.6850	1.4599
Body weight (kg)	0.6620	1.5105
Method-1	0.5376	1.8602
Ears Front View-2	0.5319	1.8799
Method-7	0.5281	1.8934
Method-2	0.5221	1.9154
Method-3	0.5214	1.9181
Ears Front View-1	0.5153	1.9404
Method-5	0.5107	1.9581
Method-8	0.5075	1.9704
Method-9	0.5034	1.9863
Method-6	0.4955	2.0182
Method-10	0.4924	2.0309
Method-4	0.4906	2.0383
Sex-Male	0.3426	2.9186
Neutered-Yes	0.2556	3.9126

Interpretation thumb rule: VIF ≥ 5 (highly correlated); 1 < VIF < 5 (moderately correlated); VIF = 1 (not correlated).

Table 5. Canonical discriminant analysis efficiency parameters to determine the significance of each canonical discriminant function.

Test functions	Canonical Correlation	Eigenvalue	Variance discrimination(%)	Bartlett's statistic	P-value
1 through 13	0.6173	0.6419	69.1762	3041.7512	<0.0001
2 through 13	0.3745	0.1647	17.7502	989.5693	<0.0001
3 through 13	0.2532	0.1006	10.8419	343.1375	<0.0001
4	0.1177	0.0207	2.2317	59.7078	<0.0001

Table 6. Results for the tests of equality of group means to test for difference in the means across sample groups once redundant variables have been removed.

Variable	Wilk's Lambda	F	P-value	Rank
Sex-Male	0.9016	116.8876	< 0.0001	1
Method-11	0.9233	88.9967	< 0.0001	2
Known/unknown rear-N/A	0.9298	80.9128	< 0.0001	3
Method-10	0.9362	72.9841	< 0.0001	4
Neutered-Yes	0.9393	69.2589	< 0.0001	5
Method-7	0.9410	67.2266	< 0.0001	6
Method-9	0.9522	53.7635	< 0.0001	7
Method-8	0.9538	51.9346	< 0.0001	8
Age (months)	0.9669	36.7075	< 0.0001	9

Table 6. *Cont.*

Variable	Wilk's Lambda	F	P-value	Rank
Body weight (kg)	0.9700	33.0774	< 0.0001	10
Method-2	0.9776	24.5883	< 0.0001	11
Ears Front View-2	0.9791	22.8557	< 0.0001	12
Method-5	0.9816	20.0276	< 0.0001	13
Type-Neutral	0.9824	19.2140	< 0.0001	14
Ears Front View-3	0.9866	14.6046	< 0.0001	15
Nature-Visual/Acoustic	0.9890	11.9268	< 0.0001	16
Eye colour-Bluish	0.9925	8.0946	< 0.0001	17
Eye colour-Brownish	0.9927	7.8799	< 0.0001	18

df1=72;df2=16785

Standardized discriminant coefficients, which measure the relative importance of each dependent variable across the five established discriminant functions, are presented in Supplementary Table S1.

A Press' Q value of 3956.74 (n = 4290; n' = 2506; K = 5) was computed for Response intensity levels (scored from one to five as presented in Table 1), indicating that predictions can be considered better than chance at a 95% confidence level (Chan, 2005).

Centroids for response intensity levels

Centroids for the levels of response intensity (scored from one to five as presented in Table 1) considered in this study were calculated. These centroids were determined by substituting the mean values for the observations represented in each of the five significantly detected discriminant functions (F1 to F4). Detailed results for the functions at the centroids are reported in Table 7.

Table 7. Functions at the centroids for the levels of response intensity.

Function/Response intensity	1	2	3	4	5
F1	-1.318	-0.694	0.507	0.644	-0.41
F2	-0.095	0.012	0.39	-0.633	0.245
F3	0.024	0.378	0.059	-0.03	-0.949
F4	-0.117	0.313	-0.035	-0.003	0.169

Data mining CHAID decision tree

CHAID decision tree is provided in Supplementary Figure 1.

Discussion

Globally, the animals evaluated in the present study were more inclined toward proactivity than reactivity, that is, they tend to get actively engaged with environmental stressors, have a feed-forward memory, have low glucocorticoid-based stress response, and are less flexible to environmental cues. Such a finding would be explained to a large extent by the behavioural and physiological-type coping strategies that camels have developed through the centuries for energy optimization in desert-type habitats with extreme conditions, as well as their domestic character. However, the existence of variability in the stress response also reflects the implication of different factors on coping styles, which should be thoroughly considered when predicting the response of animals to stressful situations and, within the context of selective breeding, when selecting those individuals with the most desired behavioural patterns for a specific functionality. Further, in relation to this interindividual variability in the response, as can be concluded based on the percentage of classification of the discriminant analysis, the number of classifying categories can be reduced, given that there is noticeable confusion between some of them.

The variables that most discriminate among animals for their coping response (Supplementary Figure 1) are the type of test used (which includes the nature of the stimulus and type of reinforcement), sex, age, body weight, ears front view, and neutering status. With regard to the type of test used, animals were more reactive to methods 1, 2, 3, 4, 5, and 6, which fundamentally use visual stimuli and negative reinforcement. In contrast, for the methods 7, 8, 9, 10, and 11, which used negative reinforcement and a combination of visual and auditory stimuli, the animals showed higher proactive responses. From these results, it can be concluded that it is best to use negative reinforcement and a combination of visual and auditory stimuli for the evaluation of the individual response to environmental stimuli and training the camels for interactive experiences with humans. When compared with existing literature on this specific matter for other animal species, there is a wide variability as to what type of reinforcement is best to successfully intervene on approach/avoidance behaviors in an animal setting (Baker & Wong, 2019; Brajon et al., 2015; Diverio et al., 2017; Fernandez, 2020; Freymond et al., 2014). This discrepancy could be attributed to handling treatment and specific environmental conditions at the rearing location, but also to the sample size and composition of the qualitative and quantitative behavior assessment scales used in each investigation.

Concerning the combination of visual and auditory stimuli, given the fact that the camels evaluated participate in tourist routes in which the animals are disposed in a single line (caravan) and follow the guidelines of the human team in charge of leading the activity, it is expected that a significant role is played by both visual stimuli (especially to see what is ahead) and auditive stimulus (inter- and intra-especific communication signals). If animals are exposed to a combination of stimuli and are desensitized by means of negative reinforcement techniques, it would help reduce stress levels and enhance behavioral anticipation before stimuli of a diverse nature that may appear simultaneously. In addition, method 11, in which there were congeners around, provides evidence of the relevance of social support to master environmental stressors in a gregarious species such as camels (Padalino et al., 2014). Social support has been reported to affect coping styles in a wide range of animal species, such as non-human primates, rodents, dogs, farm animals, and birds (Hennessy, Kaiser, & Sachser, 2009; Kikusui, Winslow, & Mori, 2006; Rault, 2012; Reimert et al., 2014). For sex, females tend to be generally more reactive, which may be related to sex-linked differences, mostly mediated by reproductive steroid hormones and cyclicity, in neurotransmitter and neuromodulatory systems that are correlated with a higher general prevalence of stress- and fear-eliciting behaviors in female mammals (Donner & Lowry, 2013; Keiser et al., 2017; Kokras & Dalla, 2014; Maeng & Milad, 2015; Palanza, 2001). The usually practiced castration of males and the positive-biased involvement of this sex in leisure tourism activities, can be an additional reason for these results. Besides, in those species with differentiated parental involvement in offspring care, the sex that gets involved in the lesser proportion (in camels, the male) is prone to take higher-risk strategies, seek for novelty, and be more sensitive to reward and impulsivity (Palanza, 2001).

Taking into account the interrelationship between sex and age, some differences can be appreciated and are important to contemplate when acquiring an animal whose past history is relatively unknown and which wants to be involved in a specific domestication protocol. Male dromedaries become more proactive when they are exposed to unknown stimuli at a certain age (around 208 months of age), while the reactivity tends to be enhanced in females in the same scenario at an average age of 112 months. Hence, males remain generally more reactive until older ages with respect to females, but become more proactive from a certain age. These results coincide with those by Pastrana et al. (2021), who stated that adult male dromedaries are more cautious and curious animals and linked this finding to inherited traits in males of resource-defense polygynous mammals but also to the accumulation of practical knowledge that could help group decision making and survival as long as age increases. Additionally, these authors point out that, by initiating the domestication protocols at the same age, female dromedaries appear to be ready to participate in ride experiences earlier than males. Such a condition would be explained on the basis that females reach sexual maturity earlier than males; therefore, their ability to participate in leisure riding activities after an adapted domestication protocol is greater since their cognitive development, mediated largely by sexual hormones (Luine, 2014), will be superior. In short, these findings should be taken as an indicator to initiate female domestication protocols as soon as possible to avoid a greater probability of reactivity as the animal grows and reproduces and, in the case of males, to encourage proactive attitudes as quickly as possible and after castration.

In fact, neutering status also played a discriminating role in behavioural-type coping responses in dromedary camels. In particular, castrated animals were more proactive. It could be explained by the effects of castration on the reduction of the probability of unwanted behaviors associated with the intrinsic activity of sex hormones. In light of the arguments about the relationship between sexual hormones and cognitive maturity outlined above, the protocol that is followed in this camel breed to castrate animals is that the animals are neutered once they have reached sexual maturity and have been initiated in the domestication protocol for their functionality, to ensure that they reach sufficient serum levels of sex hormones for a proper organic maturity and avoid a harmful level from a behavioural viewpoint (Oliveira, 2009; Pastrana et al., 2021). Closely related, other effects of castration in camels include robustness and physical endurance (Pigière & Henrotay, 2012; Ucko & Dimbleby, 2007). Thus, castrated animals are usually heavier. As for the implication of the variable body weight on coping styles in dromedary camels, heavier animals, which are usually castrated, tend to be less reactive.

With reference to the perception of the evaluator of the position of the ears of the camel from a frontal or lateral view, considering the relative low range of mobility that these animals have in this body region, it would be expected that only the frontal view has discriminating potential. In a lateral view, if the movement is slight, a change of position would hardly be appreciated. But if the ears are seen from the front, even if there is a slight change in position, a change in the longitudinal axis of the ear will be more appreciable. Specifically, a segment of the auricular pavilion will be appreciated if the ears move forward and a proportion of the dorso-medial side of the ear if they are backwards. In the current study, the more backward the ears are, the greater the proactivity of the camel is expected. Typically, when dromedary camels have their ears backwards, they are considered to be in an angry or upset position, which is common to dominant/aggressive animals, and these are commonly the most proactive individuals. Moreover, in the case of the use of a combination of visual and auditory stimuli, these latter being generally unknown to the animal and disposed behind the subject, the position of the ears backward would indicate that the animal is trying to identify the stimulus that is behind to subsequently try to solve the situation instead of being immobilized.

For the rest of the variables with discriminating potential, their effect was comparatively small. On the one hand, the impact of eye colour on proactivity or reactivity would be related to variability in visual acuity in relation to heterogeneity in iris pigmentation. Visual acuity is expected to be lower as long as the iris pigmentation is more heterogeneous (Frank et al., 2000), which in turn may influence the approach/avoidance response of the animals towards the surrounding stimuli. Then, the significant but relatively low impact of the variables nature of the stimulus, type of reinforcement, position of stimuli, and familiarity of the animal with them, would reinforce the importance of using the combination of the presentation of stimuli, either visual or auditive, and reinforcement techniques rather than using them separately.

Contrastingly, the owner/trainer and the regime of physical exercise did not exert a significant influence on the coping styles of dromedary camels. Such an outcome adds further evidence that the camels evaluated, which are bred in spaces relatively different from each other but for the same functionality, are domestic animals that would, in general, respond positively to different stimuli. That is, the stress response of dromedary camels is not significantly affected by potential variations in the man-made environment in which the animals are bred relative to the bond that exists between the animal and the staff in charge of their breeding and physical-psychological training.

The coat colour and particularities did not also have a significant impact on behavioral-type stress responses in our animal sample. For leadership behavior it has effectively played a significant role (Iglesias Pastrana et al., 2021) but for the camel behaviour perceived by the client during tourist routes, which would be in close relationship with the behavioural features evaluated in this study and despite of mere experimental design effects might be represented, it also did not have a significant effect (Pastrana et al., 2021). Pleiotropic effects are inferred for genes responsible for coat and eye colour on temperament features such as calmness and nervousness (Ducrest, Keller, & Roulin, 2008; Finn et al., 2016; Keeler, 1942; Kim et al., 2010; Pérez-Guisado, Lopez-Rodríguez, & Muñoz-Serrano, 2006; Podberscek & Serpell, 1996; Trut, 1999), and some congenital disorders such as deafness and ocular anomalies in different animal species (Schonthaler et al., 2005; Volpato, Dioli, & Di Nardo, 2017), which can notably determine the level of individual engagement on exploratory activities and other energetic tasks, and in turn the probability to emerge as group leader. However, coping styles comprise cognitive-processing traits, which are more complex dimensions and that are influenced, among other factors, by desensitization protocols. Furthermore, when evaluating leadership behaviour in dromedary camels, the herd structure was not distorted, thus the intraherd dominance-subordination structure is an influencing factor, which coul be affected by external colouration as reported for other animal species (Bro-Jørgensen, 2002; Geist, 1987; Gerald, 2001; Guthrie, 1971; Parsons & Baptista, 1980; West & Packer, 2002); whereas during the assessment of coping behaviours, the animals are isolated from the group for their individual evaluation. From these statements, it is deduced, on the one hand, that leadership behavior and social dominance within the herd in camels could conceal the real cognitive abilities of camels, similarly to the results for cognitive performance in fallow deer (Pastrana et al., 2022). Likewise, it can be concluded that a camel with a coat colour potentially associated with congenital disorders and undesired behavioural features that could difficult its training for a specific functional role, should not be excluded from their participation in leisure riding or therapy but to adapt a protocol to approach and train it.

Conclusions

A genetic background for camel behavior, mediated by both coping strategies for energy optimization in desert-type ecosystems and domestication, can explain the generally proactive response of dromedary camels when coping with new environmental stressors. However, non-negligible variability does exist in coping styles in dromedaries, and that is fundamentally attributable to behavioural assessment tools, sex, and body language signals. Negative reinforcement strategies and the use of a combination of visual and auditory stimuli are the most optimal tools to increase camels' approaching behaviour towards new stimuli, thus favoring the training of camels for diverse activities that include active interaction with relatively unknown elements. Given their gregarious character, social support promotes proactive coping behaviour in this animal species. Additionally, sexual hormones and selection play an active role in the manner in which the dromedary camel copes with stressors. Male dromedaries become more proactive as age increases, whereas this condition enhances reactive coping responses in females. Hence, camel training protocols are recommended to be initiated at the earliest ages possible in order to reduce the probability of undesired reactivity as the animal grows and to encourage proactive attitudes as quickly as possible in females and males, respectively. In a close relationship, the castration of the animals once sexual maturity is reached and domestication protocol for their functional aptitude is initiated, will stimulate body growth and physical endurance, as well as proactive coping responses. With reference to interspecific communication signals, when the position of the ears is evaluated from the front view of the animal, the more backward the ears are, the greater the proactivity of the camel is expected. This conglomerate of information will allow owners and breeders to select leisure camels for reduced reactivity and fearfulness, although further research including more animals and functional aptitudes would enrich the empirical knowledge in this regard with its potential applications in animal welfare promotion scenarios and the exploration of new niches for conservation purposes.

Author contributions: Conceptualization, C.I.P., F.J.N.G. and A.K.M.; Data curation, C.I.P. and F.J.N.G.; Formal analysis, C.I.P., F.J.N.G. and A.K.M.; Funding acquisition, E.C. and J.V.D.B.; Investigation, C.I.P. and F.J.N.G.; Methodology, C.I.P., F.J.N.G. and A.K.M.; Project administration, E.C. and J.V.D.B.; Resources, E.C. and J.V.D.B.; Software, C.I.P., F.J.N.G. and A.K.M.; Supervision, F.J.N.G., E.C. and J.V.D.B.; Validation, F.J.N.G. and J.V.D.B.; Visualization, E.C.; Writing—original

draft, C.I.P. and F.J.N.G.; Writing—review & editing, F.J.N.G., E.C. and J.V.D.B. All authors have read and agreed to the published version of the manuscript.

Funding: The present research was carried out in the financing framework of the international project CA.RA.VA.N—'Toward a Camel Transnational Value Chain' (Reference APCIN-2016-00011-00-00) and during the covering period of a predoctoral contract (FPU Fellowship) funded by the Spanish Ministry of Science and Innovation and was developed under the context a Ramón y Cajal Post-Doctoral fellowship financially supported by MCIN/AEI/10.13039/501100011033 and European Union "NextGenerationEU"/PRTR" (Recovery, Transformation and Resilience Plan—Funded by the European Union—NextGenerationEU).

Data availability statement: The data presented in this study are available on request from the first author.

Acknowledgments: The authors would also like to thank 'Aires Africanos' Eco-tourism Company, Oasis Park Fuerteventura, and 'Camelus' Camellos de Almería, for their direct technical help and assistance.

Conflicts of interest: The authors declare no conflict of interest.

Ethics declaration statement: All farms included in the study followed specific codes of good practices and therefore, the animals received humane care in compliance with the national guide for the care and use of laboratory and farm animals in research. Written consent from the owners was obtained for their participation. The study was conducted in accordance with the Declaration of Helsinki. The Spanish Ministry of Economy and Competitivity through the Royal Decree Law 53/2013 and its credited entity, the Ethics Committee of Animal Experimentation from the University of Córdoba, permitted the application of the protocols present in this study as cited in the 5th section of its 2nd article, as the animals assessed were used for credited zootechnical use. This national Decree follows the European Union Directive 2010/63/UE, from the 22 September of 2010.

References

Abdullah, A., Said, I. B., & Ossen, D. R. (2019). A sustainable bio-inspired cooling unit for hot arid regions: Integrated evaporative cooling system in wind tower. *Applied Thermal Engineering*, 161, 114201.

Al-Jassim, R., & Sejian, V. (2015). Climate change and camel production: impact and contribution. *Journal of Camelid Science*, 8, 1-17.

Baker, M. R., & Wong, R. Y. (2019). Contextual fear learning and memory differ between stress coping styles in zebrafish. *Scientific reports*, 9(1), 9935.

Barreto, R. E., & Volpato, G. L. (2011). Ventilation rates indicate stress-coping styles in Nile tilapia. *Journal of biosciences*, 36(5), 851-855.

Benus, R., Bohus, B., Koolhaas, J., & Van Oortmerssen, G. (1991). Heritable variation for aggression as a reflection of individual coping strategies. *Experientia*, 47, 1008-1019.

Berger, J., Brubaker, A., Willits, N., & Coss, R. (2013). Novelty Seeking & Startle Response in Adult Domesticated Horses. Proceedings of the 9th International Equitation Science Conference, International Society for Equitation Science, University of Delaware (USA).

Bolhuis, J. E., Schouten, W. G., Schrama, J. W., & Wiegant, V. M. (2005). Individual coping characteristics, aggressiveness and fighting strategies in pigs. *Animal Behaviour*, 69(5), 1085-1091.

Bouâouda, H., Achâaban, M. R., Ouassat, M., Oukassou, M., Piro, M., Challet, E., El Allali, K., & Pévet, P. (2014). Daily regulation of body temperature rhythm in the camel (*Camelus dromedarius*) exposed to experimental desert conditions. *Physiological Reports*, 2(9), e12151.

Boujenane, I. (2019). Comparison of body weight estimation equations for camels (*Camelus dromedarius*). *Tropical animal health and production*, 51, 1003-1007.

Brajon, S., Laforest, J.-P., Schmitt, O., & Devillers, N. (2015). The way humans behave modulates the emotional state of piglets. *PLoS One*, 10(8), e0133408.

Bro-Jørgensen, J. (2002). Overt female mate competition and preference for central males in a lekking antelope. *Proceedings of the National Academy of Sciences*, 99(14), 9290-9293.

Budzyńska, M. (2014). Stress reactivity and coping in horse adaptation to environment. *Journal of Equine Veterinary Science*, 34(8), 935-941.

Bunting, K. V., Steeds, R. P., Slater, L. T., Rogers, J. K., Gkoutos, G. V., & Kotecha, D. (2019). A practical guide to assess the reproducibility of echocardiographic measurements. *Journal of the American Society of Echocardiography*, 32(12), 1505-1515.

Çakmakçı, C., Karaca, S., & María, G. A. (2021). Does coping style affect behavioral responses and growth performance of lambs weaned at different ages? *Journal of Veterinary Behavior*, 42, 64-74.

Chan, Y. (2005). Biostatistics 303. Discriminant analysis. *Singapore medical journal*, 46(2), 54.

Correa, L. M., Zapata, B., Goddard, P., & Bonacic, C. (2019). The relationship between coping styles and responses to handling in captive guanacos (*Lama guanicoe*). *Small Ruminant Research*, 177, 103-105.

Diverio, S., Menchetti, L., Riggio, G., Azzari, C., Iaboni, M., Zasso, R., Di Mari, W., & Santoro, M. M. (2017). Dogs' coping styles and dog-handler relationships influence avalanche search team performance. *Applied Animal Behaviour Science*, 191, 67-77.

Donner, N. C., & Lowry, C. A. (2013). Sex differences in anxiety and emotional behavior. *Pflügers Archiv-European Journal of Physiology*, 465, 601-626.

Ducrest, A.-L., Keller, L., & Roulin, A. (2008). Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends in ecology & evolution*, 23(9), 502-510.

Fernandez, E. J. (2020). Training petting zoo sheep to act like petting zoo sheep: An empirical evaluation of response-independent schedules and shaping with negative reinforcement. *Animals*, 10(7), 1122.

Ferrari, C., Pasquaretta, C., Carere, C., Cavallone, E., von Hardenberg, A., & Réale, D. (2013). Testing for the presence of coping styles in a wild mammal. *Animal Behaviour*, 85(6), 1385-1396.

Finn, J. L., Haase, B., Willet, C. E., van Rooy, D., Chew, T., Wade, C. M., Hamilton, N.A., & Velie, B. D. (2016). The relationship between coat colour phenotype and equine behaviour: A pilot study. *Applied Animal Behaviour Science*, 174, 66-69.

Fleiss, J. L., & Cohen, J. (1973). The equivalence of weighted kappa and the intraclass correlation coefficient as measures of reliability. *Educational and psychological measurement*, 33(3), 613-619.

Fowler, M. (2011). *Medicine and surgery of camelids*: John Wiley & Sons.

Frank, R. N., Puklin, J. E., Stock, C., & Canter, L. A. (2000). Race, iris color, and age-related macular degeneration. *Transactions of the American Ophthalmological Society*, 98, 109.

Freymond, S. B., Briefer, E. F., Zollinger, A., Gindrat-von Allmen, Y., Wyss, C., & Bachmann, I. (2014). Behaviour of horses in a judgment bias test associated with positive or negative reinforcement. *Applied Animal Behaviour Science*, 158, 34-45.

Gaughan, J. (2011). Which physiological adaptation allows camels to tolerate high heat load–and what more can we learn. *Journal of Camelid Science*, 4, 85-88.

Geist, V. (1987). On speciation in Ice Age mammals, with special reference to cervids and caprids. *Canadian Journal of Zoology*, 65(5), 1067-1084.

Gerald, M. S. (2001). Primate colour predicts social status and aggressive outcome. *Animal Behaviour*, 61(3), 559-566.

Geuens, M., & De Pelsmacker, P. (2002). Developing a short affect intensity scale. *Psychological reports*, 91(2), 657-670.

González Ariza, A., Arando Arbulu, A., León Jurado, J. M., Navas González, F. J., Delgado Bermejo, J. V., & Camacho Vallejo, M. E. (2021). Discriminant canonical tool for differential biometric characterization of multivariety endangered hen breeds. *Animals*, 11(8), 2211.

González, F. J. N., Vidal, J. J., Jurado, J. M. L., Arbulu, A. A., McLean, A. K., & Bermejo, J. V. D. (2018). Genetic parameter and breeding value estimation of donkeys' problem-focused coping styles. *Behavioural processes*, 153, 66-76.

Guthrie, R. (1971). A new theory of mammalian rump patch evolution. *Behaviour*, 38(1-2), 132-145.

Hennessy, M. B., Kaiser, S., & Sachser, N. (2009). Social buffering of the stress response: diversity, mechanisms, and functions. *Frontiers in neuroendocrinology*, 30(4), 470-482.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S. and Delgado, J. V. (2020). Ethological characterization of the Canarian camel breed. *Archivos de zootecnia*, 69(265), 108-115.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Arando Arbulu, A., & Delgado Bermejo, J. V. (2021). The Youngest, the Heaviest and/or the Darkest? Selection Potentialities and Determinants of Leadership in Canarian Dromedary Camels. *Animals*, 11(10), 2886.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Barba Capote, C. J., & Delgado Bermejo, J. V. (2020a). Effect of research impact on emerging camel husbandry, welfare and social-related awareness. *Animals*, 10(5), 780.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Nogales Baena, S., & Delgado Bermejo, J. V. (2020b). Camel Genetic Resources Conservation through Tourism: A Key Sociocultural Approach of Camelback Leisure Riding. *Animals*, 10(9), 1703.

Keeler, C. E. (1942). The association of the black (non-agouti) gene with behavior: In the Norway Rat. *Journal of Heredity*, 33(11), 371-384.

Keiser, A. A., Turnbull, L. M., Darian, M. A., Feldman, D. E., Song, I., & Tronson, N. C. (2017). Sex differences in context fear generalization and recruitment of hippocampus and amygdala during retrieval. *Neuropsychopharmacology*, 42(2), 397-407.

Kikusui, T., Winslow, J. T., & Mori, Y. (2006). Social buffering: relief from stress and anxiety. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 361(1476), 2215-2228.

Kim, Y. K., Lee, S. S., Oh, S. I., Kim, J. S., Suh, E. H., Houpt, K. A., Lee, H.C., Lee., H.J., & Yeon, S. C. (2010). Behavioural reactivity of the Korean native Jindo dog varies with coat colour. *Behavioural Processes*, 84(2), 568-572.

Kokras, N., & Dalla, C. (2014). Sex differences in animal models of psychiatric disorders. *British journal of pharmacology*, 171(20), 4595-4619.

Koo, T. K., & Li, M. Y. (2016). A guideline of selecting and reporting intraclass correlation coefficients for reliability research. *Journal of chiropractic medicine*, 15(2), 155-163.

Koolhaas, J., De Boer, S., Coppens, C., & Buwalda, B. (2010). Neuroendocrinology of coping styles: towards understanding the biology of individual variation. *Frontiers in neuroendocrinology*, 31(3), 307-321.

Koolhaas, J., Korte, S., De Boer, S., Van Der Vegt, B., Van Reenen, C., Hopster, H., De Jong, I.C., Ruis, M.A.W., & Blokhuis, H. (1999). Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews*, 23(7), 925-935.

Landis, J. R., & Koch, G. G. (1977). An application of hierarchical kappa-type statistics in the assessment of majority agreement among multiple observers. *Biometrics*, 363-374.

Luine, V. N. (2014). Estradiol and cognitive function: past, present and future. *Hormones and behavior*, 66(4), 602-618.

Maeng, L. Y., & Milad, M. R. (2015). Sex differences in anxiety disorders: interactions between fear, stress, andgonadal hormones. *Hormones and behavior*, 76, 106-117.

Martins, C. I., Silva, P. I., Conceição, L. E., Costas, B., Höglund, E., Øverli, Ø., & Schrama, J. W. (2011). Linking fearfulness and coping styles in fish. *PLoS One*, 6(11), e28084.

Navas, F. J., Jordana, J., León, J. M., Arando, A., Pizarro, G., McLean, A. K., & Delgado, J. V. (2017). Measuring and modeling for the assessment of the genetic background behind cognitive processes in donkeys. *Research in veterinary science*, 113, 105-114.

Navas González, F. J., Jordana Vidal, J., León Jurado, J. M., Arando Arbulu, A., McLean, A. K., & Delgado Bermejo, J. V. (2018a). Genetic parameter and breeding value estimation of donkeys' problem-focused coping styles. *Behavioural Processes*, 153, 66-76.

Navas González, F. J., Jordana Vidal, J., Pizarro Inostroza, G., Arando Arbulu, A., & Delgado Bermejo, J. V. (2018b). Can Donkey Behavior and Cognition Be Used to Trace Back, Explain, or Forecast Moon Cycle and Weather Events? *Animals*, 8(11), 215.

Navas González, F. J., Vidal, J. J., León Jurado, J. M., McLean, A. K., & Delgado Bermejo, J. V. (2020). Nonparametric analysis of noncognitive determinants of response type, intensity, mood, and learning in donkeys (*Equus asinus*). *Journal of Veterinary Behavior*, 40, 21-35.

Oliveira, R. F. (2009). Social behavior in context: hormonal modulation of behavioral plasticity and social competence. *Integrative and Comparative Biology*, 49(4), 423-440.

Øverli, Ø., Korzan, W. J., Höglund, E., Winberg, S., Bollig, H., Watt, M., Forster, G.L., Barton, B.A., Øverli, E., Renner, K.J., & Summers, C.H. (2004). Stress coping style predicts aggression and social dominance in rainbow trout. *Hormones and behavior*, 45(4), 235-241.

Padalino, B., Aubé, L., Fatnassi, M., Monaco, D., Khorchani, T., Hammadi, M., & Lacalandra, G. M. (2014). Could dromedary camels develop stereotypy? The first description of stereotypical behaviour in housed male dromedary camels and how it is affected by different management systems. *PLoS One*, 9(2), e89093.

Palanza, P. (2001). Animal models of anxiety and depression: how are females different? *Neuroscience & Biobehavioral Reviews*, 25(3), 219-233.

Parsons, J., & Baptista, L. F. (1980). Crown color and dominance in the white-crowned sparrow. *The Auk*, 97(4), 807-815.

Pastrana, C. I., González, F. J. N., Ciani, E., Ariza, A. G., & Bermejo, J. V. D. (2021). A tool for functional selection of leisure camels: Behaviour breeding criteria may ensure long-term sustainability of a European unique breed. *Research in Veterinary Science*, 140, 142-152.

Pastrana, C. I., Gonzalez, F. J. N., Inostroza, M. G. P., Arbulu, A. A., Bermejo, J. V. D., & Aguilera, M. J. R. (2022). Study of variability of cognitive performance in captive fallow deer (*Dama dama*) through g and c factors. *Journal of Veterinary Behavior*, 47, 70-85.

Pérez-Guisado, J., Lopez-Rodríguez, R., & Muñoz-Serrano, A. (2006). Heritability of dominant–aggressive behaviour in English Cocker Spaniels. *Applied Animal Behaviour Science*, 100(3-4), 219-227.

Pigière, F., & Henrotay, D. (2012). Camels in the northern provinces of the Roman Empire. *Journal of Archaeological Science*, 39(5), 1531-1539.

Podberscek, A. L., & Serpell, J. A. (1996). The English Cocker Spaniel: preliminary findings on aggressive behaviour. *Applied Animal Behaviour Science*, 47(1-2), 75-89.

Rault, J.-L. (2012). Friends with benefits: social support and its relevance for farm animal welfare. *Applied Animal Behaviour Science*, 136(1), 1-14.

Reimert, I., Bolhuis, J. E., Kemp, B., & Rodenburg, T. B. (2014). Social support in pigs with different coping styles. *Physiology & behavior*, 129, 221-229.

Schonthaler, H. B., Lampert, J. M., von Lintig, J., Schwarz, H., Geisler, R., & Neuhauss, S. C. (2005). A mutation in the silver gene leads to defects in melanosome biogenesis and alterations in the visual system in the zebrafish mutant fading vision. *Developmental biology*, 284(2), 421-436.

Shahda, M. M., Abd Elhafeez, M. M., & El Mokadem, A. A. (2018). Camel's nose strategy: New innovative architectural application for desert buildings. *Solar Energy*, 176, 725-741.

Trut, L. N. (1999). Early Canid Domestication: The Farm-Fox Experiment: Foxes bred for tamability in a 40-year experiment exhibit remarkable transformations that suggest an interplay between behavioral genetics and development. *American Scientist*, 87(2), 160-169.

Ucko, P. J., & Dimbleby, G. W. (2007). *The domestication and exploitation of plants and animals*: Transaction Publishers.

Vindas, M. A., Gorissen, M., Höglund, E., Flik, G., Tronci, V., Damsgård, B., Thörnqvist, P.O., Nilsen, T.O., Winberg, S., Øverli, Ø., & Ebbesson, L.O.E. (2017). How do individuals cope with stress? Behavioural, physiological and neuronal differences between proactive and reactive coping styles in fish. *Journal of Experimental Biology*, 220(8), 1524-1532.

Volpato, G., Dioli, M., & Di Nardo, A. (2017). Piebald camels. *Pastoralism*, 7(1), 3.

Wechsler, B. (1995). Coping and coping strategies: a behavioural view. *Applied Animal Behaviour Science*, 43(2), 123-134.

West, P. M., & Packer, C. (2002). Sexual selection, temperature, and the lion's mane. *Science*, 297(5585), 1339-1343.

Wilson, R. T. (2012). *Ecophysiology of the Camelidae and desert ruminants*: Springer Science & Business Media.

Windberger, U., Auer, R., Seltenhammer, M., Mach, G., & Skidmore, J. A. (2019). Near-Newtonian Blood Behavior–Is It Good to Be a Camel? *Frontiers in Physiology*, 10, 906.

Zidar, J., Balogh, A., Favati, A., Jensen, P., Leimar, O., & Løvlie, H. (2017). A comparison of animal personality and coping styles in the red junglefowl. *Animal Behaviour*, 130, 209-220.

Zozulya, A. A., Gabaeva, M. V., Sokolov, O. Y., Surkina, I. D., & Kost, N. V. (2008). Personality, coping style, and constitutional neuroimmunology. *Journal of immunotoxicology*, 5(2), 221-225.

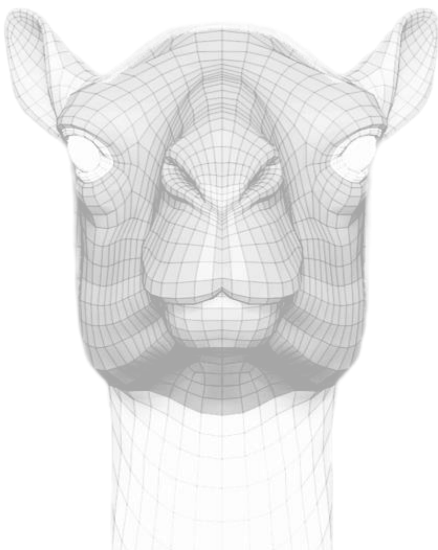
4.3 Cognitive processes and environment- and animal-dependent factors modulating Intelligence Quotient (IQ) and behavioural performance in dromedary camels

Carlos Iglesias Pastrana[1], Francisco Javier Navas González[1], Elena Ciani[2], Amy Katherine McLean[3] and Juan Vicente Delgado Bermejo[1]

[1]Department of Genetics, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain

[2]Department of Biosciences, Biotechnologies and Environment, Faculty of Veterinary Sciences, University of Bari 'Aldo Moro', 70121 Bari, Italy

[3]Department of Animal Science, University of California Davis, 95616 California, USA



Quality indicator information provided on the publication
Latest information available (2022)

Status of the manuscript: Submitted

Journal (year, volume, page(s)): *Animal Behaviour*

International database in which it is indexed: Journal of Citation Reports (JCR)

Thematic area in the reference database: Zoology

Impact index of the journal in the year of the article's publication: 2.5

Rank/number of thematic area journals: 20/176 (Q1)

Abstract

The exploration into the cognitive intelligence of dromedary camels sheds lights on the genetic structure underlying intelligence and general cognition in this animal species, and enriches the empirical knowledge into the diversity of cognitive abilities found across animal species. By means of discriminant canonical analyses, the present research study aims at disentangling the cognitive processes that most influence Intelligence Quotient (IQ) and the animal-dependent factors that greatly affect behavioural performance in dromedary camels mainly relegated to leisure tourism activities. The comfortability of camels when separated from the main herd emerged as the most distinguishing factor between individuals for overall IQ, which in turn may be revealing the existence of a collective intelligence in this social species but also a non-negligible impact of long-term memory of past experiences and social dominance on the cognitive performance in camels. Such conditioning factors also influence the individual disposition to enter and leave housing facilities and to be handled. Furthermore, the lesser the dependence on the group, the more curious and less emotionally stable camels tend to be, which would diminish the quality of the attention and concentration towards the stimuli presented and trainer's instructions. Qualitative attributes such as sex, neutering status, physical exercise, ownership/herd size and eye colour were found to be significantly discriminating factors for the dependence on the group, docility, ease of handling, and concentration. Within a context of camel rearing and production, the results of the present study can inform the tailoring of effective training methods, improved management practices and selective breeding programs for superior cognitive performance, as well as the exploration of new potential functional niches for this emerging livestock species.

Keywords

Cognition, intelligence quotient, *Camelus dromedarius*, quantitative genetics, qualitative attributes, selective breeding

Introduction

The millennium process of co-habitation and functional specialization at livestock scenarios not only has shaped the morphology of the animals, but also the psyche (Hansen Wheat et al., 2019). The study of animal intelligence and cognition traits - generally termed as 'cognitive intelligence' in the field of basic and applied psychology- has traditionally been focused on species such as non-human primates, mice, dolphins, and birds. However, as our understanding of animal cognition expands, it becomes increasingly apparent that cognitive intelligence is not limited to a select few species (Pastrana et al., 2022; Shettleworth, 2001; Wynne & Udell, 2020).

Apart from the benefits at increasing the knowledge on the ecological and evolutionary significance of cognitive intelligence (Dukas, 2004; Pritchard et al., 2016), and its applicability for species comparative studies on cognitive development (Olmstead & Kuhlmeier, 2015), the quantification of the phenotypic variability for intelligence and cognition traits is decisive to study the genetic structure underlying cognitive processes in non-human animals (Plomin, 2001). At a population level, up to approximately 40 % of the differences between individuals for cognitive performance can be ascribed to a psychometric construct, 'g factor' or 'general intelligence factor' (Deary, Penke, & Johnson, 2010; Reader, Hager, & Laland, 2011), but also potentially to 'c factor' or 'collective intelligence' for species with defined hierarchical social structures and that may be affecting the cognitive performance of the animal aggrupation (Rowe, Hattie, & Hester, 2021). Both psychometric constructs are typically extracted from statistically reduction scores such as intelligence quotient (IQ), a composite measure of the correlations between the performance of an individual on different cognitive tasks and their comparison with the expected skills according to its chronological age (Matzel & Sauce, 2017).

At domestic settings, more specifically at those farming emplacements in which a daily human-animal interaction is the main source of economic profit (i.e., assisted interventions), selecting and screening for high-IQ animals could enrich the mid- to long-term profitability of the sector. Educational and training programs will be expected to improve the mutual bonds that are established between owners/trainers, animals and surrounding environment, as well as help at effectively control, in terms of both time and economic resources, the type of reactions displayed by the animals when approach varied stimuli (González et al., 2019).

Although being increasingly reared with food production purposes and some preliminary experiences have been carried out on camel-assisted interventions, dromedary camels continue to be largely disregarded for their behavioural characterization (Al-Obaidi & Abdullah, 2017; Iglesias Pastrana et al., 2020; Larsson & Brothers, 2019), thus their cognitive capabilities and genetic background that may affect human-camel interaction at man-made environments are misconsidered. Apart from the common misconception of camels as mere beasts of burden, Ancient Greek fables and treatise on animal symbolism in medieval culture cited camels as docile (Bádenas de la Peña, Facal, & García Gual, 1978) and submissive (Morales Muñiz, 1996) animals, respectively. In addition, camels are commonly recognized to be more intelligent than other ruminants but lesser than horses and dogs (Al-Ani, 2004; Al-Obaidi & Abdullah, 2017). In fact, the 'phronesis' or ability to think about practical matters ('practical wisdom') can be found according to Aristotle in these animal species (López Gómez, 2009). However, empirically-based studies on camel selection for behavioural criteria are clearly sparse. What it is available so far in this regard is a methodological proposal for the indirect genetic selection of reared-for-leisure dromedary camels that is based on the correlations existing between the camel behavioural performance during the interactive experience, the tourists' subjective perception of camel behavioural features and the general satisfaction of participants about the camel ride (Pastrana et al., 2021).

Therefore, the aim of the present research is the quantification, by means of application of human-analogous IQ score, of the phenotypic variability for thirteen cognitive processes in dromedary camels. The animal model used was the Canarian dromedary camel, an autochthonous endangered breed that is fundamentally relegated to leisure riding activities and could be potentially valorize for valuable niches such as assisted-therapy (Pastrana et al., 2021). We have examined the role that different genetically-based factors might play at interindividual variability for cognition-related traits in this animal species, thus enriching the list of suitable selection criteria for the design of adapted breeding programs. Additionally, those cognitive processes that most modulate individual Intelligence Quotient (IQ) in dromedary camels has been unraveled. Overall, the quantification of IQ in dromedary camels has the potential to be applicated for both animal training and welfare evaluation and promotion purposes. In the first case, dromedaries that exhibit superior cognitive performance may make training plans more effective in terms of time, technical and economic resources that are needed to be invested. Regarding animal welfare, individual IQ could be used to select animals that would combat potentially painful processes in a more efficient way, taking into account the role of cognition in the subjective perception of pain through evaluation, learning and decision-making processes. In the same context, a punctual decrease in cognitive performance could also be taken as indicative of the patency of painful processes, as these affect cognitive outputs (Khera & Rangasamy, 2021).

Material and methods

Animal sample and study context

Data collection occurred from September 2019 to January 2021 and involved a total of 130 individuals from the Canarian camel breed. Among these individuals, there were 58 females and 72 males. These camels were located in three distinct breeding locations across Spain: Huelva (Doñana National Park, coordinates 36.972330, −6.427498), Almería (coordinates 36.902180, −2.429520), and Fuerteventura (coordinates 28.186777, −14.158361).

To ensure the suitability of the animals for the study, comprehensive clinical examinations were conducted to assess their well-being and eligibility. It's worth noting that both the age and live weight of the camels did not follow a normal distribution ($p < 0.05$).

The live body weight of the camels was calculated using the following formula (Equation 1) proposed by Boujenane (2019):

$$\text{Live Weight} = 6.46 \times 10^{-7} (HW + ChG + HG)^{3.17}$$

where HW represents height at the withers, ChG denotes chest girth, and HG signifies hump girth.

The age range of female Canarian dromedary camels in the study varied from 40 to 423 months, while male Canarian dromedary camels ranged from 18 to 385 months in age. This broad age range was chosen to accommodate all animals included in the study, as the stimulus battery used for assessing coping styles/reactivity was suitable for all age groups. This decision was particularly important due to the endangered status of the breed, and having comprehensive information about individual animals was indispensable.

Regarding live weight, female Canarian dromedary camels exhibited weights ranging from 327.03 to 687.13 Kg, while their male counterparts weighed between 342.72 and 777.56 Kg.

Recording of behavioural traits

The methodology applied is described in Navas González et al. (2019), Navas et al. (2017), Navas González et al. (2018a), Navas González et al. (2018b) and Navas González et al. (2020).

We organized the information into two different clusters. The first cluster, labeled "cognition," comprised seven traits directly related to the camels' nonspecific cognitive processes, particularly their capacity to perceive information from their environment. The second cluster, referred to as "intelligence," encompassed six traits associated with cognitive processes and mental abilities that allowed camels to retain environmental information as knowledge, which could be applied to adapt to specific situations. A detailed breakdown of each cognitive trait and its human extrapolation is available in Table 1.

To facilitate analysis, we transformed these categorical traits into distinct linear scales. Within these scales, camels assigned a score of 1 represented the lowest extreme in behavioral patterns, while a score of 5 denoted the highest extreme. For a

Table 1. Definition of the thirteen cognitive processes encompassing the intelligence and general cognition clusters examined in dromedary camels, along with their human analogy.

Cluster	Cognitive process	Definition	Human analogy (Navas González et al., (2019)
Intelligence	Concentration	The animal collaborates during the assessment session and does not get distracted by the environment.	Attention
	Curiosity	The animal is interested in the novel stimuli being presented and moves toward them.	Curiosity
	Memory	The animal remembers the stimuli being presented.	Memory
	Stubbornness	The dromedary camel rejects following the requests of the assessor.	Cognitive rigidity/ decision-making
	Docility	The dromedary camel easily follows the orders of the instructor.	Docility/decision-making
	Alertness	The animal shows a vigilant or alert status focusing on the stimulus around.	Alertness
General cognition	Dependence	The dromedary camel is comfortable when separated from the main herd.	Separation anxiety
	Trainability	Ability of the animal to be trained into the fulfillment of the tests.	Cognitive training
	Cooperation	The dromedary camel cooperates with its handlers during the daily tasks.	Cognitive cooperation
	Emotional stability	The animal is not predictable from one stimulus to another.	Anticipation/predictability
	Perseverance	The animal is patient when completing several sequential tests.	Patience. Related to decision-making. Patience is studied as a decision-making problem, involving the choice of either a small reward in the short term, against a more valuable reward in the long term
	Get in/out of stables	The animal shows no problem when leaving or entering its housing facilities.	Fear/cognitive appraisal/ coping
	Ease of handling	The animal shows sympathy toward humans.	Cognitive empathy/attitudes toward animals

comprehensive understanding of the thirteen intelligence- and cognition-related traits considered, along with detailed definitions of the scale scores, please refer to Table 2.

We established the definitions of the cognitive processes examined in this study, outlined the scales for their measurement, and identified potential environmental factors that could influence them. Our approach was guided by the protocols introduced in Momozawa et al. (2005) and by drawing analogies to human cognitive processes as detailed in Navas et al. (2017).

Table 2. Description of the thirteen cognitive processes and the definition of their scales studied in dromedary camels.

Intelligence Cluster			
Cognitive process	**Definition**	**Scale**	**Description**
Concentration	The animal collaborates during the assessment session and does not get distracted by the environment.	1	Distracted
		2	Poor
		3	Inconstant
		4	Intermediate
		5	Concentrated
Curiosity	The animal is interested in the novel stimuli being presented and moves towards them.	1	Never (0%)
		2	Rarely (5-10%)
		3	Sometimes (50%)
		4	Frequently (70%)
		5	Always (100%)
Memory	The animal remembers the stimuli being presented.	1	Scattered
		2	Poor short-term memory
		3	Average short-term memory
		4	Average long-term memory
		5	Good long-term memory
Stubbornness	The dromedary camel rejects following the requests of the assessor.	1	Stubborn (Cautious)
		2	Indifferent
		3	Moaner
		4	Reluctant
		5	Obedient
Docility	The dromedary camel easily follows the orders of the instructor.	1	Stubborn
		2	Indifferent
		3	Moaner
		4	Reluctant
		5	Obedient
Alertness	The animal shows a vigilant or alert status focusing on the stimulus around.	1	Untamed
		2	Unwilling
		3	Reticent
		4	Adaptable
		5	Docile
General Cognition Cluster			
Cognitive process	**Definition**	**Scale**	**Description**
Dependence	The dromedary camel is comfortable when separated from the main herd	1	Dependent
		2	Restless
		3	Stable
		4	Adapted
		5	Calm

Table 2. *Cont.*

General Cognition Cluster			
Cognitive process	**Definition**	**Scale**	**Description**
Trainability	Ability of the animal to be trained into the fulfilment of the tests	1	Never (0%)
		2	Rarely (5-10%)
		3	Sometimes (50%)
		4	Frequently (70%)
		5	Always (100%)
Cooperation	The dromedary camel cooperates with its handlers during the daily tasks	1	Never (0%)
		2	Rarely (5-10%)
		3	Sometimes (50%)
		4	Frequently (70%)
		5	Always (100%)
Emotional stability	The animal is not predictable form one to another stimulus	1	Unpredictable
		2	Surprising
		3	Stable
		4	Balanced
		5	Predictable
Perseverance	The animal is patient when completing several sequential tests.	1	Impatient
		2	Generally impatient but easily handled
		3	Patient but pushes the operator occasionally
		4	Patient without pushing the operator
		5	Awaits the operator's orders
Get In/Out of Stables	The animal shows no problem when leaving or entering its housing facilities.	1	Never (0%)
		2	Rarely (5-10%)
		3	Sometimes (50%)
		4	Frequently (70%)
		5	Always (100%)
Ease at Handling	The animal shows sympathy towards humans.	1	Mistrustful towards humans in general
		2	Mistrustful towards unknown people
		3	Comfortable with familiar people, but mistrustful of unknown people
		4	Comfortable with the human presence
		5	Increased sympathy for human presence

The thirteen cognitive processes were categorized into two groups: seven traits related to general cognitive processes observed directly in the field, and six traits specifically associated with intelligence-related cognitive processes. These groupings were determined using Principal Component Analysis (PCA) criteria, as outlined in Navas et al. (2017).

The standardization and development of the tests and measurement scales were detailed in Navas et al. (2017) and Navas González et al. (2018a). We also conducted statistical assessments to ensure that the tests effectively measure the intended constructs and possess internal reliability, as reported in previous studies in Navas et al. (2017) and Navas González et al. (2018b).

We meticulously recorded all data pertaining to the cognitive abilities of the dromedary camels during the development of a six-stage operant conditioning test. A single trained appraiser consistently recorded information concerning four behavioral variables for each stage and across all animals. Each dromedary camel was allotted a maximum of 450 seconds to complete the operant conditioning test, translating to 75 seconds for each phase and implemented treatment. No extra time was granted to the dromedary camels to complete the test.

Operant conditioning behavioural test

The operant conditioning behavioral test took place in an open area familiar to the dromedary camels, which was part of their daily activity zone. In this test, each animal encountered six consecutive reinforcement treatments, one during each of the six stages within the operant conditioning test. Handlers A and B administered six distinct reinforcement treatments, some of which involved unfamiliar elements while others comprised known factors. These elements could be visual (within the dromedary camels' line of sight) and/or acoustic (generating sounds, such as "motivator" or claps, which may or may not be within the dromedary camels' visual range). The elements were presented to the dromedary camels from different positions, either in front or from a rear position, consistently at a distance of 2 meters from the animals. A cameraperson (handler C) concurrently recorded the experiences at 1080p, 50 Hz, with a shutter speed of 1/250 seconds. This recording was used to evaluate the dromedary camels' performance post-experiment and to assess for any intraobserver discrepancies. The timing of events was controlled by the cameraperson (handler C). Further details of the operant conditioning test can be found in Navas González et al. (2018a).

Reliability of the test and scoring system

The scores for each individual were recorded consistently by the same three trained judge for all stimuli and animals. Intraobserver discrepancies were not observed, as all on-field scores matched the scores obtained upon reviewing the recorded tapes.

A preliminary analysis involving Cohen's κ test was conducted during the initial stages of the study (Iglesias et al., 2020) to assess intra-observer reliability and ascertain agreement among the judgments by the each of the assessors for 30 individuals (23.1% of the total sample) across the categorical variables of response type, mood, and response intensity.

Once intraobserver effect had been discarded, as recommended by Bunting et al. (2019), we used the Intraclass Correlation Coefficient (ICC) as a reference method to assess the reproducibility and reliability of numeric measurements as three different trained operators had measured the same variable across all the animals involved in the study (interobserver reliability).

There are no fixed standards for acceptable ICC reliability values. A low ICC may indicate poor agreement among raters or measurements and may also be linked to limited subject variability, a small sample size, or a small number of raters involved. As a general guideline, we recommend using at least 30 diverse samples and involving a minimum of 3 raters when conducting a reliability study. Under these conditions, ICC values can be interpreted as follows: less than 0.5 indicates poor reliability, 0.5 to 0.75 suggests moderate reliability, 0.75 to 0.9 signifies good reliability, and values above 0.90 indicate excellent reliability (Koo & Li, 2016).

Following the criteria set by Fleiss and Cohen (1973), we interpreted ICC values as follows: less than 0.4 (low), 0.4 to 0.59 (reasonable), 0.6 to 0.74 (good), and 0.75 to 1.0 (excellent) to determine if we achieved sufficient reproducibility and repeatability. We used the "Two-Way Random" model, as recommended by Koo and Li (2016), and calculated 95% confidence intervals using the formula 95% kappa Confidence Interval (95%CI) = $\kappa \pm 1.96\ SE\kappa$, utilizing the reliability analysis routine in SPSS Statistics for Windows, Version 25.0, IBM Corp. (2017).

Reliability of the test and scoring system

In human terms, the concept of mental age measures how an individual's performance compares to what is typically expected for their chronological age within a specific cognitive process (Gerrig & Zimbardo, 2002).

In contemporary human IQ tests, the median raw score of the norming sample is designated as IQ 100. This occurs when the chronological age and mental age align or when an individual attains a score expected at their chronological age (Hunt, 2010). Each standard deviation (SD) unit from this value corresponds to increments or decrements of 15 IQ points (Gottfredson, 2009).

To establish an analogous animal scale, we computed the mean score attained by the dromedary camels in our study population during the multiphase operant conditioning test for each of the thirteen cognitive processes (scored from 1 to 5). Subsequently, we focused on the highest mean score within the scale (ranging from 1 to 5) achieved, on average, by dromedary camels at the lowest possible age level for each cognitive process. This score served as the reference point, equivalent to the average range (IQ 100), signifying the mental age at which a particular dromedary camel would be expected to achieve that specific cognitive process score. This starting point served as the basis for moving upward or downward within the 1 to 5 scale (Table 3) to determine IQ categories below and above the average. Quantitatively, these increases or decreases followed 15-point intervals per SD unit.

Table 3. Mean mental age (in months) at which Canarian dromedary camels reach a particular level within the qualitative score scale for each of the thirteen cognitive processes studied.

Cluster	Cognitive process/Score	1	2	3	4	5
Intelligence	Concentration	152	150	161	169	166
	Curiosity	144	159	171	169	160
	Memory	65	136	159	159	197
	Stubbornness	79	214	157	176	159
	Docility	65	171	170	180	159
	Alertness	18	163	163	163	163
General cognition	Dependence	170	144	138	169	187
	Trainability	153	130	176	172	170
	Cooperation	18	164	175	165	162
	Emotional stability	168	156	182	166	160
	Perseverance	49	242	169	161	185
	Get In/Out of Stables	151	122	171	162	173
	Ease at Handling	53	172	177	163	162

To extend our findings to humans, we considered a dromedary camel's IQ to be in the average range, analogous to human IQ 100, when its mental age matched its chronological age. Dromedary camels scoring below this point, where their mental age equaled their chronological age, were classified as having IQ scores below the average range. It is important to note that overestimation could occur for individuals significantly below or above the average because dromedary camels could reach the highest average level (5) for various cognitive processes at very early ages.

The IQ of each dromedary camel, representing their mental age, was calculated as the average of mental ages or IQs across all thirteen cognitive skills for each animal. We computed IQ using the following mathematical formula: IQ = (mental age/chronological age) × 100 (National Council on Measurement in Education, 2017). The dromedary camel’s IQ distribution through the calculation of polynomial regression equations (6^{th} order) and R squared (R^2) values is shown in Figure 1.

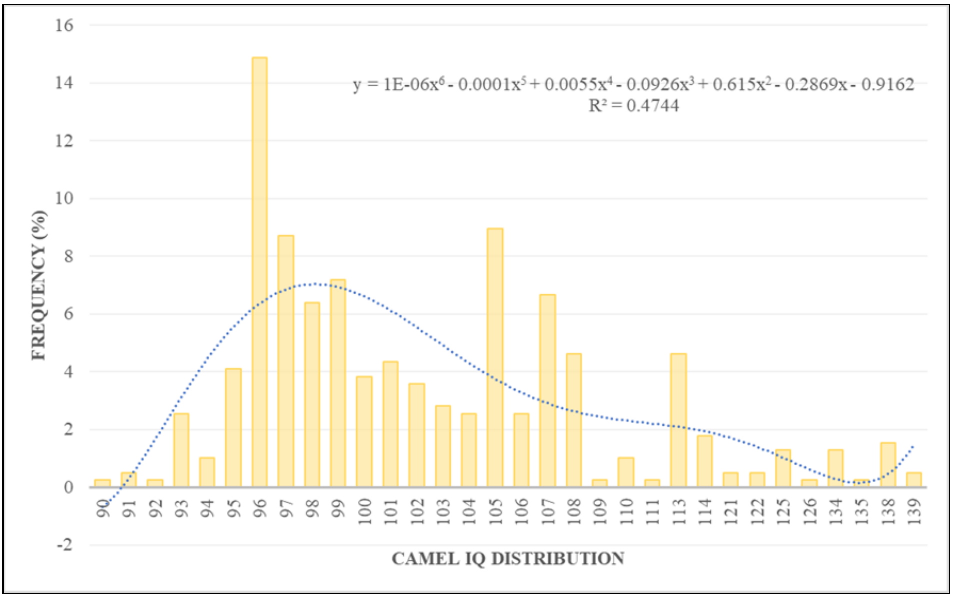


Figure 1. Dromedary camel sample IQ distribution graph, adjusted R2 and polynomial regression equation (6th order).

Statistical analysis

In accordance with the methodologies presented by González Ariza et al. (2021), our initial approach involved conducting a discriminant canonical analysis.

The first objective was to develop a tool capable of assessing the most optimal linear combinations of cognitive processes scores (independent variables comprising the thirteen cognitive processes and scales reported in Table 1 and 2) that explain average Intelligence Quotient (dependent variable).

Second, we aimed to develop a tool capable of assessing the most optimal linear combinations of cognitive processes normalized Intelligence Quotients (independent variables comprising the normalized Intelligence Quotient for the thirteen cognitive processes and scales reported in Table 1 and 2) that explain the clustering patterns defined by factors such as rater, physical exercise, eye colour, coat colour, coat particularities, owner, neutering status, and sex (dependent variables).

For the classification, prediction, interpretation, and manipulation of observations associated with the aforementioned dependent variables linked to each of the two objectives, we employed the Chi-squared automatic interaction detection (CHAID) decision tree method. This methods allowed for a discrete analysis of the independent variables and the relationships that it describes with the normalized Intelligence Quotient levels for the thirteen cognitive processes referred in Table 1 and Table 3.

To assess the reliability of the CHAID decision tree model, we conducted cross-validation. This involved evaluating the model's predictive performance when applied to new data samples, comparing it to the training sample. Cross-validation provided valuable insights into how effectively the model could generalize to unseen data. To validate the CHAID decision tree and determine whether the selected predictors effectively explained differences across average Intelligence Quotient and normalized Intelligence Quotient levels for the thirteen cognitive processes, we employed a ten-fold cross-validation approach.

Results

Table 4 presents the descriptive statistics for each of the thirteen cognitive processes investigated.

Table 4. Descriptive statistics for the thirteen cognitive processes scored in Canarian dromedary camels.

Cluster	Cognitive process	N	Range	Minimum	Percentile 25	Percentile 50 (Mean)	Percentile 75	Maximum
Intelligence	Concentration	390	4	1	3	4	5	5
	Curiosity	390	4	1	4	5	5	5
	Memory	390	4	1	3	4	4	5
	Stubbornness	390	4	1	4	5	5	5
	Docility	390	4	1	4	5	5	5
	Alertness	390	3	2	3	5	5	5
General cognition	Dependence	390	4	1	3	4	5	5
	Trainability	390	4	1	2	4	5	5
	Cooperation	390	3	2	4	5	5	5
	Emotional stability	390	4	1	4	5	5	5
	Perseverance	390	4	1	4	4	4	5
	Get in/out of stables	390	4	1	4	4	5	5
	Ease at handling	390	4	1	4	5	5	5

For all cognitive processes, there was highly significant and from poor to excellent agreement among the three observers. Detailed results are presented in Table 5.

The first aim (developing a tool capable of assessing the most optimal linear combinations of cognitive processes scores, being these the independent variables comprising the thirteen cognitive processes and scales reported in Table 1 and 2), that explain average Intelligence Quotient (dependent variable), was achieved after following 3 rounds of multicollinearity analyses. For the second aims, that is aimed at developing a tool capable of assessing the most optimal linear combinations of cognitive processes normalized Intelligence Quotients (independent variables comprising the normalized

Table 5. Intraclass Correlation Coefficient analysis to test for inter-observer reliability.

Poor	Moderate	Good	Excellent
Alertness: 0.190 *Memory*: 0.443 *Perseverance*: 0.479	*Get in/out of stables*: 0.551 *Concentration*: 0.548 *Trainability*: 0.670 *Dependence*: 0.739	*Docility*: 0.879	*Cooperation*: 0.910 *Curiosity*: 0.913 *Emotional stability*: 0.919 *Stubbornness*: 0.921 *Ease of handling*: 0.936

Intelligence Quotient for the thirteen cognitive processes and scales reported in Table 1 and 2), that explain the clustering patterns defined by factors such as rater, physical exercise, eye colour, coat colour, coat particularities, owner, neutering status, and sex, 9 rounds of multicollinearity analyses were followed. The variables included in all the discriminant canonical analyses are detailed in Table 6.

Table 6. Summary of the value of tolerance and VIF after multicollinearity analysis of cognition-related traits in Canarian dromedary camels.

Average IQ and individual score per cognitive process evaluated		
Statistic	**Tolerance (1-R^2)**	**VIF (1/Tolerance)**
Get In/Out of Stables	0.8103	1.2341
Memory	0.7218	1.3855
Alertness	0.6976	1.4336
Perseverance	0.6086	1.6431
Dependence	0.4812	2.0781
Curiosity	0.4684	2.1348
Emotional stability	0.4136	2.4178
Concentration	0.3868	2.5856
Trainability	0.3314	3.0176
Ease at Handling	0.2686	3.7225
Cooperation	0.2229	4.4858
Influence of animal extrinsic and intrinsic factors (rater, physical exercise, eye colour, coat colour, coat particularities, owner, neutering status, and sex) on IQ normalized per cognitive process evaluated		
Statistic	**Tolerance (1-R^2)**	**VIF (1/Tolerance)**
Ease at Handling-IQ Normalized	0.4578	2.1842
Docility-IQ Normalized	0.4305	2.3229
Dependence-IQ Normalized	0.3200	3.1250
Concentration-IQ Normalized	0.3199	3.1255

Interpretation thumb rule: VIF ≥ 5 (highly correlated); 1 < VIF < 5 (moderately correlated); VIF = 1 (not correlated).

Pillai's trace criteria for all the discriminant analysis performed in order to achieve all the tasks referred in the two objectives to accomplish in this study are reported in Table 7.

The functions identified through the discriminant analysis which demonstrated significant discriminant ability for each of the nine discriminant analyses performed to fulfill the 2 objectives proposed in the present study are shown in Table 8. The maximum number of functions identified was found for discriminant analysis 5 (DA 5) which

Table 7. Pillai's Trace Criteria for the 9 discriminant analysis performed to accomplish the two objectives in this study.

Discriminant Analysis	Objective	Trace	F (Observed value)	F (Critical value)	DF1	DF2	p-value	alpha
DA 1	**Objective 1**	0.0882	1.5853	1.5562	22	756	0.0432	0.05
DA 2	**Objective 2**	0.0195	0.9480	1.9504	8	770	0.4759	0.05
DA 3		0.1849	9.8056	1.9504	8	770	< 0.0001	0.05
DA 4		0.0068	0.3261	1.9504	8	770	0.9562	0.05
DA 5		0.5192	8.1398	1.4837	28	1528	< 0.0001	0.05
DA 6		0.0818	2.0100	1.6501	16	1540	0.0101	0.05
DA 7		0.2351	8.1823	1.7605	12	1155	< 0.0001	0.05
DA 8		0.1970	23.6137	2.3951	4	385	< 0.0001	0.05
DA 9		0.0967	10.3044	2.3951	4	385	< 0.0001	0.05

The primary objective (Objective 1) was fulfilled after the performance of Discriminant Analysis 1 (DA1) and entailed the development of a tool capable of identifying the most effective linear combinations of cognitive process scores. These independent variables encompassed the thirteen cognitive processes and scales outlined in Tables 1 and 2. The objective was to elucidate their collective influence on the average Intelligence Quotient, which served as the dependent variable.

Furthermore, our secondary goal (Objective 2) was to create a tool designed to evaluate the most optimal linear combinations of normalized Intelligence Quotients for the thirteen cognitive processes and scales detailed in Tables 1 and 2. The clustering patterns determined by following independent factors were considered: rater (DA 2), physical exercise (DA 3), eye colour (DA 4), coat colour (DA 5), coat particularities (DA 6), owner (DA 7), neutering status (DA 8) and sex (DA 9).

Table 8. Canonical discriminant analysis efficiency parameters to determine the significance of each canonical discriminant test function.

DA 1: Average IQ and individual score per cognitive process evaluated					
Test functions	**Canonical Correlation**	**Eigenvalue**	**Variance discrimination(%)**	**Bartlett's statistic**	**P-value**
1 through 2	0.2700	0.0855	71.9537	34.8028	0.0406
2	0.1237	0.0333	28.0463	5.8951	0.8240
DA 2: Influence of rater on IQ normalized per cognitive process evaluated					
Test functions	**Canonical Correlation**	**Eigenvalue**	**Variance discrimination(%)**	**Bartlett's statistic**	**P-value**
1 through 2	0.1074	0.0762	87.7715	7.5581	0.4778
2	0.0893	0.0106	12.2285	3.0886	0.3782
DA 3: Influence of physical exercise on IQ normalized per cognitive process evaluated					
Test functions	**Canonical Correlation**	**Eigenvalue**	**Variance discrimination(%)**	**Bartlett's statistic**	**P-value**
1 through 2	0.4291	0.2257	99.6617	78.7534	<0.0001
2	0.0277	0.0008	0.3383	0.2953	0.9609
DA 4: Influence of eye colour on IQ normalized per cognitive process evaluated					
Test functions	**Canonical Correlation**	**Eigenvalue**	**Variance discrimination(%)**	**Bartlett's statistic**	**P-value**
1 through 2	0.0636	0.0041	59.9237	2.6081	0.9565
2	0.0520	0.0027	40.0763	1.0456	0.7902

Table 8. *Cont.*

DA 5: Influence of coat colour on IQ normalized per cognitive process evaluated					
Test functions	Canonical Correlation	Eigenvalue	Variance discrimination(%)	Bartlett's statistic	P-value
1 through 4	0.5564	0.4483	63.1131	231.4190	<0.0001
2 through 4	0.4517	0.2564	36.0964	89.5631	<0.0001
3 through 4	0.0654	0.0043	0.6055	2.1466	0.9951
4	0.0362	0.0013	0.1850	0.5030	0.9732
DA 6: Influence of coat particularities on IQ normalized per cognitive process evaluated					
Test functions	**Canonical Correlation**	**Eigenvalue**	**Variance discrimination(%)**	**Bartlett's statistic**	**P-value**
1 through 4	0.2358	0.0589	68.7128	32.1898	0.0094
2 through 4	0.1543	0.0244	28.4500	10.1939	0.3350
3 through 4	0.0492	0.0024	2.8364	0.9336	0.9197
4	0.0008	0.0000	0.0008	0.0003	0.9867
DA 7: Influence of owner on IQ normalized per cognitive process evaluated					
Test functions	**Canonical Correlation**	**Eigenvalue**	**Variance discrimination(%)**	**Bartlett's statistic**	**P-value**
1 through 3	0.3635	0.1522	57.0194	96.3715	<0.0001
2 through 3	0.3207	0.1147	42.9551	41.8217	<0.0001
3	0.0082	0.0001	0.0255	0.0262	0.9870
DA 8: Influence of neutering status on IQ normalized per cognitive process evaluated					
Test functions	**Canonical Correlation**	**Eigenvalue**	**Variance discrimination(%)**	**Bartlett's statistic**	**P-value**
1	0.4439	0.2453	100.0000	84.6908	<0.0001
DA 9: Influence of sex on IQ normalized per cognitive process evaluated					
Test functions	**Canonical Correlation**	**Eigenvalue**	**Variance discrimination(%)**	**Bartlett's statistic**	**P-value**
1	0.3110	0.1071	100.0000	39.2586	<0.0001

assessed the influence of coat colour on IQ normalized per cognitive process evaluated, and for the discriminant analysis 6 (DA 6) which assessed the influence of coat particularities on IQ normalized per cognitive process evaluated. Among all the functions, F1 displayed the highest discriminatory power in all discriminant analyses, explaining a minimum significant 57.02% of the variance (in DA 7 which studied the influence of owner on IQ normalized per cognitive process evaluated) and a maximum of 100% (in DA 8 which studied the influence of neutering status on IQ normalized per cognitive process evaluated, and in DA 9 which studied the influence of sex on IQ normalized per cognitive process evaluated).

Concerning the interpretation of canonical coefficients and loadings, the variables investigated in this study were ranked based on their discriminative capacity. A test comparing group means of the dependent variables involved in the discriminant canonical analysis was performed, as shown in Table 9. Higher F-values and lower values of Wilks' Lambda indicate greater discriminatory power.

Furthermore, the standardized discriminant coefficients, which measure the relative importance of each dependent variable across the established discriminant functions,

Table 9. Results for the tests of equality of group means to test for difference in the means across sample groups once redundant variables have been removed.

Variable	Wilk's Lambda	F	P-value	Rank
DA 1: Average IQ and individual score per cognitive process evaluated				
Variable	**Wilk's Lambda**	**F**	**P-value**	**Rank**
Dependence	0.9527	9.6046	< 0.0001	1
Trainability	0.9813	3.6912	0.0258	2
Concentration	0.9920	1.5682	0.2097	
Get In/Out of Stables	0.9954	0.8937	0.4100	
Emotional Stability	0.9963	0.7213	0.4868	
Alertness	0.9977	0.4538	0.6356	
Cooperation	0.9979	0.3990	0.6713	
Memory	0.9982	0.3580	0.6993	
Perseverance	0.9992	0.1478	0.8626	
Curiosity	0.9993	0.1380	0.8711	
Ease at Handling	0.9997	0.0566	0.9450	
DA 2: Influence of rater on IQ normalized per cognitive process evaluated				
Variable	**Wilk's Lambda**	**F**	**P-value**	**Rank**
Concentration-IQ Normalized	0.9972	0.5498	0.5775	
Docility-IQ Normalized	0.9977	0.4477	0.6394	
Ease at Handling-IQ Normalized	0.9985	0.2843	0.7527	
Dependence-IQ Normalized	0.9990	0.1980	0.8204	
DA 3: Influence of physical exercise on IQ normalized per cognitive process evaluated				
Variable	**Wilk's Lambda**	**F**	**P-value**	**Rank**
Concentration-IQ Normalized	0.8527	33.4239	< 0.0001	1
Ease at Handling-IQ Normalized	0.8560	32.5488	< 0.0001	2
Docility-IQ Normalized	0.8666	29.7812	< 0.0001	3
Dependence-IQ Normalized	0.8982	21.9401	< 0.0001	4
DA 4: Influence of eye colour on IQ normalized per cognitive process evaluated				
Variable	**Wilk's Lambda**	**F**	**P-value**	**Rank**
Dependence-IQ Normalized	0.9969	0.5995	0.5496	
Concentration-IQ Normalized	0.9975	0.4841	0.6166	
Ease at Handling-IQ Normalized	0.9979	0.4016	0.6695	
Docility-IQ Normalized	0.9982	0.3403	0.7117	
DA 5: Influence of coat colour on IQ normalized per cognitive process evaluated				
Variable	**Wilk's Lambda**	**F**	**P-value**	**Rank**
Dependence-IQ Normalized	0.6931	24.1622	< 0.0001	1
Concentration-IQ Normalized	0.7639	16.8633	< 0.0001	2
Ease at Handling-IQ Normalized	0.7790	15.4813	< 0.0001	3
Docility-IQ Normalized	0.7819	15.2247	< 0.0001	4
DA 6: Influence of coat particularities on IQ normalized per cognitive process evaluated				
Variable	**Wilk's Lambda**	**F**	**P-value**	**Rank**
Dependence-IQ Normalized	0.9491	5.1571	0.0005	1
Docility-IQ Normalized	0.9553	4.5089	0.0014	2
Ease at Handling-IQ Normalized	0.9595	4.0602	0.0031	3
Concentration-IQ Normalized	0.9601	4.0047	0.0034	4

Table 9. *Cont.*

DA 7: Influence of owner on IQ normalized per cognitive process evaluated				
Variable	**Wilk's Lambda**	**F**	**P-value**	**Rank**
Dependence-IQ Normalized	0.8818	17.2393	< 0.0001	1
Concentration- IQ Normalized	0.9001	14.2814	< 0.0001	2
Ease at Handling-IQ Normalized	0.9203	11.1395	< 0.0001	3
Docility-IQ Normalized	0.9279	10.0028	< 0.0001	4
DA 8: Influence of neutering status on IQ normalized per cognitive process evaluated				
Variable	**Wilk's Lambda**	**F**	**P-value**	**Rank**
Concentration-IQ Normalized	0.8455	70.9213	< 0.0001	1
Docility-IQ Normalized	0.8481	69.5010	< 0.0001	2
Ease at Handling-IQ Normalized	0.8536	66.5330	< 0.0001	3
Dependence-IQ Normalized	0.8937	46.1558	< 0.0001	4
Df1=1;Df2=388				
Variable	**Wilk's Lambda**	**F**	**P-value**	**Rank**
Ease at Handling-IQ Normalized	0.9519	19.6144	< 0.0001	1
Docility-IQ Normalized	0.9527	19.2468	< 0.0001	2
Concentration-IQ Normalized	0.9587	16.7273	< 0.0001	3
Dependence-IQ Normalized	0.9935	2.5278	0.1127	

df1=1;df2=388

are presented in Figure 2 for the first objective (DA 1) and Supplementary Figure 1 (second objective, from DA 2 to DA 9).

Press' Q values reported in Table 10 were computed and indicated that predictions can be considered better than chance at a 95% confidence level (Chan, 2005).

Centroids for the levels of average Intelligence Quotient (DA 1, objective 1), and qualitative categories considered for rater, physical exercise, eye colour, coat colour, coat particularities, owner, neutering status and sex (DA 2 to Da 9, objective 2), were calculated. These centroids were determined by substituting the mean values for the observations represented in each of the significantly detected discriminant functions (Table 8). Detailed results for the functions at the centroids are reported in Table 11.

Lastly, the CHAID decision tree for the levels of average Intelligence Quotient (DA 1, objective 1) and qualitative categories considered for rater, physical exercise, eye colour, coat colour, coat particularities, owner, neutering status and sex (DA 2 to Da 9, objective 2), are respectively provided in Supplementary Figures from 2 to 10.

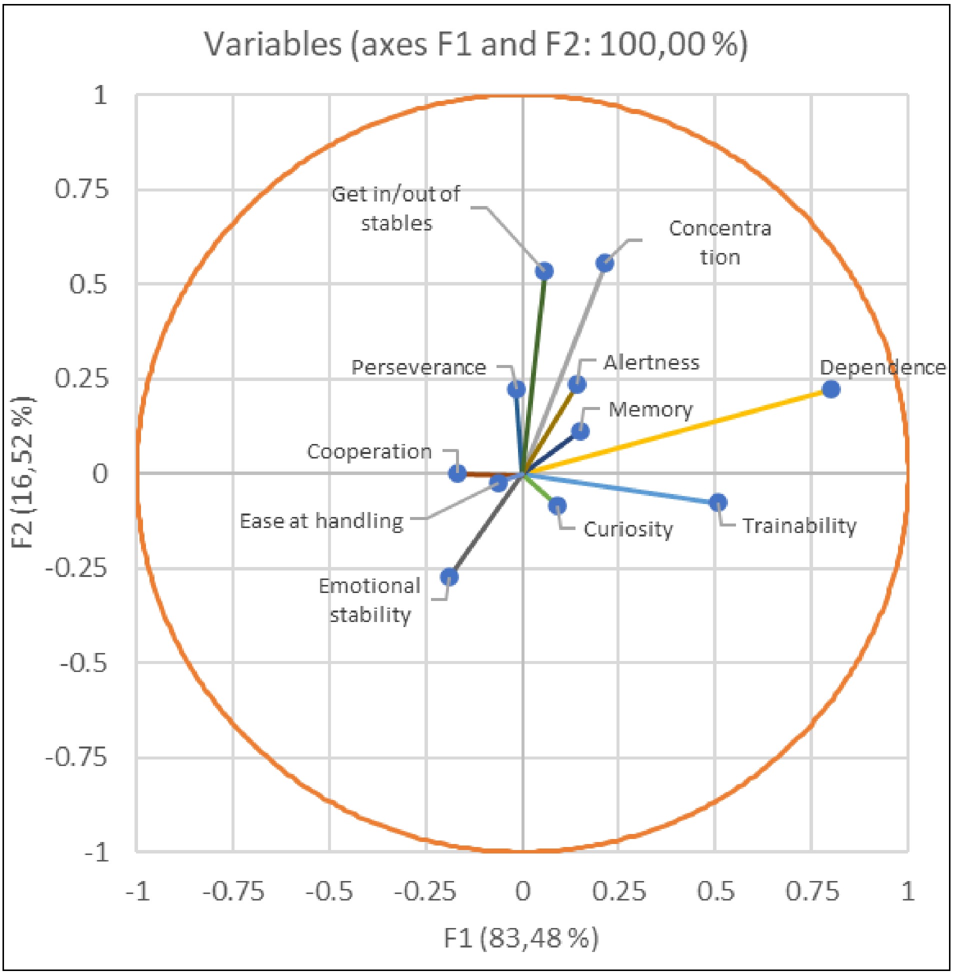


Figure 2. Standardized discriminant coefficients for cognitive processes scores upon average Intelligence Quotient in Canarian dromedary camels.

Table 10. Cross Validation Press' Q values.

Discriminant Analysis	Objective	Purpose	N	n	K	Press' Q
DA 1	**Objective 1**	Cognitive Processes Scores vs Average IQ	390	224	3	101.953846
DA 2	**Objective 2**	Normalized IQ vs Rater Effect	390	114	3	2.95384615
DA 3		Normalized IQ vs Level of Exercise Effect	390	254	3	177.415385
DA 4		Normalized IQ vs Eye Colour Effect	390	358	3	599.815385
DA 5		Normalized IQ vs Coat Colour Effect	390	111	8	90.843956
DA 6		Normalized IQ vs Coat Particularities Effect	390	163	5	115.785256
DA 7		Normalized IQ vs Owner Effect	390	207	4	163.969231
DA 8		Normalized IQ vs Neutering status Effect	390	279	2	72.3692308
DA 9		Normalized IQ vs Sex Effect	390	268	2	54.6564103

Table 11. Functions at the centroids for the levels of global IQ, rater, physical exercise, eye colour, coat colour, coat particularities, owner, neutering status and sex.

Function/Average IQ	Above average	Average	Below average
F1	-0.2703	-0.0434	0.2996
F2	0.0286	-0.6208	0.0207
Function/Rater	**1**	**2**	**3**
F1	-0.2043	0.3888	-0.1845
F2	-0.1235	-0.0043	0.1278
Function/Physical exercise	**No**	**Training**	**Yes**
F1	0.3015	1.0562	-0.4524
F2	-0.0252	0.0731	0.0118
Function/Eye colour	**Brownish**	**Brownish with blue spots**	**Bluish**
F1	-0.0153	-0.0106	0.2661
F2	0.0083	-0.3377	0.0024

Function/Coat colour	White	Cinnamon	Bay	Ashed	Black	Chestnut	Roan	Blonde
F1	2.5065	-0.1236	-0.0857	3.4343	-0.1261	0.1070	-0.5312	-0.4545
F2	-2.0609	-0.0424	0.0796	2.3216	0.0769	0.2736	-0.2520	-0.2490
F3	-0.0126	-0.0290	-0.0228	0.1343	-0.0239	-0.0207	-0.0425	0.1641
F4	-0.0137	0.0639	-0.0192	0.0140	-0.0078	-0.0204	-0.0407	-0.0007

Function/Coat particularities	Solid color	White-haired zones in extremities	White-haired zones in head and neck	White-haired zones in extremities, head and neck	White-haired zones practically all over the body
F1	0.3308	-0.2153	0.8365	-0.0795	-0.1449
F2	-0.1660	-0.1104	0.6110	0.1176	0.0608
F3	-0.0198	0.0649	0.1809	-0.0277	-0.0471
F4	0.0000	0.0000	0.0009	-0.0006	0.0024

Function/Owner	1	2	3	4
F1	-0.1794	-0.1190	1.1098	-0.0387
F2	0.3967	-0.3246	0.0925	-0.3061
F3	0.0001	-0.0062	-0.0015	0.0206

Function/Neutering status	Non neutered	Neutered
F1	0.4366	-0.5591
Function/Sex	**Female**	**Male**
F1	0.3636	-0.2929

Discussion

Contrary to the unmerited popular conception of camels as unintelligent animals (Al-Obaidi & Abdullah, 2017), the results of the present study demonstrate that dromedaries can be effectively evaluated for cognition traits related with both intelligence and general cognition processes, based on an analogous, validated methodology for humans and other livestock species (González et al., 2019). Within a context of selective breeding, more specifically at those camel production environments in which animal behavioural features are decisive for their profitability, these animals can be indeed ranked for their cognitive performance and thus their Intelligence Quotient. Although a high proportion of the camels evaluated have a below-average IQ, it is patent a huge variability on the proportions of animals that have a global cognitive performance over average (Figure X), thus an ample scope for selection of camels based on cognitive abilities is plausible.

Good (ICC between 0.75-0.9) and excellent (ICC greater than 0.9) reliability did exist between raters when scoring those cognitive processes that mostly evaluate how the camels cooperate with the instructors during the development of the evaluation test. However, moderate (ICC between 0.5-0.75) and poor (ICC lesser than 0.5) inter-rater reliability (Koo & Li, 2016) can be found for those traits in which the animal attention towards the stimuli being presented and their potentially distraction by the surrounding environment during the assessment session are the principal cognitive components evaluated. Concentration and attention are known to be greatly dependent on both intrinsic and extrinsic motivational and emotional factors (Eysenck, 2012; Robinson et al., 2012; Vallerand & Ratelle, 2002), as well as on intraherd dominance structure in social groups (Colas-Zelin et al., 2012; Kar, Whiting, & Noble, 2017; Shepherd, Deaner, & Platt, 2006), and can be inferred from body language signals such as the ears' position (Houpt, 2018). Hence, although evaluators being previously trained for behaviour assessment, the fact that camels are social animals with a defined intraherd hierarchy (Schulte & Klingel, 1991) that is probably unknown for the evaluators when performing the behavioural assessment activities, together with the likelihood of expression of separation anxiety and the relatively restricted movements of the ears in camels (Fowler, 2011), it can be expected high interobserver variability for the quantitative evaluation of those camel behavioural traits strongly linked to concentration/attention. These results are in accordance with the percentage of correct classification (38.21%) for the discriminant analysis that used the evaluator as grouping variable and the IQ for each cognitive process as set of predictors.

From a practical perspective, when aiming to adapt the tasks to be filled by the animals during both training and working sessions, and subsequently select the best candidates for their expected higher performance, the understanding of the relationships between the cognitive processes evaluated and IQ becomes indispensable. Based on the decision tree and high percentage of correct classification (86.92%) of the discriminant analysis that identified the differences among cognitive processes for their particular influence on IQ, objective inferences for a practical usefulness in camel selective breeding based on cognitive criteria can be done. The cognitive process that best allows distinguishing between animals for their overall IQ is the comfortability of the camel when removed from the main herd. Apart from the mere fact that camels are gregarious animals, such finding could be also expected given the fact that the main functionality of the camels evaluated is leisure tourism, for which several camels are seeked to get involved (Pastrana et al., 2021).

Indeed, dromedary camels with an above-average IQ are more dependent on the herd than those animals with a below-average IQ, which feel more comfortable when separated from the herd. On the one hand, this could be taken as an evidence of the existence of a group intelligence in a gregarious species such as the camel, that is, something similar to c factor or 'collective intelligence' (Pratt, 2019). On the other hand, concerning the animals with a below-average IQ and generally feeling more comfortable when separated from the herd and guided by a familiar instructor, this could be taken as a reflection of active avoidance, in individuals at lower positions within the hierarchical-social structure, of agonistic behaviors from conspecifics located at higher positions of the social hierarchy (Allan & Gilbert, 1997; Reddon, Ruberto, & Reader, 2021); although this situation may evidently cause a lower cognitive performance in subordinate animals (Colas-Zelin et al., 2012; Pastrana et al., 2022). In terms of functional aptitude, those camels that are most dependent on the main herd would be more likely to participate in leisure tourism activities, while the camels with lesser dependency on the group could be suitable for assisted-therapies. In the last case, considering that those camels that have lesser dependence on the main herd are also characterized for a higher perseverance, which can be explained on the basis of the association between subordination and lower response level but higher memory retention (Santos et al., 2021), could be beneficially used for individualized and varied therapy sessions. Both a higher perseverance or patience when completing consecutive tests and a striking memory retention, could lead to a better decision-making ability of the camels for pursuing the obtention of a small reward in the short term rather than a more rewarding recompense in the long term (Coutlee & Huettel, 2012; Wang & Ruhe, 2007). Hence, the camel with such cognitive characteristics could display a better ability to be effectively and safely trained into the fulfillment of different tasks (trainability).

The dependence on the group is also expected to be influencing the easiness with which camels enter and leave housing facilities, being fear and the coping styles used by these animals the main underlying and influencing features in this regard (Hofmann, 2008; Kikusui, Winslow, & Mori, 2006). Although the performance for the cognitive process 'get in/out of stables' is variable among animals in the study population, relatively higher proportions of animals with below-average IQ can be detected when their performance for this specific process is either at the lower or upper limits of the specific scoring scale. In the case of camels that show hardly any impediment when entering or leaving the pens, they could be more submissive animals because they are in lower hierarchical position and that follow the instructions of the trainer, who is a person to whom the animals already know and with which they have an established bond. Then, as previously discussed, this subordination could be responsible for cognitive impairment and thus lower global performance. On the other hand, the animals that do show problems when getting in/out of stables could be camels that may have dominant roles within the social group, condition that leads them to have the need to exert constant influence/control over the group (Cheng et al., 2013). In other words, they are more likely to be more dependent on a collective intelligence, hence displaying lower performance for those traits that imply isolation from the group.

Moreover, a potential influence of long-term memory of past events can be modulating the individual disposition to leave and enter facilities. The below-average IQ in those camels that are less dependent on the herd and potentially more submissive animals, but have greater memory, could be associated with the animal's refusal to carry out specific tasks by association with certain past experiences. In fact, related literature confirms the great ability of camels to remember different episodes of their lives (Al-Ani, 2004; Cantimpratensis, 1973). Overall, these results emphasize the importance of knowing the dominance and subordination relationships between animals within a group so that the intra-herd handling practices can be adjusted and long-term, welfare-promotion human-camel bonds be implemented. This way, the dependence of the group in the camels could be effectively controlled trough the guidance of an instructor they trust on (cooperation). Then, the ability of the camels to be successfully trained into the fulfillment of specific tasks by following the instructions of the trainer (docility), will be improved.

Notwithstanding the aforementioned scenarios, in order to achieve a good performance of the animals during the training and working sessions, it becomes imperative to ensure that the concentration of the camels on the presented stimuli and their cooperation with the trainer's instructions are as effective and equilibrated as possible. Concretely, such cognitive processes are expected to be greatly modulated by the emotional stability of the individual as well as the curiosity and alertness of the animal towards the stimulus being presented (Ainley, 2006; Lee & Son, 2022; McElreath et al., 2003; Spasova, 2012). In general, camels that are less dependent on the group and with a below-average IQ tend to be more curious animals, which coincides with the conclusions presented by Schutte and Malouff (2019), who argue that autonomy is a key factor in the development and manifestation of curiosity. Curiosity may be a positive emotion that is activated by boredom and the need to be engaged in new experiences (Collins, Litman, & Spielberger, 2004), then helps the individual to expand its perspectives and construct new resources (Fredrickson & Joiner, 2018). Therefore, the lesser dependence of these camels on the motivation and ability of the group to carry out tasks and make decisions, and their autonomy of choice to explore new stimuli around, might determine their greater individual likelihood to initiate group movements (leadership behavior). These animals are more focused at increasing group members' fitness instead of sexual competition and force another congeners into submission. In addition, the active interaction with the environment promotes the synthesis of the hormone serotonin, which is known to have antagonistic potential towards the effects, either active or residual, of sex hormones at the central level (Giammanco et al., 2005; Siegel & Douard, 2011). In fact, according to Iglesias Pastrana et al. (2021), gelded dromedaries, which tend to be more submissive and scored relatively lower in the hierarchical rank, are more prone to lead group movements or collective activities. Hence, the results of the present investigation serves to elucidate that leadership behaviour in this animal species could be leading to the misinterpretation of the real cognitive performance of the animals, and provides further evidence that leadership, although conceptually related to dominance, is functionally distinct from this last dimension.

Additionally, the fact that the camels that are less dependent on the group and more curious about the novel stimuli being presented have a below-average IQ, could be explained by the interference of curiosity in the animal's ability to maintain full attention and concentration in the trainer's instructions, thus conditioning a lower global cognitive performance during the whole assessment task (Chang & Shih, 2019). Indeed, the less curiosity, the greater the docility of animals, apart from a higher customer satisfaction at camel ride experiences (Pastrana et al., 2021). Therefore, for utilitarian purposes, it would be advisable to introduce new stimuli gradually and in a controlled manner to all animals at the same time, so that possible conditioning effects arising from the presentation of novel stimuli (neophobia) (Iglesias et al., 2018) disappears in those animals with more defensive characters such as bulls, but also excessive exploration in high curious animals. Thus, fear and diversive curiosity will be decreased in account of the promotion of animal's concentration on the trainer's instructions when using these stimuli.

High interest in the novel stimulus presented also implicates both less emotional stability and inconsistent alert status towards the stimuli around in the camels. Actually, when camels are effectively focusing on the stimulus around and they are more predictable from one to another stimulus, their overall cognitive performance is comparatively superior. Such finding would have its basis on the fact that calm animals, when they direct its attention and concentration on the desired stimuli and trainer's instructions, do so in a more focused way and would respond according to previous knowledge, therefore their cognitive abilities to generate a specific, adapted response will be greater and more effective (Burkart & Van Schaik, 2010; Nathan et al., 2006).

Taking into account the discussed interrelationships between cognitive processes and IQ and in order to facilitate the selection of animals according to their potential suitability for a specific functional niche and the adaption of the training protocols, it is fundamental to know what is the influence of different animal-dependent factors on the normalized, individual cognition performance. With this purpose, the list of cognitive processes that serve to explain in greater proportion the differences in camels' cognitive performance and that therefore deserve greater attention for the individualized evaluation of animals are 'concentration', 'dependence', 'docility', and 'ease of handling'.

These results can be expected given the main functionality to which the evaluated animals are dedicated (leisure riding).

With respect to sex-attributed differences (percentage of correct classification of the discriminant analysis = 68.72%), female dromedaries are generally easier to handle when compared to males and concentrated more during the assessment/training activities. These results coincide with those by Pastrana et al. (2021), who found that female dromedaries are ready to participate in leisure ride experiences earlier than their counterparts. By contrast, male dromedaries show less sympathy toward humans and are more variable for their docility, which could be attributed partially to the effects of sex hormones. The existence of castrated and non-castrated males in the study sample would explain these results. However, if neutering status is evaluated as a potential influencing factor of camel cognition (percentage of correct classification of the discriminant analysis = 71.54%), it can be observed that non-castrated camels are more sympathetic toward humans, which could be ascribed to the fact that all the females in the study population, which are easier to handle as discussed earlier for the sex-linked effects, and a relative proportion of males, are not castrated. Besides, the specific protocol that is followed for the castration of the camel of the breed evaluated could have some explanatory power for such results, since animals begin to domesticate before being castrated so that cognitive maturity, largely mediated by sex hormones, is enough to ensure cognitive maturity but without reaching undesirable levels from an ethological point of view (i.e., agonistic behaviors) (Iglesias Pastrana et al., 2021; Oliveira, 2009).

Male dromedaries are also less dependent on the group. Although the study camels are bred in single-sex herds, when they participate in activities such as leisure riding, animals of both sexes get involved and are disposed in a single file that is generally lead by a male, so the relatively minor dependence of the group in males could be rely on the influence of specific behavior patterns in natural camel populations. Classically, a group of females is led by an older male (Ahmed, Sadiq, & Abdullah, 2019). Additionally, in regards of the effects of neutering status on the individual dependence of the group, camels are generally more dependent when castrated. Such finding would be linked to the effects of sex hormones, since the absence of chemical signaling by these hormones is expected to decrease the incidence of agonistic interactions (i.e., sexual competition) and promote non-sexual affiliative interactions between congeners (Kalagassy, Carbone, & Houpt, 1999; Yang, Comninos, & Dhillo, 2018). Nevertheless, this greater dependence on the group of castrated animals will also condition a lower concentration of these animals during the individual training/working sessions.

In relation to the impact of the training protocol in terms of human resources involved (owner) (percentage of correct classification of the discriminant analysis = 57.44%), the smaller the size of the flock, the lesser the dependence of the group, the better the concentration and the greater the docility and easiness of handling. A smaller size of the group would be facilitating a closer, safer and relatively more individualized handling of the animals (Grandin, 2020), apart from the fact that the possible relationships of dominance and submission between the animals of a smaller group would be easier to recognize and therefore adapted measures to minimize their influence on the cognitive performance of the animals can be adopted. Furthermore, the active involvement of the camels in domestication and training regimes for a specific functionality (percentage of correct classification of the discriminant analysis = 65.13%), have a significant effect mainly on the easiness of animal handling. Although it would be expected that active involvement of the animals in such protocols would improve their easiness of handling, it can be noticed that a relative proportion of the study camels that display notable sympathy toward humans when handled, are indeed not actively participating in domestication/training protocols. This finding would be adding further evidences to the statements previously argued on the potential influence of memory for past experiences on the greater or lesser receptivity of camels to interact with humans. As a reiteration, the active involvement of leisure camels in training protocols, as these last imply the participation of several animals, could end up conditioning a greater dependency of the animals in the group. Hence, camels would display a lower concentration if they have to be separated from the group to carry out a different action. In this scenario, it could be useful to define smaller-size stable, functional groups, either single- or mixed-sex, so that the depletion on cognitive performance because of stress and separation anxiety can be avoided.

Lastly, in regards of the role of phaneroptic-related characters on the individual cognitive performance in dromedaries, non-negligible effects can be observed for eye colour (percentage of correct classification of the discriminant analysis = 92.31%). Those animals with light-colored iris have lesser levels of concentration and docility, and higher dependency on the group and rejection towards humans when being handled. According to different authors, such cognitive outputs are linked to a lower visual acuity that is correlated to the heterogeneity in iris pigmentation, and other congenital disorders such as deafness that are associated to pleiotropic effects for genes responsible of pigmentation (Frank et al., 2000; Komáromy et al., 2011; Schonthaler et al., 2005; Volpato, Dioli, & Di Nardo, 2017). In turn, these conditions will influence the approach/avoidance responses of the animals towards the presented stimuli. Such findings, together with the conclusions stated on the leadership behaviour in dromedary camels (Iglesias Pastrana et al., 2021), being blue-eyed camels more prone to lead collective movements, serve to further demonstrate that leadership can be influenced by emotional stability (nervousness) and potentially conceal real cognitive abilities of the animals.

For other phaneroptic traits such as coat color and particularities, in addition to the relatively homogeneous distribution of the proportions of each color and particularities category between the different quantitative categories for the normalized IQ of each discriminating cognitive process, the percentages of correct classification of the discriminant analyses for such qualitative characters have the lowest values (36.15% and 46.15% for the grouping variable 'coat colour' and 'coat particularities', respectively). These results demonstrate that the specific effect of these factors and each of their possible categories on the normalized IQ for concentration, dependence, docility, and ease of handling in dromedary camels would not be so easily recognizable and substantially discriminating. It could be associated with the existence of multiple, small-effect interaction processes between genes with high level of variability and that are responsible, in relative proportion, for characters related to melanogenesis and behavioural patterns. On the basis of the high variability for coat colour phenotypes in camels (Alhaddad & Alhajeri, 2019) and the knowledge on the affectation of social dominance by coat colour in other mammal species (Bro-Jørgensen, 2002; Geist, 1987; Gerald, 2001; Guthrie, 1971; West & Packer, 2002), future applied studies are encouraged to indagate into the genomic basis of melanic body color and social dominance in camels, as well as the correlations between the genetic markers that might be significantly associated with these characteristics. Then, genetic selection schemes for these livestock species will be substantially enriched.

Conclusions

The present investigation challenges the misconception of camels as unintelligent subjects and demonstrates that this animal species can be comprehensively assessed for cognitive traits underlying intelligence and general cognition processes by using a human-analogous IQ scoring method. A high level of interindividual variability for cognitive performance was revealed among the evaluated camels, suggesting the potential for selective breeding based on cognitive abilities in this livestock species. Reliability analyses indicated good and excellent inter-rater agreement for cognitive processes that evaluated animal cooperation with handlers, whereas lower reliability was found for those traits essentially measuring attention and concentration. Animal intrinsic and extrinsic motivational and emotional factors, the intra-herd social structure, and the relative difficulty to asses attention basing on body language signals in camels, can be explaining such lack of interobserver agreement. Within a practical framework, understanding the relationship between cognitive processes and IQ is crucial for the tailoring of camel training programs and the selection of individuals for their superior performance. The comfortability of camels when separated from the main herd emerged as the most distinguishing factor between individuals for overall IQ. This finding is particularly relevant in the context of camel leisure tourism, where these animals are sought for their involvement in group activities. Camels with above-average IQ showed a higher dependency on the main herd, while those with below-average IQ exhibited greater comfort when separated from congeners and guided by a familiar instructor. These observations suggest the presence of group intelligence in dromedary camels and the influence of social hierarchies on cognitive performance. Furthermore, camels with lower dependence on the group and higher perseverance may be suitable for individualized and varied assisted-therapy sessions due to their decision-making abilities, higher concentration and memory retention. The easiness of entering and leaving housing facilities was also influenced by the dependence on the group, fear, and coping styles. Camels that encountered fewer obstacles during this process may be more submissive and easier to be trained, while those facing difficulties were likely to have dominant roles within the social group and generally more dependent on a group intelligence. Long-term memory of past events may be also impacting on the individual disposition to enter and leave housing facilities and to be handled. Such findings emphasize the importance of considering dominance and subordination relationships within camel herds to improve intra-herd handling practices and establish sympathetic, long-term human-camel bonds. Camels that are less dependent on the group and exhibit below-average IQ tend to be also more curious and display lesser emotional stability, which may interfere with their ability to maintain full attention and concentration in both the stimuli presented and the trainer's instructions. Gradual introduction of novel stimuli and controlled exposure can mitigate the effects of curiosity, fear, and diversive exploration, thus enhancing concentration. In regards of the effects of different animal-dependent factors on the cognitive performance in camels, concentration, dependence, docility and ease of handling are the processes mostly biased and that best discriminate among qualitative categories for each influencing factor. Female dromedaries camels are generally easier to handle and more focused during training and working activities. Male camels displayed less sympathy toward humans and exhibited greater variability in docility, potentially determined by sex hormones effects. Strongly linked, non-castrated camels demonstrated greater sympathy toward humans compared to castrated camels. Additionally, the smaller the size of the flock, the lesser the dependence of the group, the better the concentration and the greater the docility and easiness of handling, probably due to the existence of a closer and safer camel-trainer bond. Besides, the construction of smaller-size stable, functional groups, either single- or mixed-sex, would avoid the potential depletion on cognitive performance because of stress and separation anxiety effects. Lastly, camel with light-colored iris have lesser levels of concentration and docility, and higher dependency on the group and rejection towards humans when being handled. This can be linked, according to literature, to a lower visual and auditive acuity that may be associated to pleiotropic effects for genes responsible of melanogenesis.

Author contributions: Conceptualization, C.I.P., F.J.N.G. and A.K.M.; Data curation, C.I.P. and F.J.N.G.; Formal analysis, C.I.P., F.J.N.G. and A.K.M.; Funding acquisition, E.C. and J.V.D.B.; Investigation, C.I.P. and F.J.N.G.; Methodology, C.I.P., F.J.N.G. and A.K.M.; Project administration, E.C. and J.V.D.B.; Resources, E.C. and J.V.D.B.; Software, C.I.P., F.J.N.G. and A.K.M.; Supervision, F.J.N.G., E.C. and J.V.D.B.; Validation, F.J.N.G. and J.V.D.B.; Visualization, E.C.; Writing—original draft, C.I.P. and F.J.N.G.; Writing—review & editing, F.J.N.G., E.C. and J.V.D.B. All authors have read and agreed to the published version of the manuscript.

Funding: The present research was carried out in the financing framework of the international project CA.RA.VA.N—'Toward a Camel Transnational Value Chain' (Reference APCIN-2016-00011-00-00) and during the covering period of a predoctoral contract (FPU Fellowship) funded by the Spanish Ministry of Science and Innovation and was developed under the context a Ramón y Cajal Post-Doctoral fellowship financially supported by MCIN/AEI/10.13039/501100011033 and European Union "NextGenerationEU"/PRTR" (Recovery, Transformation and Resilience Plan—Funded by the European Union—NextGenerationEU).

Data availability statement: The data presented in this study are available on request from the first author.

Acknowledgments: The authors would also like to thank 'Aires Africanos' Eco-tourism Company, Oasis Park Fuerteventura, and 'Camelus' Camellos de Almería, for their direct technical help and assistance.

Conflicts of interest: The authors declare no conflict of interest.

Ethics declaration statement: All farms included in the study followed specific codes of good practices and therefore, the animals received humane care in compliance with the national guide for the care and use of laboratory and farm animals in research. Written consent from the owners was obtained for their participation. The study was conducted in accordance with the Declaration of Helsinki. The Spanish Ministry of Economy and Competitivity through the Royal Decree Law 53/2013 and its credited entity, the Ethics Committee of Animal Experimentation from the University of Córdoba, permitted the application of the protocols present in this study as cited in the 5th section of its 2nd article, as the animals assessed were used for credited zootechnical use. This national Decree follows the European Union Directive 2010/63/UE, from the 22 September of 2010.

References

Ahmed, Z. O., Sadiq, A. T., & Abdullah, H. S. (2019). Solving the Traveling Salesman's Problem Using Camels Herd Algorithm. Proceedings of 2nd Scientific Conference of Computer Sciences (SCCS).

Ainley, M. (2006). Connecting with learning: Motivation, affect and cognition in interest processes. *Educational Psychology Review*, 18, 391-405.

Al-Ani, F. K. (2004). *Camel: management and diseases*: CABI Books.

Al-Obaidi, A. T. S., & Abdullah, H. S. (2017). Camel herds algorithm: A new swarm intelligent algorithm to solve optimization problems. *International Journal on Perceptive and Cognitive Computing*, 3(1).

Alhaddad, H., & Alhajeri, B. H. (2019). Cdrom archive: a gateway to study camel phenotypes. *Frontiers in genetics*, 10, 48.

Allan, S., & Gilbert, P. (1997). Submissive behaviour and psychopathology. *British Journal of Clinical Psychology*, 36(4), 467-488.

Bádenas de la Peña, P., Facal, J. L., & García Gual, C. (1978). *Fábulas de Esopo/Vida de Esopo/Fábulas de Babrio*: Editorial Gredos.

Boujenane, I. (2019). Comparison of body weight estimation equations for camels (*Camelus dromedarius*). *Tropical animal health and production*, 51, 1003-1007.

Bro-Jørgensen, J. (2002). Overt female mate competition and preference for central males in a lekking antelope. *Proceedings of the National Academy of Sciences*, 99(14), 9290-9293.

Bunting, K. V., Steeds, R. P., Slater, L. T., Rogers, J. K., Gkoutos, G. V., & Kotecha, D. (2019). A practical guide to assess the reproducibility of echocardiographic measurements. *Journal of the American Society of Echocardiography*, 32(12), 1505-1515.

Burkart, J. M., & Van Schaik, C. P. (2010). Cognitive consequences of cooperative breeding in primates? *Animal cognition*, 13, 1-19.

Cantimpratensis, T. (1973). *Liber de natura rerum*: Text (Vol. 1): Walter De Gruyter.

Chan, Y. (2005). Biostatistics 303. Discriminant analysis. *Singapore medical journal*, 46(2), 54.

Chang, Y.-Y., & Shih, H.-Y. (2019). Work curiosity: A new lens for understanding employee creativity. *Human Resource Management Review*, 29(4), 100672.

Cheng, J. T., Tracy, J. L., Foulsham, T., Kingstone, A., & Henrich, J. (2013). Two ways to the top: evidence that dominance and prestige are distinct yet viable avenues to social rank and influence. *Journal of personality and social psychology*, 104(1), 103.

Colas-Zelin, D., Light, K. R., Kolata, S., Wass, C., Denman-Brice, A., Rios, C., Szalk, K., & Matzel, L. D. (2012). The imposition of, but not the propensity for, social subordination impairs exploratory behaviors and general cognitive abilities. *Behavioural Brain Research*, 232(1), 294-305.

Collins, R. P., Litman, J. A., & Spielberger, C. D. (2004). The measurement of perceptual curiosity. *Personality and individual differences*, 36(5), 1127-1141.

Coutlee, C. G., & Huettel, S. A. (2012). The functional neuroanatomy of decision making: prefrontal control of thought and action. *Brain resea*rch, 1428, 3-12.

Deary, I. J., Penke, L., & Johnson, W. (2010). The neuroscience of human intelligence differences. *Nature Reviews Neuroscience*, 11(3), 201-211.

Dukas, R. (2004). Evolutionary biology of animal cognition. *The Annual Review of Ecology, Evolution, and Systematic*s, 35, 347-374.

Eysenck, M. (2012). *Attention and arousal: Cognition and performance*: Springer.

Fleiss, J. L., & Cohen, J. (1973). The equivalence of weighted kappa and the intraclass correlation coefficient as measures of reliability. *Educational and psychological measurement*, 33(3), 613-619.

Fowler, M. (2011). *Medicine and surgery of camelids*: John Wiley & Sons.

Frank, R. N., Puklin, J. E., Stock, C., & Canter, L. A. (2000). Race, iris color, and age-related macular degeneration. *Transactions of the American Ophthalmological Society*, 98, 109.

Fredrickson, B. L., & Joiner, T. (2018). Reflections on positive emotions and upward spirals. *Perspectives on Psychological Science*, 13(2), 194-199.

Geist, V. (1987). On speciation in Ice Age mammals, with special reference to cervids and caprids. *Canadian Journal of Zoology*, 65(5), 1067-1084.

Gerald, M. S. (2001). Primate colour predicts social status and aggressive outcome. *Animal Behaviour*, 61(3), 559-566.

Gerrig, R. J., & Zimbardo, P. G. (2002). *American Psychological Association: Glossary of Psychological Terms*: Pearson Education, Education, Incorporated (COR).

Giammanco, M., Tabacchi, G., Giammanco, S., Di Majo, D., & La Guardia, M. (2005). Testosterone and aggressiveness. *Medical Science Monitor*, 11(4), 136-145.

González Ariza, A., Arando Arbulu, A., León Jurado, J. M., Navas González, F. J., Delgado Bermejo, J. V., & Camacho Vallejo, M. E. (2021). Discriminant canonical tool for differential biometric characterization of multivariety endangered hen breeds. *Animals*, 11(8), 2211.

González, F. J. N., Vidal, J. J., Jurado, J. M. L., McLean, A. K., & Bermejo, J. V. D. (2019). Dumb or smart asses? Donkey's (*Equus asinus*) cognitive capabilities share the heritability and variation patterns of human's (*Homo sapiens*) cognitive capabilities. *Journal of Veterinary Behavior*, 33, 63-74.

Gottfredson, L. S. (2009). *Logical fallacies used to dismiss the evidence on intelligence testing*: APA PsycBooks.

Grandin, T. (2020). *Improving animal welfare: A practical approach*: CABI Books.

Guthrie, R. (1971). A new theory of mammalian rump patch evolution. *Behaviour*, 38(1-2), 132-145.

Hansen Wheat, C., Fitzpatrick, J. L., Rogell, B., & Temrin, H. (2019). Behavioural correlations of the domestication syndrome are decoupled in modern dog breeds. *Nature communications*, 10(1), 2422.

Hofmann, S. G. (2008). Cognitive processes during fear acquisition and extinction in animals and humans: Implications for exposure therapy of anxiety disorders. *Clinical psychology review*, 28(2), 199-210.

Houpt, K. A. (2018). *Domestic animal behavior for veterinarians and animal scientists*: John Wiley & Sons.

Iglesias, C., Navas, F., Pizarro, G., Arando, A., Cumplido, A., & Delgado, J. (2018). Evaluating neophobia in a captive herd of fallow deers. *Archivos de Zootecnia*, 67(260), 596-603.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S. and Delgado, J. V. (2020). Ethological characterization of the Canarian camel breed. *Archivos de zootecnia*, 69(265), 108-115.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Arando Arbulu, A., & Delgado Bermejo, J. V. (2021). The Youngest, the Heaviest and/or the Darkest? Selection Potentialities and Determinants of Leadership in Canarian Dromedary Camels. *Animals*, 11(10), 2886.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Barba Capote, C. J., & Delgado Bermejo, J. V. (2020). Effect of research impact on emerging camel husbandry, welfare and social-related awareness. *Animals*, 10(5), 780.

Kalagassy, E. B., Carbone, L. G., & Houpt, K. A. (1999). Effect of castration on rabbits housed in littermate pairs. *Journal of Applied Animal Welfare Science*, 2(2), 111-121.

Kar, F., Whiting, M. J., & Noble, D. W. (2017). Dominance and social information use in a lizard. *Animal cognition*, 20(5), 805-812.

Khera, T., & Rangasamy, V. (2021). Cognition and pain: a review. *Frontiers in psychology*, 12, 673962.

Kikusui, T., Winslow, J. T., & Mori, Y. (2006). Social buffering: relief from stress and anxiety. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 361(1476), 2215-2228.

Komáromy, A. M., Rowlan, J. S., La Croix, N. C., & Mangan, B. G. (2011). Equine Multiple Congenital Ocular Anomalies (MCOA) syndrome in PMEL17 (Silver) mutant ponies: five cases. *Veterinary ophthalmology*, 14(5), 313-320.

Koo, T. K., & Li, M. Y. (2016). A guideline of selecting and reporting intraclass correlation coefficients for reliability research. *Journal of chiropractic medicine*, 15(2), 155-163.

Larsson, M., & Brothers, D. (2019). Camel-Assisted Interventions (CAI): Furry co-workers for human development. Proceedings of the International Society of Applied Ethology.

Lee, J.-h., & Son, C. (2022). The Effect of negative emotion on concentration through emotional regulation: mediated moderation of Metacognitive Awareness. *Journal of Rational-Emotive & Cognitive-Behavior Therapy*, 1-13.

López Gómez, C. (2009). Inteligencia animal en Aristóteles. *Discusiones Filosóficas*, 10(15), 69-81.

Matzel, L., & Sauce, B. (2017). *IQ (The intelligence quotient). Encyclopedia of Animal Cognition and Behavior*: Springer.

McElreath, R., Clutton-Brock, T. H., Fehr, E., Fessler, D. M., Hagen, E. H., Hammerstein, P., Kosfeld, M., Milinski, M., Silk, J.B., Tooby, J., & Wilson, M.I. (2003). Group report: The role of cognition and emotion in cooperation. *Genetic and cultural evolution of cooperation*, 125-152.

Momozawa, Y., Kusunose, R., Kikusui, T., Takeuchi, Y., & Mori, Y. (2005). Assessment of equine temperament questionnaire by comparing factor structure between two separate surveys. *Applied Animal Behaviour Science*, 92(1-2), 77-84.

Morales Muñiz, D. C. (1996). El simbolismo animal en la cultura medieval. *Espacio Tiempo y Forma. Serie III, Historia Medieval*, (9).

Nathan, P. J., Lu, K., Gray, M., & Oliver, C. (2006). The neuropharmacology of L-theanine (N-ethyl-L-glutamine) a possible neuroprotective and cognitive enhancing agent. *Journal of herbal pharmacotherapy*, 6(2), 21-30.

Navas, F. J., Jordana, J., León, J. M., Arando, A., Pizarro, G., McLean, A. K., & Delgado, J. V. (2017). Measuring and modeling for the assessment of the genetic background behind cognitive processes in donkeys. *Research in veterinary science*, 113, 105-114.

Navas González, F. J., Jordana Vidal, J., León Jurado, J. M., Arando Arbulu, A., McLean, A. K., & Delgado Bermejo, J. V. (2018a). Genetic parameter and breeding value estimation of donkeys' problem-focused coping styles. *Behavioural Processes*, 153, 66-76.

Navas González, F. J., Jordana Vidal, J., Pizarro Inostroza, G., Arando Arbulu, A., & Delgado Bermejo, J. V. (2018b). Can Donkey Behavior and Cognition Be Used to Trace Back, Explain, or Forecast Moon Cycle and Weather Events? *Animals*, 8(11), 215.

Navas González, F. J., Jordana Vidal, J., León Jurado, J. M., McLean, A. K., & Delgado Bermejo, J. V. (2019). Dumb or smart asses? Donkey's (*Equus asinus*) cognitive capabilities share the heritability and variation patterns of human's (*Homo sapiens*) cognitive capabilities. Journal of Veterinary Behavior, 33, 63-74.

Navas González, F. J., Vidal, J. J., León Jurado, J. M., McLean, A. K., & Delgado Bermejo, J. V. (2020). Nonparametric analysis of noncognitive determinants of response type, intensity, mood, and learning in donkeys (*Equus asinus*). *Journal of Veterinary Behavior*, 40, 21-35.

Oliveira, R. F. (2009). Social behavior in context: hormonal modulation of behavioral plasticity and social competence. *Integrative and Comparative Biology*, 49(4), 423-440.

Olmstead, M. C., & Kuhlmeier, V. A. (2015). *Comparative cognition*: Cambridge University Press.

Pastrana, C. I., González, F. J. N., Ciani, E., Ariza, A. G., & Bermejo, J. V. D. (2021). A tool for functional selection of leisure camels: Behaviour breeding criteria may ensure long-term sustainability of a European unique breed. *Research in Veterinary Science*, 140, 142-152.

Pastrana, C. I., Gonzalez, F. J. N., Inostroza, M. G. P., Arbulu, A. A., Bermejo, J. V. D., & Aguilera, M. J. R. (2022). Study of variability of cognitive performance in captive fallow deer (*Dama dama*) through g and c factors. *Journal of Veterinary Behavior*, 47, 70-85.

Plomin, R. (2001). The genetics of g in human and mouse. *Nature Reviews Neuroscience*, 2(2), 136-141.

Pratt, S. C. (2019). Collective intelligence in social animals. In *Encyclopedia of Animal Behavior* (pp. 754-761): Elsevier.

Pritchard, D. J., Hurly, T. A., Tello-Ramos, M. C., & Healy, S. D. (2016). Why study cognition in the wild (and how to test it)? *Journal of the Experimental Analysis of Behavior*, 105(1), 41-55.

Reader, S. M., Hager, Y., & Laland, K. N. (2011). The evolution of primate general and cultural intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 1017-1027.

Reddon, A. R., Ruberto, T., & Reader, S. M. (2021). Submission signals in animal groups. *Behaviour*, 159(1), 1-20.

Robinson, L. J., Stevens, L. H., Threapleton, C. J., Vainiute, J., McAllister-Williams, R. H., & Gallagher, P. (2012). Effects of intrinsic and extrinsic motivation on attention and memory. *Acta psychologica*, 141(2), 243-249.

Rowe, L. I., Hattie, J., & Hester, R. (2021). g versus c: comparing individual and collective intelligence across two meta-analyses. *Cognitive Research: Principles and Implications*, 6(1), 1-24.

Santos, M. J., Merlo, S. A., Kaczer, L., & Pedreira, M. E. (2021). Social context shapes cognitive abilities: associative memories are modulated by fight outcome and social isolation in the crab *Neohelice granulata*. *Animal Cognition*, 24, 1007-1026.

Schonthaler, H. B., Lampert, J. M., von Lintig, J., Schwarz, H., Geisler, R., & Neuhauss, S. C. (2005). A mutation in the silver gene leads to defects in melanosome biogenesis and alterations in the visual system in the zebrafish mutant fading vision. *Developmental biology*, 284(2), 421-436.

Schulte, N., & Klingel, H. (1991). Herd structure, leadership, dominance and site attachment of the camel, *Camelus dromedarius*. *Behaviour*, 118(1-2), 103-114.

Schutte, N. S., & Malouff, J. M. (2019). Increasing curiosity through autonomy of choice. *Motivation and Emotion*, 43, 563-570.

Shepherd, S. V., Deaner, R. O., & Platt, M. L. (2006). Social status gates social attention in monkeys. *Current biology*, 16(4), R119-R120.

Shettleworth, S. J. (2001). Animal cognition and animal behaviour. *Animal behaviour*, 61(2), 277-286.

Siegel, A., & Douard, J. (2011). Who's flying the plane: Serotonin levels, aggression and free will. *International journal of law and psychiatry*, 34(1), 20-29.

Spasova, Z. (2012). The effect of weather and its changes on emotional state–individual characteristics that make us vulnerable. *Advances in Science and Research*, 6(1), 281-290.

Vallerand, R. J., & Ratelle, C. F. (2002). Intrinsic and extrinsic motivation: A hierarchical model. *Handbook of self-determination research*, 128, 37-63.

Volpato, G., Dioli, M., & Di Nardo, A. (2017). Piebald camels. *Pastoralism*, 7(1), 3.

Wang, Y., & Ruhe, G. (2007). The cognitive process of decision making. *International Journal of Cognitive Informatics and Natural Intelligence (IJCINI)*, 1(2), 73-85.

West, P. M., & Packer, C. (2002). Sexual selection, temperature, and the lion's mane. *Science*, 297(5585), 1339-1343.

Wynne, C. D., & Udell, M. A. (2020). *Animal cognition: Evolution, behavior and cognition*: Bloomsbury Publishing.

Yang, L., Comninos, A. N., & Dhillo, W. S. (2018). Intrinsic links among sex, emotion, and reproduction. *Cellular and molecular life sciences*, 75, 2197-2210.

4.4 The youngest, the heaviest and/or the darkest? Selection potentialities and determinants of leadership in Canarian dromedary camels

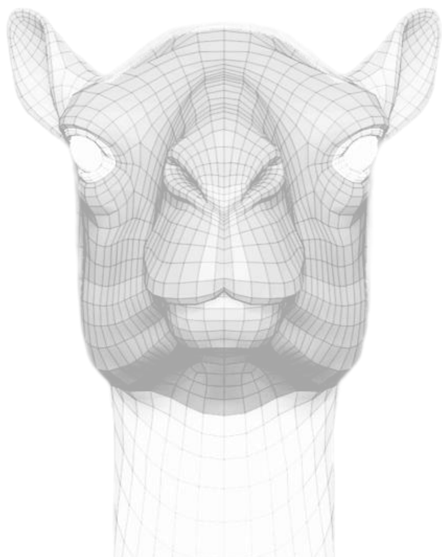
Carlos Iglesias Pastrana[1], Francisco Javier Navas González[1,2], Elena Ciani[3], Ander Arando Arbulu[4] and Juan Vicente Delgado Bermejo[1]

[1]Department of Genetics, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain

[2]Andalusian Institute of Agricultural and Fisheries Research and Training (IFAPA), Alameda del Obispo, 14004 Cordoba, Spain

[3]Department of Biosciences, Biotechnologies and Biopharmaceutics, Faculty of Veterinary Sciences, University of Bari 'Aldo Moro', 70121 Bari, Italy

[4]Animal Breeding Consulting, University of Córdoba, 14014 Cordoba, Spain



Quality indicator information provided on the publication

Status of the manuscript: Published

Journal (year, volume, page(s)): *Animals* 2021, *11*, 2886

International database in which it is indexed: Journal of Citation Reports (JCR)

Thematic area in the reference database: Veterinary Sciences

Impact index of the journal in the year of the article's publication: 3.231

Rank/number of thematic area journals: 16/145 (Q1)

Abstract

Several idiosyncratic and genetically correlated traits are known to extensively influence leadership in both domestic and wild species. For minor livestock such as camels, however, this type of behavior remains loosely defined and approached only for sex-mixed herds. The interest in knowing those animal-dependent variables that make an individual more likely to emerge as a leader in a single-sex camel herd has its basis in the sex-separated breeding of Canarian dromedary camels for utilitarian purposes. By means of an ordinal logistic regression, it was found that younger, gelded animals may perform better when eliciting the joining of mates, assuming that they were castrated just before reaching sexual maturity and once they were initiated in the pertinent domestication protocol for their lifetime functionality. The higher the body weight, the significantly ($p < 0.05$) higher the score in the hierarchical rank when leading group movements, although this relationship appeared to be inverse for the other considered zoometric indexes. Camels with darker and substantially depigmented coats were also significantly ($p < 0.05$) found to be the main initiators. Routine intraherd management and leisure tourism will be thus improved in efficiency and security through the identification and selection of the best leader camels.

Keywords

Dromedary camel, sex-separated breeding, intraherd leadership, animal handling improvement, pleiotropic genes, morphofunctional selection

Introduction

Selective mimetism can be understood as the joining decisions made by individuals based on external factors such as proximity to other individuals. This form of behavioral coordination makes, for instance, gregarious animals more likely to engage in a movement when in close proximity of other congeners (Cédric Sueur, Petit, & Deneubourg, 2009). Selective mimetism may bidimensionally operate at both time and space levels across the members composing a group but always dynamically seeks the stability of a specific behavioral pattern (Yamaguchi, Tanaka, & Yachida, 1997).

In this context, the members of the social intraherd network may tend to follow one or more leader(s) (Šárová et al., 2010), which are animals that more frequently initiate collective movements (Petit & Bon, 2010). These animals are often preferably selected by herdsmen/conservationists in domestic/rewilding scenarios for the maintenance of group cohesion in farmland activities (Butt, Shortridge, & WinklerPrins, 2009) and free-roaming herds (Ramos et al., 2018). Consequently, the study of the initiation and propagation of collective movements on the basis of sociodemographic attributes may not only permit better understanding of how species-specific social structure affects animal space use patterns, but also reveal breeding criteria to facilitate the labor of domestic gregarious animals' handlers.

As stated in Ramos et al. (2018), leadership is expected to be a complex, multifactorial interaction process, far from a strictly despotic action. Various characteristics have been indicated in literature to affect movement control in animal groups. For example, for some mammalian wild species, the oldest individual, who is supposed to better know the surrounding environment, may frequently act as the leader (Berry & Bercovitch, 2015; McComb et al., 2001; McComb et al., 2011). Contrastingly, although age has been reported not to condition leadership, it has been reported to be a mediator of dominance status in feral horses and zebras (Feist & McCullough, 1976; Klingel, 1968; Krueger et al., 2014), brown lemurs (Jacobs et al., 2011) and macaques (Cedric Sueur & Petit, 2008).

Among other conditioning factors, gender (Ihl & Bowyer, 2011; Ramos et al., 2015) and physiological individual state have frequently been shown to interact and be determinant for certain sex-dependent conditions. For instance, pregnant or lactating females have been suggested to lead the group towards areas where the resources for the satisfaction of their high energy requirements can be found (Fischhoff et al., 2007). For domestic species, extended knowledge on animal leadership behavior is currently available for dogs (Ákos et al., 2014), swine (Blackshaw, Thomas, & Blackshaw, 1994) and other major ungulates (Escós, Alados, & Boza, 1993; Cédric Sueur et al., 2018). However, sparse effective scientific knowledge exists within this applied field for rare, minor domestic species such as camels (Iglesias Pastrana et al., 2020).

In regard to hierarchy determination and leadership, the most common observational findings in camel mixed-sex herds depict an older male in the lead who is followed by the rest of the congeners (Al-Obaidi & Abdullah, 2017) and the internal division or large herds into smaller numerous subgroups (Schulte & Klingel, 1991). However, the patterns of social relationships within single-sex camel herds have not been evaluated yet.

Deepening the knowledge in this field may assist in defining handling standards adapted to the species' social ecology. Furthermore, because of the gregariousness nature of camels (Monaco, Padalino, & Lacalandra, 2015) and the emerging socioeconomic interests in this species' productive exploitation (Zarrin et al., 2020), it is imperative to be conscious of animal-dependent traits that differentially contribute to the establishment of intraherd social rank and how these can be used to make handling easier through individual selection. The immediate need for this approach is justified on account of the practice of sex-separated breeding for some local camel breeds (i.e., Canarian camels) for utilitarian purposes attending to sex-biased morphostructural preferences (Schulz, 2008).

In the present research, we aimed to evaluate the relative importance of sociodemographic, zoometric and phaneroptical characteristics in determining the intraherd leader- ship role in Canarian camels. The deeper the knowledge on the occurrence and dynamics of leadership in camels, the better livestock management practices can be adjusted for animal welfare promotion and the maintenance of handlers' self-security. More specifically, apropos of Canarian camel breeding strategies, leader males and females might be easily recognized so as to incite the joining of mates when forming and guiding caravans for tourism or at the entrance in the milking parlor.

Material and methods

Study sample

The study was conducted at the worldwide largest reserve of Canarian camels in Fuerteventura, Canary Islands (28°25′57″ N–14°00′11″ W). The farming environment consisted of square-shaped fenced pens with a shelter providing a shaded area in the middle of the facility and both the feeding and drinking points located along one of the lateral sides.

Four Canarian camel herds were evaluated; the study subjects were all members of these herds. All individuals were recognized by natural markings such moles, scars and fur color patterns. Additionally, the animals were identified with delible numbers placed on the subjects by an operator.

Camel herds were stable (no change, neither introduction nor removal, of any member had been effected prior to the study) and thus selected because intraherd dominance and hierarchy had already been defined and established. Herd structure was as follows: herd one comprised 21 she-camels; herd two, 29 she-camels; herd three, 26 male-camels (20 gelded, 6 entire); and herd four, 24 male-camels (21 gelded, 3 entire). As a result, a total of one hundred Canarian camels (50 cows and 50 male-camels (41 gelded, 9 entire) with average ages (±SD) of 158.36±62.03 months were subjects of the study. The gelded male-camels in the study had been gelded after reaching sexual maturity and after being trained to develop their functional role. Hierarchy within herds was determined following Sueur, Petit and Deneubourg (2009) and Seltmann et al. (2013), who reported that the specific organization of individuals during collective movements may constitute the basis for the mechanisms underlying the emergence of complex systems, even if these are not necessarily complex and can be based on local rules, such as hierarchy in a particular herd, and their determinants, such as activity within the herd (Ward et al., 2013).

A priori definitions and considerations

Provided that the present study has its basis in the determination of motorial selective mimetism, *a priori* definitions are provided to clarify the manner in which concepts were understood and measurements were therefore taken. As suggested by Seltmann et al. (2013), special attention was provided to establishing the conceptual difference between a group movement and any locomotor activity occurring on a daily basis while animals perform their regular activities. In this regard, the following concepts and within-herd roles were predetermined and defined:

(a) <u>Initiator/leader</u>: the individual moves directly towards the corridor, where they are restrained for veterinary and other official control activities or duties, and crosses it to a contiguous fenced pen without pausing for more than two seconds. To be considered as an initiation movement, at least two more individuals have to be positioned directly at the entrance of the corridor and just behind the animal crossing it. Three animals are the maximum that can fit, in single file, into the corridor at the same time.

(b) <u>Termination</u>: the initiation movement ends when the initiator totally crosses the corridor, enters the contiguous fenced pen, and stops for at least 3 min.

(c) <u>Followers</u>: those group members crossing the corridor behind the initiator. They have to arrive at the contiguous fenced pen no later than 3 min after the termination of the movement and approach the initiator at a minimum distance of 3 m.

(d) <u>Successful movement</u>: a group movement was considered successful if the initiator had two followers minimum.

Rank determination

Once within-herd roles had been defined, intraherd rank was determined. Camels were ranked in a descending order from one to fifty (higher value in the order), such that the camel ascribed the first position (score of 1) was the leader/initiator, while that ascribed with the fiftieth position was the last animal in the hierarchy. Video sampling was used to investigate the types and underlying mechanisms of decision making before and after an individual initiated a movement (became the leader/initiator). Herd movements were recorded using two cameras by two operators (A and B) (Sony RX100M3, 25 fps), with one observer (A) placed on the front of the corridor, the other (B) at the main congregation point of the group. An auxiliary operator (C) annotated the identity of group members con- ducting predeparture behavior simultaneously (incentive movements or back glances (Sueur, Deneubourg, & Petit, 2011)). Videos recorded lasted for 33.31±32.26 seconds on average (±SD).

An incentive movement was defined as a directed walk of an animal for a distance shorter than an initiation movement that does not result within 2 seconds in feeding, social interactions or lying down.

A back glance was defined as a turn of an individual's head of more than 90°. Back glances during feeding or social interactions were not considered to be relevant for pre-departure behavior and therefore excluded. If the directions of predeparture behaviors formed an angle exceeding 45°, the directions were considered to be different (Sueur, Deneubourg, & Petit, 2010).

Once one individual initiated a group movement, one observer (operator B) focused on the initiator and recorded the identity of the initiator, the time of their departure and the identity of followers. Operator C recorded the exact progression order of the joining individuals and the times of their departures. A joiner was defined as an individual moving at an angle of less than 45° to the initiator's trajectory and crossing an imaginary line situated 4 m (a third of the minimum distance one individual had to move to initiate a group movement) behind the initiator's start point within 10 min. If the initiator started in the center of the group and individuals ahead of it walked at least 6 m at an angle of less than 45° to the initiator's trajectory, they were counted as joiners as well. When the initiator returned to the group, the observation was cancelled.

No disruption of the progression order occurred, as the area in which the experiment was conducted was isolated from external influences apart from the animals and the operators conducting the experiment.

Information about dominance relations between individuals was acquired via *ad libitum* recording of agonistic behavior following the premises described in literature (Bhakat & Chaturvedi, 2004; Bhakat, Chaturvedi, & Sahani, 2004; Mohammed, Mohamed, & Osman, 2020).

No conflict was recorded, as herds had already been conformed prior to the experiments, structure was solid, and herd structure was not distorted, as no new animals were either included or extracted. Although animals were relocated for the experiment, whole herds were relocated to the same testing area at the same time, as literature has suggested (Prins, 1989) that there appears to be little effect of location on animals that are habituated to perform transhumant movements. In this regard, our study considered the findings by authors such as Schulte and Klingel (1991), who found that no stable leadership in camels was observed, although individual preferences in the walking order existed when the camels left and entered the enclosure.

Statistical analysis

Prior assumption testing

The Shapiro–Francia W′ test (for $50 < n < 2500$ samples) and Levene's test were used to discard gross violations of parametric assumptions (normality and homoscedasticity). The Shapiro–Francia W′ test was performed using the Shapiro–Francia normality routine of the test and distribution graphics package of the Stata Version 16.0 software. Homoscedasticity was tested using Levene's test with the explore procedure of the descriptive statistics package in SPSS Statistics (Version 25.0, IBM Corp., Armonk, NY, USA) (Corp., 2017).

The chi-square (X^2) test of independence was used to determine the inclusion of variables in the model and to test the probability of the chi-square test on the log ratio, which is equivalent to the Fisher's F test (Yoo et al., 2017), which in turn would test whether every individual had the same probability to be in the analyses. The purpose of the ordinal logistic regression model designed for the present study was to assess conditioning variables that were proximately associated with camel intraherd hierarchy. The variables for which a statistically significant association with camel intraherd hierarchy at a 5% significance level ($p < 0.05$) were used for further analysis using the ordinal logistic regression model.

Ordinal logistic regression

Ordinal logistic regression was used to fit the below statistical model, which describes how the chance of an animal being placed at a specific position within the hierarchy (intraherd hierarchy status) established in camel herds depended on a number of covariates or predictors. We defined Y as an ordinal outcome with J categories. Thus, we modelled the cumulative probability of responding to a level smaller or equal to j with the probability $P(Y \leq j)$ for j from 1 to the number of categories of Y. The analytical expression of the model is as follows:

$$logit(P(Y \leq j)) = \beta_{j0} + \beta_{j1}x_1 + \cdots + \beta_{jp}x_p$$

for $j = 1,\ldots, J - 1$ and p predictors. Because the parallel lines' assumption, the intercepts were different for each category, but the slopes were constant across categories.

The knowledge of the distribution of intraherd hierarchy status yielded the likelihood of the sample. To estimate the β parameters of the model (the coefficients of the linear function), the likelihood function was maximized. As opposed to linear regression, an exact analytical solution does not exist; hence, an iterative algorithm had to be applied.

Maximization of the likelihood function was performed using the Newton–Raphson algorithm with 100 iterations and a convergence level of 0.000001, which are given as default by XLSTAT Version 2014.5.03 (Addinsoft, 2014).

The set of independent covariates and categorical predictors consisted of four blocks: biometrics, phaneroptics, age and sex/sexual status. The first block comprised the variables of height at withers (HW, cm), chest girth (CG, cm), hump girth (HG, cm) and body weight (kg); the second block comprised the variables of coat color, coat particularities (delimited white-haired zones) and eye color; the third block represented the age of the animal and the fourth block comprised the variables of sex and neutering status.

Variables in the first block were chosen because of the implications of overall body condition (Iglesias et al., 2020) and body size on the determination of camel intraherd hierarchy (Alhajeri et al., 2021; Norbert & Hans, 1991). The second block was considered because of the implication of phaneroptics with behavioral traits (Volpato, Dioli, & Di Nardo, 2017). The third and fourth blocks were included as well, as the variables measured therein have often been reported to be either determinants or confounding in the determination of camel hierarchy status in camels and other species (El Wathig & Faye, 2013; Horová, Brandlová, & Gloneková, 2015; Ishag, Eisa, & Ahmed, 2011; Schulte & Klingel, 1991).

Results

Prior assumption testing

A gross violation of normality assumption occurred in all variables ($p < 0.05$). Homoscedasticity was violated as well ($p < 0.01$); hence, a nonparametric approach was applied.

Ordinal logistic regression model

Model quality

Afterwards, we determined whether the set of variables evaluated in this study may have significantly conditioned (i.e., have been responsible for) intraherd hierarchy status (position of the animals in the hierarchic ranking) by comparing the model as it was defined with a simpler model with only one intercept. In this case, as the probability of these variables modelling for intraherd hierarchy status was lower than 0.001 (Tables 1 and 2), the variables chosen were concluded to statistically significantly condition and model for intraherd hierarchy status.

Table 1. Test of the null hypothesis H0: Y = 0 (variable: intraherd hierarchy status).

Statistic	DF	Chi-Square	Pr > Chi^2
-2Log(Likelihood)	19	39.753	0.004
Score	19	41.264	0.002
Wald	19	35.518	0.012

Table 2. Goodness of fit statistics for intraherd hierarchy status model.

Statistic	Full Model
Observations	100
Sum of weights	100
Df	32
-2Log(Likelihood)	720.675
R^2 (McFadden)	0.052
R^2 (Cox and Snell)	0.328
R^2 (Nagelkerke)	0.328
AIC	856.675
SBC/BIC	857.173
Iterations	6

Df: degrees of freedom; AIC: Akaike's Information Criterion; SBC/BIC: Schwarz's Bayesian Criterion/Bayesian Information Criterion.

Table 2 provides several indicators of the quality of the model (or goodness of fit). These results were equivalent to the R^2 and to the analysis of variance table in linear regression and ANOVA. The most important value was the probability of the chi-square test on the log ratio. This is equivalent to the Fisher's F test, and it is used to evaluate whether the variables bring significant information by comparing the model as it is defined with a simpler model with only one constant. In this case, as the probability was lower than 0.0001 (Table 1), we could conclude that data could be significantly modelled by the set of variables chosen.

Parameter analysis

Table 3 provides details on the model and presents a measure of the effect of the variables considered on the categories of the response variable. There is one intercept for each category of the response variable and one set of coefficients, since the parallel curves hypothesis is supposed to be met.

When the regression coefficient for a specific category within a variable was equal to 0.000, this meant that said category was taken as the reference to measure the higher or lower repercussions of the subsequent categories in the same variable. The standardized regression coefficient measured the times that a certain level or category

Table 3. Standardized regression coefficients for the factors and covariates considered in the model for the intraherd hierarchy status.

Source	Hierarchy categories	Standardized Regression coeficient (β)	Standard Error	Wald Chi-Square	Pr > Wald X^2	Wald Lower bound (95%)	Wald Upper bound (95%)
Intercept	1	63.212	44.324	2.034	0.154	-23.662	150.087
	2	62.437	44.313	1.985	0.159	-24.415	149.289
	3	61.965	44.306	1.956	0.162	-24.873	148.802
	4	61.613	44.300	1.934	0.164	-25.213	148.440
	5	61.325	44.295	1.917	0.166	-25.491	148.142
	6	61.072	44.290	1.901	0.168	-25.734	147.878
	7	60.848	44.285	1.888	0.169	-25.949	147.645
	8	60.650	44.283	1.876	0.171	-26.142	147.442
	9	60.466	44.282	1.865	0.172	-26.325	147.257
	10	60.287	44.281	1.854	0.173	-26.502	147.076
	11	60.110	44.278	1.843	0.175	-26.674	146.894
	12	59.939	44.275	1.833	0.176	-26.839	146.717
	13	59.773	44.273	1.823	0.177	-27.001	146.546
	14	59.608	44.271	1.813	0.178	-27.161	146.377
	15	59.443	44.269	1.803	0.179	-27.322	146.208
	16	59.277	44.268	1.793	0.181	-27.487	146.042
	17	59.114	44.268	1.783	0.182	-27.651	145.878
	18	58.949	44.267	1.773	0.183	-27.813	145.711
	19	58.785	44.265	1.764	0.184	-27.973	145.543
	20	58.619	44.264	1.754	0.185	-28.136	145.374
	21	58.445	44.262	1.744	0.187	-28.308	145.198
	22	58.326	44.261	1.737	0.188	-28.424	145.077
	23	58.206	44.260	1.729	0.188	-28.542	144.955
	24	58.085	44.259	1.722	0.189	-28.662	144.831
	25	57.959	44.258	1.715	0.190	-28.786	144.703
	26	57.828	44.256	1.707	0.191	-28.913	144.569
	27	57.689	44.254	1.699	0.192	-29.048	144.425
	28	57.539	44.251	1.691	0.194	-29.191	144.270
	29	57.379	44.248	1.682	0.195	-29.345	144.102
	30	57.295	44.246	1.677	0.195	-29.425	144.015
	31	57.211	44.245	1.672	0.196	-29.508	143.931
	32	57.129	44.246	1.667	0.197	-29.592	143.849
	33	57.046	44.247	1.662	0.197	-29.678	143.769
	34	56.961	44.248	1.657	0.198	-29.764	143.686
	35	56.871	44.250	1.652	0.199	-29.856	143.599
	36	56.778	44.251	1.646	0.199	-29.952	143.509
	37	56.680	44.253	1.641	0.200	-30.053	143.414
	38	56.577	44.254	1.634	0.201	-30.160	143.313
	39	56.467	44.256	1.628	0.202	-30.273	143.207
	40	56.348	44.257	1.621	0.203	-30.394	143.090
	41	56.218	44.258	1.614	0.204	-30.525	142.961
	42	56.075	44.258	1.605	0.205	-30.669	142.819

Table 3. *Cont.*

Source	Hierarchy categories	Standardized Regression coeficient (β)	Standard Error	Wald Chi-Square	Pr > Wald X^2	Wald Lower bound (95%)	Wald Upper bound (95%)
Intercept	43	55.915	44.258	1.596	0.206	-30.829	142.659
	44	55.740	44.258	1.586	0.208	-31.003	142.483
	45	55.545	44.257	1.575	0.209	-31.198	142.288
	46	55.313	44.258	1.562	0.211	-31.430	142.057
	47	55.015	44.258	1.545	0.214	-31.729	141.759
	48	54.597	44.260	1.522	0.217	-32.151	141.344
	49	53.893	44.266	1.482	0.223	-32.867	140.652
Animal inherent	HW (cm)	-0.050	0.016	9.452	0.002	-0.082	-0.018
	CG (cm)	-0.016	0.010	2.646	0.104	-0.035	0.003
	HG (cm)	-0.015	0.005	8.186	0.004	-0.026	-0.005
	Weight (kg)	0.001	0.000	8.087	0.004	0.000	0.002
	Age (months)	0.000	0.000	8.976	0.003	0.000	0.000
Sex	Female	0.000	0.000				
	Male	1.233	1.675	0.542	0.462	-2.050	4.517
Coat colour	Roan	0.000	0.000				
	Chestnut	3.396	1.729	3.858	0.050	0.007	6.785
	Bay	6.261	2.545	6.052	0.014	1.273	11.249
	Cinnamon	5.820	1.948	8.922	0.003	2.001	9.639
	Blonde	4.315	2.869	2.263	0.132	-1.307	9.938
	Black	8.267	11.400	0.526	0.468	-14.076	30.610
	White	-0.415	15.652	0.001	0.979	-31.094	30.263
Coat particularities (delimited white-haired zones)	All over	0.000	0.000				
	Extremities	2.012	2.226	0.817	0.366	-2.351	6.375
	Extremities, head and neck	3.635	1.692	4.616	0.032	0.319	6.951
	Solid colour (no white)	2.125	2.231	0.907	0.341	-2.248	6.497
	Head and neck	12.766	7.532	2.873	0.090	-1.996	27.529
Eye colour	Brown	0.000	0.000				
	Blue	6.669	2.936	5.159	0.023	0.914	12.423
	Brownish with blue spots	2.158	13.531	0.025	0.873	-24.363	28.678
Sex status	Whole	0.000	0.000				
	Gelded	5.938	1.883	9.948	0.002	2.248	9.627

had a higher (positive standardized coefficient) or lower (negative standardized coefficient) repercussion.

The interpretation of parameters was not immediate. Based on the results in Table 3, it was concluded that the model equation for each position n in the intraherd hierarchy status was as follows:

Log(P(Order ≤ n)/P(Response > n) = 0.050 x HW (cm) - 0.016 x CG (cm) - 0.015 x HG (cm) + 0.001 x Weight (kg) - 0.000 x Age (months) + 3.396 x Chestnut + 6.261 x Bay + 5.820 x Cinnamon + 3.635 x White marks in Extremities, head and neck + 0.669 x Blue Eyes + 5.938 x Gelded.

On this table, we can see from the probability of the chi-squares that the variable most influencing intraherd hierarchy status was whether the animal was gelded or not. The intercept was not significant, but being taller (higher height at withers) and heavier (larger weight), as well as having smaller chests (shorter chest girth) and humps (shorter hump girth), significantly conditioned the animals reaching higher positions in the intraherd hierarchy rank. Age had a very low negative, significant repercussion on intraherd hierarchy status, which means that as an animal grows old, its position in the rank may slightly significantly decrease. Animals with darker coats, such as bay, cinnamon and chestnut; those with white-haired zones in their extremities, head and neck and those with blue eyes were also significantly more prone to reach higher positions in the rank.

Discussion

According to Cesarani and Pulina (2021), genetic selection–domestication induces changes in the behavioral patterns of some farm animals compared to those of their wild ancestors. In this context, hierarchy definition within a herd may be one such behavioral trait, as humans may have reconfigured wild herd structures to make the animals live in artificial groups that may not always resemble those in the wild. The same authors stated that this behavioral domestication process should be considered when planning and implementing farm animal welfare standards at the farm level.

Under the premise of camels being gregarious animals that compulsorily require social behavior expression to ensure their well-being (Schulte & Klingel, 1991), several factors are expected to influence or modulate the establishment and potential temporary modifications of the social structuration within a group of coinhabiting individuals; that is, to influence the trend of eliciting the joining of others when accomplishing a task by providing direction and motivation (leaders) and the relative disposition to associate with one's fellows (submissives).

The moderate R^2 values obtained (32.8%) may denote that the amplitude of the set of predictive factors involved in the establishment of herd hierarchy may indeed be wider and quite diverse in nature. However, even if other factors that were not registered in this research may condition this type of social hierarchical behavior (leader–follower hierarchy), the variables considered in the analyses explain almost one-third of the variability in intraherd hierarchical status in camels.

Age-influenced and sexual status-mediated effects

A slight negative relationship between age (in months) and hierarchy rank position in camels was shown (unstandardized regression coefficient β of -0.007, $p < 0.05$), which was annulled once regression coefficients were standardized. In a previous study with domestic horses, Houpt, Law, and Martinisi (1978) reached similar conclusions, as age appeared to influence neither agonistic behavior nor social structure within the herd. For companion dogs, Pal, Ghosh, and Roy (1998) reported that within-group hierarchy was also not correlated to age. In general terms, age seems not to be a major influencing factor for group hierarchy in domestic animals, although it may be linked to other cognitive features or processes that may make handling easier or more effective, such as cognitive bias (Kilgour, 2019; Navas González et al., 2020). In this regard, age could be related to certain aptitudes or behaviors derived from the cognitive development and social needs of the animals (Rodenburg & Turner, 2012), similarly as in humans (Spisak et al., 2014). Additionally, it can be assumed that both the greater physical vigor and stamina levels and the lower fearfulness associated with younger age in gregarious animal species make younger animals more likely to be endorsed as leaders.

Exploratory activities and other energetic tasks are more frequent at an early age and help in developing skills that involve the use of information independent of acquired knowledge and the demonstration of creativity to solve problems in novel situations ('fluid intelligence') (Horn & Cattell, 1967). Furthermore, the need to relate with others is greater in younger individuals, which makes them engage in more relationship-oriented activities than older congeners (Gilbert, Collins, & Brenner, 1990), which in turn increases the individual probability of being followed by congeners depending on the social status. Empirical examples in various animal species demonstrate such increased prevalence of high-energy behaviors in younger compared to older subjects (Lee & Moss, 2012; Lilley, Kuczaj, & Yeater, 2017).

This has also been reported for free-living animal species and humans, as several researchers (Bourjade et al., 2015; McComb et al., 2011; Packard, 2010) have suggested that an increase in age is associated with a greater accumulation of knowledge or experiences that help group decision making and survival. In a closely related phenomenon, herd size has been observed to be generally larger in animals living in open habitats such as savannas and pastures, as better territorial and in-group defensive behavior is thereby enabled (Thaker et al., 2010).

A general explanation for this differential influence of age in leadership hierarchy could rely on the basis that animals in domestic scenarios do not need to engage in alert reactions towards external threats, since they are reared in relatively highly controlled environments. In this context, group size may not be important for survival reasons, but it may be important for animal welfare issues arising from confined housing (Morgan & Tromborg, 2007). This reinforces the hypothesis that age may not be of critical importance from the point of view of knowledge accumulation, because it is assumed that all animals in the same herd are exposed to the same stimuli and that the age range within each group is always kept as homogeneous as possible for ease of animal handling and technical efficiency for caregivers. More than sex, the sexual status of the animals was reported to influence intraherd hierarchy position. The maturation and possible temporary or permanent functional alterations of the endocrine system plays a fundamental role in the modulation of animal behavior and could, together with age and cognitive development, explain the results discussed so far alongside the implications of castration and the time of its performance on animal temperament. According to our results, gelded animals were more likely to lead group movements or collective activities. The maintenance of adequate levels of serotonin trough the active interaction with the environment (curiosity) strengthens the antagonistic potential of this neurotransmitter on the effects of sex hormones at the central level (prefrontal cortex and subcortical structures) (Batrinos, 2012). Consequently, agonistic behaviors such as aggression or sexual-related behaviors are reduced (Giammanco et al., 2005; Siegel & Douard, 2011). According to the common practice of castration in this breed, the animals are castrated once they have been initiated in the domestication protocol for their functional aptitude and have reached their sexual maturity, having reached sufficient serum levels of sex hormones to ensure proper general organic maturity (brain structures, among others) but not a harmful level from an ethological perspective (Oliveira, 2009). Such conditions may arise as age progresses, and therefore, not gelded animals are more territorial, their social circles are more restricted and the frequency of their social interaction is minimized. Furthermore, the older an animal is when castration is performed, the lower the probability is of unwanted behaviors associated with the intrinsic activity of sex hormones disappearing, because these behaviors already constitute fixed patterns in the behavioral repertoire of the individual (Hume & Wynne-Edwards, 2005).

Additionally, the castration of camels has been shown to have a great impact on body development in this species, which constitutes a further criterion of functional interest complementary to behavioral traits in working animals. Specifically, some authors (Faye, 1997; Williamson & Payne, 1978) have discussed the advantages of castration, if carried out after the animal is sexually mature, in camels relegated to working activities. These animals were found to be larger, more robust (Pigière &

Henrotay, 2012) and more enduring (Ucko & Dimbleby, 2007) under the effect of postneutering benefits in the performance of working animals. In this context, Wilson (1990) also added that, in the case of males, castration promoted a greater development of the soft palate. This anatomical structure, when voluntarily protruded outwards, could play an important role in the definition of individual social status at the intraherd level or when displaying defense against invasion by foreigners.

Leadership inference from physical external appearance

A direct connection can be drawn between the practical framework set out in the preceding paragraph and the small positive influence of body weight and the probability of becoming a leader that was revealed in our data. This finding adds more evidence to the existing literature of the zoometric variables that influence the leadership hierarchy of camels and that are in turn influenced by management practices. In this regard, more than large animals (tall, with a wide chest and big hump), which balance to negative regression coefficients, heavier animals may play a determinant role in leadership and hierarchy definition. An empirical association has been described between body weight and sexual status (neutered or non-neutered) for housed domestic horses (Montgomery, 1957), outdoor-living domestic horses (Giles et al., 2015) and female chamois (Locati & Lovari, 1991). Hence, it can be concluded that not only the individual genetic background (and other factors such as diet) but castration may have a positive influence on body development. As long as castration is practiced properly, positive impacts on the degree of organic development and integral functional performing (physical resistance and behavior) of camels could arise. By applying this rationale to management programs, the efficiency of handling practices can be substantially improved. This may translate into tangible benefits for both staff and animals as well as consumers participating in interactive activities with the animals (e.g., camelback riding tours).

By contrast, the aforementioned negative regression coefficient for the variables of HW, CG and HG (and age before standardization) may indeed be determinant for the individual probability of leading collective actions. This finding may be of valuable help at the time of designing facilities and defining herd management protocols. For instance, it may aid in constructing proper dimensions for the entrance circuits to the milking parlors for females and in deciding which females would be the best candidates to lead the group at these emplacements. When handling males, camel herders would be able to select animals that are preferred to lead the caravans in order to prevent disruptions due to fearfulness or mistrustfulness if they encounter obstacles along the routes.

Coat and eye color genetics may reflect camel temperament

A wealth of information can be found in the scientific literature on the pleiotropic effects of the genes responsible for phaneroptical characters such as coat and eye color on the development and function of neural structures (Bellone, 2010; Brunberg et al., 2013; Ducrest, Keller, & Roulin, 2008). In this context, temperament features such as calmness and nervousness were reported to be quantitatively differentiated on the basis of coat color among individuals of the same species (Keeler, 1942; Pérez-Guisado, Lopez-Rodríguez, & Muñoz-Serrano, 2006; Podberscek & Serpell, 1996; Trut, 1999) and thus further drive the selection criteria for breeding purposes.

For example, Finn et al. (2016) found that chestnut horses were more likely to approach novel objects and animals. This finding may evidence a direct consequence of domestication and bias selection towards boldness, since the bay phenotype was more prevalent prior to the species's domestication. Parallelly, horses with the Silver mutation Arg618Cys in the PMEL gene were more cautious when being presented novel stimuli or approaching novel objects (Brunberg et al., 2013). Applied research in domestic dogs showed that individuals presenting white coat color were more fearful and displayed more submissive reactions (Kim et al., 2010). In mountain sheep (Loehr et al., 2008) and lions (West & Packer, 2002), social rank was higher as coat darkened.

For the particular case of camels, Almathen et al. (2018) found a significant association between the polymorphisms in the MC1R and ASIP genes and variability in coat color in this species. However, these authors did not refer to associated behavioral changes, although it was assumed that they existed, following the conclusions found for other species. Globally, applied research in this field has suggested that the magnitude of the aforementioned pleiotropic effects appears to be greater in dark-colored animals (Finch, Bennett, & Holmes, 1984) and that light- and particolored animals also frequently suffer from congenital deafness (Volpato, Dioli, & Di Nardo, 2017) and ocular anomalies (Brunberg et al., 2013; Komáromy et al., 2011; Schonthaler et al., 2005) due to gene mutations in KIT (Holl et al., 2017), which affect training.

It is important to highlight the common perception of camel herders that animals with a variable proportion of white fur (piebaldness) are the least aggressive but also the most fearful and submissive (Launois, Faye, & Kriska, 2002), which impairs their individual ability to lead collective actions. The same conclusion has been reached in dogs (Amat et al., 2009; Pérez-Guisado et al., 2006) and foxes (Trut, Plyusnina, & Oskina, 2004) in domestic settings.

The extension and distribution of white spots conditions the degree of deafness and visual deficit. Both impairments have been reported to be associated to certain predominant behavioral patterns (Volpato, Dioli, & Di Nardo, 2017). This has been specifically dealt with in other species such as cows. In this regard, Grandin and

Deesing (1998) reported the level of depigmentation to be a strong driving agent of the dimension of impairments and consequently of the associated behavioral patterns. For instance, Holstein cows with complete depigmented white areas on their heads are among the calmest, while those that are mostly white on the body are nervous and intractable, which was supported by our study, as camels presenting white spots on their extremities, head and neck significantly scored relatively lower in the hierarchical rank.

This depigmentation throughout the body has also relatively frequently been reported to be associated with iris depigmentation and heterochromia in camels mainly reared across northwestern African countries and the Canary Islands (Volpato, Dioli, & Di Nardo, 2017). Our results suggested that blue eyed animals scored relatively lower in hierarchic rank. As it occurs in depigmented coated animals, eye color has been related to differences in reactivity to external stimuli ('eye color–reactivity hypothesis'), whether such stimuli are familiar or not. Pastoralists often regard piebald camels as reckless, stubborn and disobedient or particularly tame, even numb. Indeed, several authors have agreed that subjects with darker eyes tend to display greater reactive skills (Navas González et al., 2018) and a superior speed of locomotion (Wilhelmy et al., 2016; Worthy, 1999). In this context, Sahrawi herders describe piebald camels as having different levels of deafness, with increased deafness linked to the presence of blue eyes and white coloring of the head and toes. However, others, such as bold pie camels (black ears and nails) have normal hearing (Monteil, 1952).

Authors such as Volpato, Dioli, and Di Nardo (2017) transcribed the widespread knowledge among Sahrawi and Tuareg herders, who related complete deafness to calm behavior while contrastingly ascribing partial deafness conditions to increasingly agitated camels with unpredictable reactions (stubborn, disobedient and reluctant to understand orders). Additionally, these authors reported piebald animals to achieve a quieter and tamer secondary position in status within the herd (Migeon, 2006). According to Volpato, Dioli, and Di Nardo (2017), the basis for these animals being ranked at relatively lower positions in the intraherd hierarchy lay upon their bad night eyesight and their increased likelihood to get lost when light is low, which translated into some piebald male-camels' lower ability to manage the herd.

Conclusions

Although intraherd hierarchy may indeed be driven by a wide and diverse set of etiological factors, phaneroptics and zoometry may play a remarkable role. More than age, the sexual status of the animal (entire or castrated) influenced intraherd hierarchy position as the maturation and possible temporary or permanent functional alterations of the endocrine system play a fundamental role in the modulation of animal behavior and brain development in this species. More than large animals (tall, with a wide chest and big hump), heavier individuals may play a determinant role in leadership and hierarchy definition. Dark-coated camels scored higher in the hierarchical rank than those presenting light coats or larger extensions of white all over the body (extremities, head and neck). The basis for these animals being ranked at lower positions in the intraherd hierarchy may lie in visual and acoustic impairments, which make them prone to develop a limited ability to manage the herd. The information obtained in this study is helpful for routine intraherd management and for the genetic management of herds with the aim to define and preselect potential leaders, which is of prominent importance for the touristic application of the representatives of this breed.

Author contributions: Conceptualization, C.I.P., F.J.N.G. and J.V.D.B.; Data curation, C.I.P. and F.J.N.G.; formal analysis, F.J.N.G.; investigation, C.I.P., F.J.N.G. and A.A.A.; methodology, C.I.P., F.J.N.G. and A.A.A.; project administration, J.V.D.B.; resources, E.C. and J.V.D.B.; software, F.J.N.G.; supervision, F.J.N.G., E.C. and J.V.D.B.; validation, F.J.N.G. and E.C.; visualization, E.C. and J.V.D.B.; writing—original draft, C.I.P. and F.J.N.G.; writing—review and editing, C.I.P., F.J.N.G.; E.C., A.A.A. and J.V.D.B. All authors have read and agreed to the published version of the manuscript.

Funding: The present research was carried out in the financing framework of the international project CA.RA.VA.N—'Toward a Camel Transnational Value Chain' (Reference APCIN-2016-00011-00-00) and during the covering period of a predoctoral contract (FPU Fellowship) funded by the Spanish Ministry of Science and Innovation.

Institutional Review Board statement: The ethics review board of the University of Córdoba considered that this type of project did not fall under legislation for the protection of animals used for scientific purposes, national decree-law 113/2013 (2010-63-EU directive). Animals were not sacrificed because the data were collected during the application of regular zootechnical procedures at the farms where the animals are housed. This work was in keeping with directive 2010/63/EU of the European Parliament and of the Council of 22 September 2010 on the protection of animals used for scientific purposes and Royal Decree 53/2013, of 1 February, which establishes the basic rules applicable to the protection of animals used in experimentation and other scientific purposes, including teaching.

Data availability statement: The data presented in this study are available on request from the first author.

Acknowledgments: Thanks to the staff at Oasis Park in Fuerteventura for their attention and support.

Conflicts of interest: Authors declare no conflict of interest. The founding sponsors had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, and in the decision to publish the results.

References

Addinsoft, S. (2018). *XLSTAT software, versión 2018.5*. Addinsoft, Paris, France: Addinsoft.

Ákos, Z., Beck, R., Nagy, M., Vicsek, T., & Kubinyi, E. (2014). Leadership and path characteristics during walks are linked to dominance order and individual traits in dogs. *PLOS Computational Biology*, 10(1), e1003446.

Al-Obaidi, A. T. S., & Abdullah, H. S. (2017). Camel herds algorithm: A new swarm intelligent algorithm to solve optimization problems. *International Journal on Perceptive and Cognitive Computing*, 3(1).

Alhajeri, B. H., Alhaddad, H., Alaqeely, R., Alaskar, H., Dashti, Z., & Maraqa, T. (2021). Camel breed morphometrics: current methods and possibilities. *Transactions of the Royal Society of South Australia*, 145(1), 90-111.

Almathen, F., Elbir, H., Bahbahani, H., Mwacharo, J., & Hanotte, O. (2018). Polymorphisms in MC1R and ASIP genes are associated with coat color variation in the arabian camel. *Journal of Heredity*, 109(6), 700-706.

Amat, M., Manteca, X., Mariotti, V. M., de la Torre, J. L. R., & Fatjó, J. (2009). Aggressive behavior in the English cocker spaniel. *Journal of Veterinary Behavior*, 4(3), 111-117.

Batrinos, M. L. (2012). Testosterone and aggressive behavior in man. *International journal of endocrinology and metabolism*, 10(3), 563.

Bellone, R. (2010). Pleiotropic effects of pigmentation genes in horses. *Animal genetics*, 41, 100-110.

Berry, P. S., & Bercovitch, F. B. (2015). Leadership of herd progressions in the Thornicroft's giraffe of Zambia. *African Journal of Ecology*, 53(2), 175-182.

Bhakat, C., & Chaturvedi, D. (2004). Studies on behavioural pattern of adult camel in different systems of management. *Journal of Dairying Foods & Home Sciences*, 23, 192-196.

Bhakat, C., Chaturvedi, D., & Sahani, M. (2004). Studies on behavioural pattern of camel calf in different systems of management. *Journal of Eco-Physiology*, 7(1-2), 17-22.

Blackshaw, J. K., Thomas, F. J., & Blackshaw, A. (1994). The relationship of dominance, forced and voluntary leadership and growth rate in weaned pigs. *Applied Animal Behaviour Science*, 41(3-4), 263-268.

Bourjade, M., Thierry, B., Hausberger, M., & Petit, O. (2015). Is leadership a reliable concept in animals? An empirical study in the horse. *PloS one*, 10(5), e0126344.

Brunberg, E., Gille, S., Mikko, S., Lindgren, G., & Keeling, L. J. (2013). Icelandic horses with the Silver coat colour show altered behaviour in a fear reaction test. *Applied Animal Behaviour Science*, 146(1-4), 72-78.

Butt, B., Shortridge, A., & WinklerPrins, A. M. (2009). Pastoral herd management, drought coping strategies, and cattle mobility in southern Kenya. *Annals of the Association of American Geographers*, 99(2), 309-334.

Corp., I. (2017). *IBM SPSS Statistics for Windows (Version 25.0)*. Armonk, NY: IBM Corp.

Ducrest, A.-L., Keller, L., & Roulin, A. (2008). Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends in Ecology & Evolution*, 23(9), 502-510.

El Wathig, M., & Faye, B. (2013). Surveillance of camel trypanosomosis in Al-Jouf región, Saudi Arabia. *Camel: An International Journal of Veterinary Sciences*, 1(1), 65.

Escós, J., Alados, C., & Boza, J. (1993). Leadership in a domestic goat herd. *Applied Animal Behaviour Science*, 38(1), 41-47.

Faye, B. (1997). *Guide de l'élevage du dromadaire*: Sanofi.

Feist, J. D., & McCullough, D. R. (1976). Behavior patterns and communication in feral horses. *Zeitschrift für Tierpsychologie*, 41(4), 337-371.

Finch, V. A., Bennett, I., & Holmes, C. (1984). Coat colour in cattle: effect on thermal balance, behaviour and growth, and relationship with coat type. *The Journal of Agricultural Science*, 102(1), 141-147.

Finn, J. L., Haase, B., Willet, C. E., van Rooy, D., Chew, T., Wade, C. M., Hamilton, N.A., & Velie, B. D. (2016). The relationship between coat colour phenotype and equine behaviour: A pilot study. *Applied Animal Behaviour Science*, 174, 66-69.

Fischhoff, I. R., Sundaresan, S. R., Cordingley, J., Larkin, H. M., Sellier, M.-J., & Rubenstein, D. I. (2007). Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii*. *Animal behaviour*, 73(5), 825-831.

Giammanco, M., Tabacchi, G., Giammanco, S., Di Majo, D., & La Guardia, M. (2005). Testosterone and aggressiveness. *Medical science monitor*, 11(4).

Gilbert, G. R., Collins, R. W., & Brenner, R. (1990). Age and leadership effectiveness: From the perceptions of the follower. *Human Resource Management*, 29(2), 187-196.

Giles, S. L., Nicol, C. J., Harris, P. A., & Rands, S. A. (2015). Dominance rank is associated with body condition in outdoor-living domestic horses (*Equus caballus*). *Applied Animal Behaviour Science*, 166, 71-79.

Grandin, T., & Deesing, M. J. (1998). Genetics and Animal Welfare. In *Genetics and the behavior of domestic animals*: Academic Press.

Holl, H., Isaza, R., Mohamoud, Y., Ahmed, A., Almathen, F., Youcef, C., Gaouar, S., Antczak. D.F., & Brooks, S. (2017). A frameshift mutation in KIT is associated with white spotting in the Arabian camel. *Genes*, 8(3), 102.

Horn, J. L., & Cattell, R. B. (1967). Age differences in fluid and crystallized intelligence. *Acta psychologica*, 26, 107-129.

Horová, E., Brandlová, K., & Gloneková, M. (2015). The first description of dominance hierarchy in captive giraffe: not loose and egalitarian, but clear and linear. *PloS one*, 10(5), e0124570.

Houpt, K. A., Law, K., & Martinisi, V. (1978). Dominance hierarchies in domestic horses. *Applied Animal Ethology*, 4(3), 273-283.

Hume, J. M., & Wynne-Edwards, K. E. (2005). Castration reduces male testosterone, estradiol, and territorial aggression, but not paternal behavior in biparental dwarf hamsters (*Phodopus campbelli*). *Hormones and behavior*, 48(3), 303-310.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S., & Bermejo, J. V. (2020c). Zoometric characterization and body condition score in Canarian camel breed. *Archivos de zootecnia*, 69(265), 14-21.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Barba Capote, C. J., & Delgado Bermejo, J. V. (2020). Effect of research impact on emerging camel husbandry, welfare and social-related awareness. *Animals*, 10(5), 780.

Ihl, C., & Bowyer, R. T. (2011). Leadership in mixed-sex groups of muskoxen during the snow-free season. *Journal of Mammalogy*, 92(4), 819-827.

Ishag, I., Eisa, M. O., & Ahmed, M. (2011). Effect of breed, sex and age on body measurements of Sudanese camels (*Camelus dromedarius*). *Australian Journal of Basic and Applied Sciences*, 5(6), 311-315.

Jacobs, A., Sueur, C., Deneubourg, J. L., & Petit, O. (2011). Social network influences decision making during collective movements in brown lemurs (*Eulemur fulvus fulvus*). *International Journal of Primatology*, 32(3), 721-736.

Keeler, C. E. (1942). The association of the black (non-agouti) gene with behavior: in the Norway rat. *Journal of Heredity*, 33(11), 371-384.

Kilgour, R. (2019). *Livestock behaviour: A practical guide*: CRC Press.

Kim, Y. K., Lee, S. S., Oh, S. I., Kim, J. S., Suh, E. H., Houpt, K. A., Lee, H.C., Lee, H.J., & Yeon, S. C. (2010). Behavioural reactivity of the Korean native Jindo dog varies with coat colour. *Behavioural processes*, 84(2), 568-572.

Klingel, H. (1968). Soziale Organisation und Verhaltensweisen von Hartmann-und Bergzebras (*Equus zebra hartmannae* und *E. z. zebra*). *Zeitschrift für Tierpsychologie*, 25(1), 76-88.

Komáromy, A. M., Rowlan, J. S., La Croix, N. C., & Mangan, B. G. (2011). Equine Multiple Congenital Ocular Anomalies (MCOA) syndrome in PMEL17 (Silver) mutant ponies: five cases. *Veterinary ophthalmology*, 14(5), 313-320.

Krueger, K., Flauger, B., Farmer, K., & Hemelrijk, C. (2014). Movement initiation in groups of feral horses. *Behavioural processes*, 103, 91-101.

Launois, M., Faye, B., & Kriska, M. A. (2002). *Le dromadaire pédagogique*: CIRAD France.

Lee, P. C., & Moss, C. J. (2012). Wild female African elephants (*Loxodonta africana*) exhibit personality traits of leadership and social integration. *Journal of Comparative Psychology*, 126(3), 224.

Lilley, M. K., Kuczaj, S. A., & Yeater, D. B. (2017). Individual differences in nonhuman animals: examining boredom, curiosity, and creativity. In *Personality in nonhuman animals* (pp. 257-275): Springer.

Locati, M., & Lovari, S. (1991). Clues for dominance in female chamois: age, weight, or horn size? Aggressive *Behavior*, 17(1), 11-15.

Loehr, J., Carey, J., Ylönen, H., & Suhonen, J. (2008). Coat darkness is associated with social dominance and mating behaviour in a mountain sheep hybrid lineage. *Animal behaviour*, 76(5), 1545-1553.

McComb, K., Moss, C., Durant, S. M., Baker, L., & Sayialel, S. (2001). Matriarchs as repositories of social knowledge in African elephants. *Science*, 292(5516), 491-494.

McComb, K., Shannon, G., Durant, S. M., Sayialel, K., Slotow, R., Poole, J., & Moss, C. (2011). Leadership in elephants: the adaptive value of age. *Proceedings of the Royal Society B: Biological Sciences*, 278(1722), 3270-3276.

Migeon, C. (2006). Ma vie de chameau. *Magazine Roadbook*, 54–62.

Mohammed, A. A.-A., Mohamed, R. D., & Osman, A. (2020). Effects of stocking density on some behavioral and some blood biochemical parameters in camel during the rut period. *Egyptian Journal of Veterinary Sciences*, 51(2), 253-262.

Monaco, D., Padalino, B., & Lacalandra, G. (2015). Distinctive features of female reproductive physiology and artificial insemination in the dromedary camel species. *Emirates Journal of Food and Agriculture*, 328-337.

Monteil, V. (1952). *Essai sur le chameau au Sahara occidental*: Études mauritaniennes.

Montgomery, G. G. (1957). Some aspects of the sociality of the domestic horse. *Transactions of the Kansas Academy of Science*, 60(4), 419-424.

Morgan, K. N., & Tromborg, C. T. (2007). Sources of stress in captivity. *Applied Animal Behaviour Science*, 102(3-4), 262-302.

Navas González, F. J., Jordana Vidal, J., León Jurado, J. M., Arando Arbulu, A., McLean, A. K., & Delgado Bermejo, J. V. (2018). Genetic parameter and breeding value estimation of donkeys' problem-focused coping styles. *Behavioural processes*, 153, 66-76.

Navas González, F. J., Jordana Vidal, J., León Jurado, J. M., McLean, A. K., & Delgado Bermejo, J. V. (2020). Nonparametric analysis of noncognitive determinants of response type, intensity, mood, and learning in donkeys (*Equus asinus*). *Journal of Veterinary Behavior*, 40, 21-35.

Norbert, S., & Hans, K. (1991). Herd Structure, Leadership, Dominance and Site Attachment of the Camel, Camelus dromedarius. *Behaviour*, 118(1/2), 103-114.

Oliveira, R. F. (2009). Social behavior in context: hormonal modulation of behavioral plasticity and social competence. *Integrative and Comparative Biology*, 49(4), 423-440.

Packard, J. M. (2010). Wolf Behavior: Reproductive, Social, and Intelligent. In *Wolves (pp. 35-65)*: University of Chicago Press.

Pal, S., Ghosh, B., & Roy, S. (1998). Agonistic behaviour of free-ranging dogs (*Canis familiaris*) in relation to season, sex and age. *Applied Animal Behaviour Science*, 59(4), 331-348.

Pérez-Guisado, J., Lopez-Rodríguez, R., & Muñoz-Serrano, A. (2006). Heritability of dominant–aggressive behaviour in English Cocker Spaniels. *Applied Animal Behaviour Science*, 100(3-4), 219-227.

Petit, O., & Bon, R. (2010). Decision-making processes: the case of collective movements. *Behavioural processes*, 84(3), 635-647.

Pigière, F., & Henrotay, D. (2012). Camels in the northern provinces of the Roman Empire. *Journal of Archaeological Science*, 39(5), 1531-1539.

Podberscek, A. L., & Serpell, J. A. (1996). The English Cocker Spaniel: preliminary findings on aggressive behaviour. *Applied Animal Behaviour Science*, 47(1-2), 75-89.

Prins, H. H. T. (1989). Buffalo Herd Structure and its Repercussions for Condition of Individual African Buffalo Cows. *Ethology*, 81(1), 47-71.

Ramos, A., Manizan, L., Rodriguez, E., Kemp, Y. J., & Sueur, C. (2018). How can leadership processes in European bison be used to improve the management of free-roaming herds. *European journal of wildlife research*, 64(2), 1-16.

Ramos, A., Petit, O., Longour, P., Pasquaretta, C., & Sueur, C. (2015). Collective decision making during group movements in European bison, *Bison bonasus*. *Animal behaviour*, 109, 149-160.

Rodenburg, T., & Turner, S. (2012). The role of breeding and genetics in the welfare of farm animals. *Animal frontiers*, 2(3), 16-21.

Šárová, R., Špinka, M., Panamá, J. L. A., & Šimeček, P. (2010). Graded leadership by dominant animals in a herd of female beef cattle on pasture. *Animal behaviour*, 79(5), 1037-1045.

Schonthaler, H. B., Lampert, J. M., von Lintig, J., Schwarz, H., Geisler, R., & Neuhauss, S. C. (2005). A mutation in the silver gene leads to defects in melanosome biogenesis and alterations in the visual system in the zebrafish mutant fading vision. *Developmental biology*, 284(2), 421-436.

Schulte, N., & Klingel, H. (1991). Herd structure, leadership, dominance and site attachment of the camel, Camelus dromedarius. *Behaviour*, 118(1-2), 103-114.

Schulz, U. (2008). *El camello en Lanzarote*: Aderlan.

Seltmann, A., Majolo, B., Schülke, O., & Ostner, J. (2013). The organization of collective group movements in wild Barbary macaques (Macaca sylvanus): social structure drives processes of group coordination in macaques. *PloS one*, 8(6), e67285.

Siegel, A., & Douard, J. (2011). Who's flying the plane: Serotonin levels, aggression and free will. *International journal of law and psychiatry*, 34(1), 20-29.

Spisak, B. R., Grabo, A. E., Arvey, R. D., & Van Vugt, M. (2014). The age of exploration and exploitation: Younger-looking leaders endorsed for change and older-looking leaders endorsed for stability. *The Leadership Quarterly*, 25(5), 805-816.

Sueur, C., Deneubourg, J.-L., & Petit, O. (2010). Sequence of quorums during collective decision making in macaques. *Behavioral ecology and sociobiology*, 64(11), 1875-1885.

Sueur, C., Deneubourg, J.-L., & Petit, O. (2011). From the first intention movement to the last joiner: macaques combine mimetic rules to optimize their collective decisions. *Proceedings of the Royal Society B: Biological Sciences*, 278(1712), 1697-1704.

Sueur, C., Kuntz, C., Debergue, E., Keller, B., Robic, F., Siegwalt-Baudin, F., Richer, C., Ramos, A., & Pelé, M. (2018). Leadership linked to group composition in Highland cattle (*Bos taurus*): Implications for livestock management. *Applied Animal Behaviour Science*, 198, 9-18.

Sueur, C., & Petit, O. (2008). Organization of group members at departure is driven by social structure in *Macaca*. *International Journal of Primatology*, 29(4), 1085-1098.

Sueur, C., Petit, O., & Deneubourg, J.-L. (2009). Selective mimetism at departure in collective movements of *Macaca tonkeana*: an experimental and theoretical approach. *Animal Behaviour*, 78(5), 1087-1095.

Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., & Slotow, R. (2010). Group dynamics of zebra and wildebeest in a woodland savanna: effects of predation risk and habitat density. *PloS one*, 5(9), e12758.

Trut, L. N. (1999). Early Canid Domestication: The Farm-Fox Experiment: Foxes bred for tamability in a 40-year experiment exhibit remarkable transformations that suggest an interplay between behavioral genetics and development. *American Scientist*, 87(2), 160-169.

Trut, L. N., Plyusnina, I., & Oskina, I. (2004). An experiment on fox domestication and debatable issues of evolution of the dog. *Russian Journal of Genetics*, 40(6), 644-655.

Ucko, P. J., & Dimbleby, G. W. (2007). *The domestication and exploitation of plants and animals*: Transaction Publishers.

Volpato, G., Dioli, M., & Di Nardo, A. (2017). Piebald camels. *Pastoralism*, 7(1), 1-17.

Ward, A. J., Herbert-Read, J. E., Jordan, L. A., James, R., Krause, J., Ma, Q., Rubenstein, D.I., Sumpter, D.J.T., & Morrell, L. J. (2013). Initiators, leaders, and recruitment mechanisms in the collective movements of damselfish. *The American Naturalist*, 181(6), 748-760.

West, P. M., & Packer, C. (2002). Sexual selection, temperature, and the lion's mane. *Science*, 297(5585), 1339-1343.

Wilhelmy, J., Serpell, J., Brown, D., & Siracusa, C. (2016). Behavioral associations with breed, coat type, and eye color in single-breed cats. *Journal of Veterinary Behavior*, 13, 80-87.

Williamson, G., & Payne, W. J. A. (1978). *An introduction to animal husbandry in the tropics*: Longman.

Wilson, R. (1990). Natural and man-induced behaviour of the one-humped camel. *Journal of Arid Environments*, 19(3), 325-340.

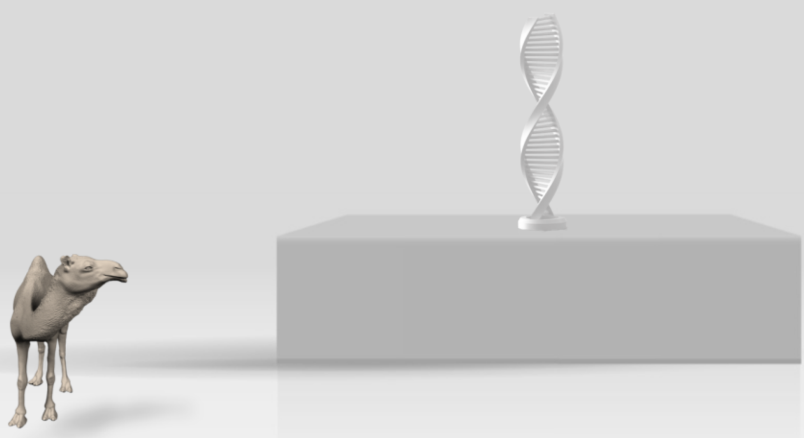
Worthy, M. (1999). *Eye color: A key to human and animal behavior*: iUniverse.

Yamaguchi, T., Tanaka, Y., & Yachida, M. (1997). Speed up reinforcement learning between two agents with adaptive mimetism. Proceedings of the 1997 IEEE/RSJ International Conference on Intelligent Robot and Systems: Innovative Robotics for Real-World Applications.

Yoo, S. K., Cotton, S. L., Sofotasios, P. C., Matthaiou, M., Valkama, M., & Karagiannidis, G. K. (2017). The Fisher–Snedecor Distribution: A Simple and Accurate Composite Fading Model. *IEEE Communications Letters*, 21(7), 1661-1664.

Zarrin, M., Riveros, J. L., Ahmadpour, A., de Almeida, A. M., Konuspayeva, G., Vargas-Bello-Pérez, E., Faye, B., & Hernández-Castellano, L. E. (2020). Camelids: new players in the international animal production context. *Tropical animal health and production*, 1-11.

CHAPTER 5
GENOME-WIDE ASSOCIATION STUDY FOR ZOOMETRICS, BIOMECHANICS AND BEHAVIOUR RELATED TRAITS IN ‘CANARIAN CAMEL’ BREED



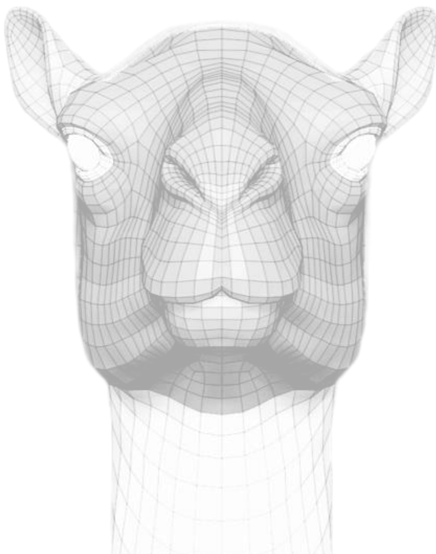
5.1 Genomic regions regulating the expression of neuro-sensory development determine body morphometrics, biomechanics and behaviour in dromedaries

Carlos Iglesias Pastrana[1], Francisco Javier Navas González[1], Martina Macri[1,2], María del Amparo Martínez Martínez[1], Elena Ciani[3] and Juan Vicente Delgado Bermejo[1]

[1]Department of Genetics, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain

[2]Animal Breeding Consulting, University of Córdoba, 14014 Cordoba, Spain

[3]Department of Biosciences, Biotechnologies and Biopharmaceutics, Faculty of Veterinary Sciences, University of Bari 'Aldo Moro', 70121 Bari, Italy



Quality indicator information provided on the publication
Latest information available (2022)

Status of the manuscript: Submitted

Journal (year, volume, page(s)): *Journal of Animal Breeding and Genetics*

International database in which it is indexed: Journal of Citation Reports (JCR)

Thematic area in the reference database: Agriculture, Dairy & Animal Science

Impact index of the journal in the year of the article's publication: 2.6

Rank/number of thematic area journals: 15/62 (Q1)

Abstract

Domestic camels are gaining recognition in animal breeding for sustainability. While primarily chosen for milk and meat production, other traits such as zoometrics, biomechanics, and behavior, important throughout domestication, are largely neglected in terms of their genomic basis. Through a genome-wide association study, sixteen and one hundred and eight genetic markers have been identified as significantly associated ($q<0.05$) at genome and chromosome-wide levels of significance, respectively, with zoometrical (width, length, and perimeter/girth), biomechanical (acceleration, displacement, spatial position, and velocity), and behavioral (general cognition, intelligence, and Intelligent Quotient (IQ)) traits in dromedary camels. In most association loci, the nearest protein-coding genes are implicated in an increased prevalence of neurodevelopmental and sensory disorders. Overall, the insights gained from the present research study represent a significant step forward in the understanding of both the genomic basis of functional traits and the effects of early domestication and modern selection on dromedary camels' health and welfare.

Keywords

Camelus dromedarius, functional traits, genome-wide association study, candidate genes, genomic selection

Introduction

Recognized for their sustainability, camels are increasingly bred for global production. With notable demand for camel milk and meat, efforts and strategies prioritize growth and milk yield traits. This sidelines traits like zoometrics, biomechanics, and behavior in genetic improvement programs for these animals (Abri & Faye, 2019; Burger, Ciani, & Faye, 2019). Thus, standardizing the incorporation of these traits into breeding criteria—linked to physical and behavioral performance—will enhance camels' potential. This applies especially to breeds and populations used in beauty contests, athletic pursuits (racing and riding), and close human interaction (assisted interventions and routine husbandry practices) (Faye, 2015; Pastrana et al., 2021).

In conservation and/or breeding programs, two essential data registries are crucial: phenotypic records of the traits of interest and genealogical information (Rúa, 2017). Estimating individual breeding values using phenotypic and pedigree information is limited for camels due to the fact that this livestock species lacks traditional pedigrees (Alhaddad & Alhajeri, 2019; Bitaraf Sani et al., 2021).

To surmount this technical constraint and enhance genetic advancement, there is a pursuit of reducing generation intervals (König, Simianer, & Willam, 2009). Progress in genomics has provided powerful instruments for thoroughly delving into the genetic composition of intricate traits and formulating selection panels for animals guided by genetic markers.

This encompasses single-gene tests (Rothschild, 2004) and genomic selection, employing arrays of genetic markers spanning the entire genome, which are recognized to correlate with particular traits (Hayes et al., 2009), both viable approaches for integration into camel selection initiatives.

Genetic polymorphisms of single candidate genes have been proposed in dromedaries for economically relevant traits such as coat colour (Almathen et al., 2018), udder and body measurements (Abdel-Aziem et al., 2015; Ishag et al., 2013; Nowier, El-Metwaly, & Ramadan, 2020), and reproductive performance (Al-Sharif et al., 2022).

Rather complex genetic breeding programs can also be developed on account of the genome-wide association studies (GWAS). In these regards, Bitaraf Sani et al. (2021) identified 99 genome-wide significant SNPs associated with birth weight, daily gain, and body weight in Iranian dromedaries. Within the same animal population, 9 significant SNPs located in 16 candidate genes and 13 significant SNPs located in 24 candidate genes were found to be associated with white and black coat color, respectively (Bitaraf Sani et al., 2022).

Additionally, Karimi et al. (2023) found 59 SNPs significantly associated with 12 morphometric traits and 37 candidate genes were classified in dromedaries from Iran. Moreover, 111 SNPs were identified as significantly associated with weight-for-age traits in Pakistani dromedary camels (Sabahat et al., 2022).

The genetic basis of other functional traits of economic relevance in camel production scenarios (e.g., athletic performance and behavioural features) remains, however, unexplored. From a purely evolutionary perspective, the identification of genomic regions that are associated with specific phenotypic traits can also aid in disentangling the effects of early domestication and historical selective breeding on camel welfare, basing on the biological functions in which the associated genes are significantly involved ('domestication syndrome' hypothesis) (Wilkins, Wrangham, & Fitch, 2014).

The present study performs genome-wide association study with the aim to identify genome sections which may condition the regulation of the expression of traits such as zoometrics, biomechanics, and behaviour in dromedary camels. The results will further support the list of genetic variants previously reported (Karimi et al., 2023) to be associated with morphometric traits in dromedaries by screening a larger number of animals and a higher-density SNP array, but also explore the genomic basis of biomechanical and behavioural traits in these livestock species. Altogether, the insights gained from this research will have the potential to inform future breeding programs, guide conservation efforts, and enriches our knowledge on the genomic features of early domestication and modern selection in camels.

Material and methods

Phenotype assessment and blood sampling

Between October 2019 and July 2020, one hundred and twenty Canarian dromedary camels (70 males and 50 females; reared at 4 different semi-extensive farms (2 farms in Canary Islands and 2 farms in mainland Spain)) were phenotyped for body morphometrics, biomechanics, and behaviour related traits. A total of thirty zoometric measures were taken from each animal as indicated by Iglesias Pastrana et al. (2022) and then aggregated depending on its geometric nature in four categories (length, height, width, and perimeter/girth measurements). Regarding biomechanical performance traits, curve estimation regression statistics was applied to the individual motion measurements for eleven key kinematic variables at ten different anatomic regions, obtained through video analyses, to calculate the coefficients of the mathematical function that best described locomotor behaviour in dromedary camels (cubic function), as described in Pastrana et al. (2023). Four additional phenotypic categories, including a relative number of kinematic variables, were defined for biomechanics-related traits (acceleration, velocity, displacement, and spatial position measurements). Behavioural traits (eleven copying styles, seven general cognition-related traits, six intelligence-related traits, and intelligent quotient (IQ) as a psychometric construct calculated from the individual performance for the general cognition and intelligence-related traits) were recorded following the protocols by González et al. (2019) and aggregated in four different categorical groups (coping styles, general cognition, intelligence, and IQ). For the genotype-phenotype association study, the phenotypic information used was the mean quantitative value per each of the categorical groups created and animal. Immediately after individual phenotyping, a blood sample from each dromedary camel was collected through jugular venipuncture in 2 mL vials containing ethylenediaminetetraacetic acid (EDTA) and stored at -20°C until genomic DNA extraction tasks.

Genotyping and standard SNP genotype quality control

High-throughput, high density SNP genotyping array was used to generate the sequence data (Axiom Camelids Genotyping 96-Array (Affymetrix, CA, USA)) as per manufacturer's instructions. This chip comprises 59,958 SNPs evenly distributed across the dromedary camel genome. Standard quality control procedures were applied to the SNP genotypes using PLINK v1.9. Markers with a call rate below 0.90, a minor allele frequency (MAF) less than 0.02, those mapping to sex chromosomes, and those exhibiting significant deviations from Hardy-Weinberg equilibrium ($P < 0.001$) were excluded from the analysis. Additionally, individuals with a genotype call rate lower than

0.95 were susceptible to being excluded from further analyses. After implementing these quality control measures, a total of 49,632 SNPs and all the animals initially included were retained for subsequent analyses. A principal component analysis (PCA) was run with PLINK v1.9 to explore the genetic population structure.

Linkage disequilibrium

Linkage disequilibrium (LD), as the degree of non-random association of allele between loci or correlation between genotypes of markers, was estimated for each pairwise combination of SNPs using the software PopLDdecay. The level and pattern of LD (r^2) between markers across the genome is an important concept to evaluate when determining the accuracy and precision of genomic association studies and genomic prediction (Zhang et al., 2019).

Genome-wide association study (GWAS) for zoometrics, biomechanics, and behaviour-related traits

Following the methodology of Macri et al. (2023), genotype-phenotype association analysis was conducted using the Genome-wide Efficient Mixed-Model Association (GEMMA) v0.98.1 package (Zhou & Stephens, 2014). For each trait, a univariate linear mixed model was fitted according to the following formula:

$$y = \mathrm{W}\alpha + \mathrm{x}\beta + \mathrm{u} + \varepsilon; \mathrm{u} \sim \mathrm{MVN_n}(0, \lambda\, \tau^{-1}\, \mathrm{K}), \text{and } \varepsilon \sim \mathrm{MVN_n}(0, \lambda\, \tau^{-1}\, \mathrm{I_n})$$

where y represents an n-vector of zoometrical, biomechanical and behavioural phenotypes for n = 120 individuals; W is an $n \times c$ matrix (c = number of fixed factors) that includes a column of 1s and the fixed effects, namely, sex (2 levels) and age category (3 levels); α is a c-vector denoting the corresponding fixed effects, including the intercept; x represents a n-vector of marker genotypes; β represents the marker's effect size (allele substitution effect); u is a n-vector of random individual effects that are normally distributed, u ~ N(0, $\lambda\, \tau^{-1}$ K), where τ^{-1} denotes the residual error variance, λ represents the ratio between the two variance components, and K is a SNP genotypes-derived $n \times n$ known relatedness matrix. Lastly, ε represents a n-vector of errors, and I_n represents an $n \times n$ identity matrix; while MVN_n depicts the multivariate normal distribution with n dimensions. P-values obtained for each association were then adjusted for multiple testing with the False Discovery Rate (FDR) method. Below 0.05 q-value associations were deemed statistically significant. Manhattan plots were generated using the "qqman" R package. The estimation of the proportion of phenotypic variance that can be explained by a specific SNP (PVE) was performed using the following formula (Shim et al., 2015):

$$PVE = \frac{2\beta^2 \, MAF\,(1 - MAF)}{2\beta^2 \, MAF\,(1 - MAF) + [se(\beta)]^2 \, 2N \, MAF\,(1 - MAF)}$$

where β represents the SNP variant estimated effect size, se(β) represents the β estimate standard error, *MAF* denotes the minor allele SNP frequency, and *N* is the size of the sample. P lambda function from the R package QCEWA was used to calculate lambda (λ) inflation factors, and quantile-quantile (Q-Q) plots were generated using the ggqqplot function. Biomart tool from Ensembl was used to retrieve those genes that were located within a flanking region of ±50 kb of the significant SNPs (Karimi et al., 2023).

Results and discussion

Altogether, the results from the present study are in accordance with the 'domestication syndrome' for mammals, and more specifically, with the genomic signatures of domestication in Old World camels reported by Fitak et al. (2020). These authors detected recent, positive selection for 107 candidate genes linked to neural crest deficiencies and altered thyroid hormone-based signaling in camel species. The current research proposes new candidate genes potentially linked to the effects of early domestication and modern selection in dromedaries, and highlights the importance of the long-term maintenance, at human-controlled environments, of the size- and behaviour-assortative mating that occurs between conspecifics in natural animal populations.

Genotypic clustering reflects intergroup differentiation and slight introgression: inference of the maintenance of assortative natural mating

PCA based on 50K genotypes revealed raising farm to be a significant clustering criteria for dromedary camels (Figure 1). In this regard, breeding practices carried out in the camel breed studied can explain the results observed. For instance, farms 2 and 3 are the largest reserves of Canarian dromedaries and they are genetically interconnected through the exchange of living animals for breeding purposes. At these emplacements, dromedaries are sorted in subgroups homogeneously defined by their sex, age, and phenotypic characters. These raising farms are also the main source for living animals of Farm 1 (Iglesias Pastrana et al., 2020, 2021). By contrast, Farm 4's genetic connection with the other farms occurs less frequently, which may thus by the basis for its relatively singular genetic structure.

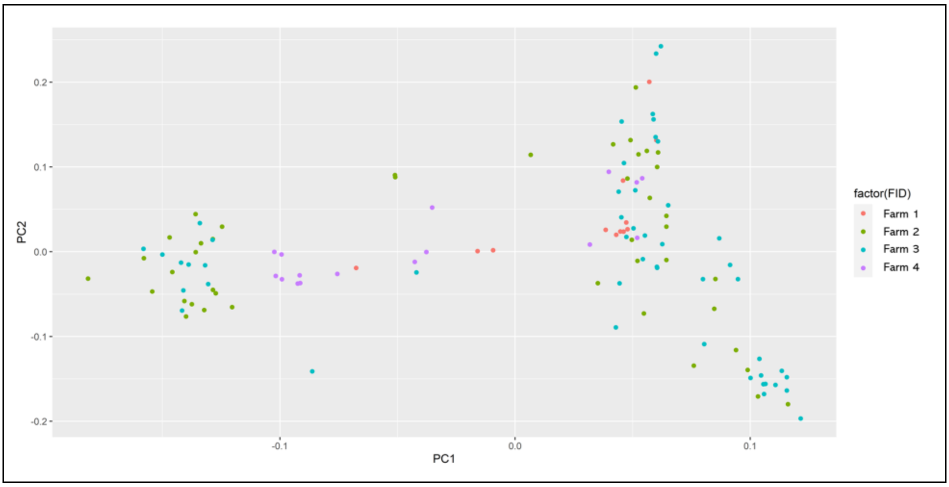


Figure 1. Principal components analysis (PCA) results displaying the clustering of 120 Canarian dromedary camels raised at 4 farms according to their 50K genotypes.

This clustering pattern, which evidences differentiation between and within farms for genotypic information, can also explain the phenotypic diversity encountered in the study sample. Descriptive statistics (minimum (Min), maximum (Max), mean, and standard deviation (SD)) for the 12 categorical phenotypes recorded in 120 dromedary camels is presented in Table 1. According to the SD values, high interindividual variability particularly exists for body morphometrics and intelligent quotient. Both environmental pressures and functional specialization at domestic scenarios shape the morphology and psyche of the animals (Hansen Wheat et al., 2019). However, little variation is patent for physical performance traits in this animal species. Such a finding can be attributed to the fact that camel gait is a highly conserved ancestral trait (Webb, 1972).

Overall, the population substructure revealed in the present study can be indicative of the positive impact of the human-driven selection of dromedary camels for the maintenance of the size- and behaviour-assortative mating that occurs between conspecifics in natural populations (Janicke et al., 2019). Under the condition of gregarious animal species, assortative mating is of paramount importance for camels in terms of intragroup energy efficiency and optimization (i.e., energy investment towards reproduction) for survival in arid and semi-arid environments.

Linkage disequilibrium pattern supports the suitability of the study population and density of the SNP array used for accurate high-resolution genomic mapping

Following the premises of McKay et al. (2007), moderate LD (r^2 = 0.20) is certainly present at a distance of 100 kb between markers, which indicates that a minimum of

Table 1. Descriptive statistics (minimum (Min), maximum (Max), mean, and standard deviation (SD)) for the zoometrics, biomechanics and behaviour traits recorded in 120 dromedary camels.

Phenotype category	Trait/unit of measurement	Min	Max	Mean±SD
Zoometrics	Length (cm)	48.22	80.98	70.46±5.03
	Heigth (cm)	54.93	77.03	64.66±3.96
	Width (cm)	26.79	41.78	36.01±2.72
	Perimeter/girth (cm)	52.06	83.77	72.02±5.18
Biomechanics	Acceleration (coefficients of the cubic regression model)	-0.06	0.05	0.00±0.02
	Velocity (coefficients of the cubic regression model)	-0.06	0.05	-0.01±0.02
	Displacement (coefficients of the cubic regression model)	-0.10	0.07	-0.04±0.05
	Spatial position (coefficients of the cubic regression model)	-0.31	-0.06	-0.22±0.07
Behaviour	Copying styles (intensity of response)	1	5	2.88±0.68
	General cognition (intensity of response)	1	5	3.99±0.52
	Intelligence (intensity of response)	1	5	4.00±0.58
	Intelligent Quotient (IQ) (points)	92.04	137.97	102.36±8.17

22,000 (2.2GB/100Kb at $r^2 = 0.2$, where 2.2GB is the dromedary camel genome size) SNPs are required to cover the genome and capture LD information for species-specific genome-wide association studies. Such a threshold is effectively overcome in our study, given that after implementing quality control measures, a total of 49,632 SNPs and all the animals initially included were retained for subsequent analyses. The LD decay plot is shown in Figure 2.

Prevalence and incidence of sensory and cognitive impairments underlie variations in camel body morphometrics

Seven SNPs at genome-wide level (Figure 3 and Table 2) and twenty-nine SNPs at chromosome-wide level displayed significant associations with the dromedary camel's zoometrical traits. In total, twenty-three different candidate genes were identified (Table 2). None of these genes coincide with those reported previously in other studies that investigated the genetic basis of growth and morphometric traits in dromedaries.

PVRIG, *STAG3*, *GAL3ST4*, *TRAPPC14*, and *LAMTOR4* genes are impacting both width and perimeter/girth measurements in dromedary camels. These genes are reported in literature among candidate neurodegenerative/neuropsychiatric (alterations in eye size and morphology, microcephaly, abnormal ciliogenesis, cilia instability, decreased

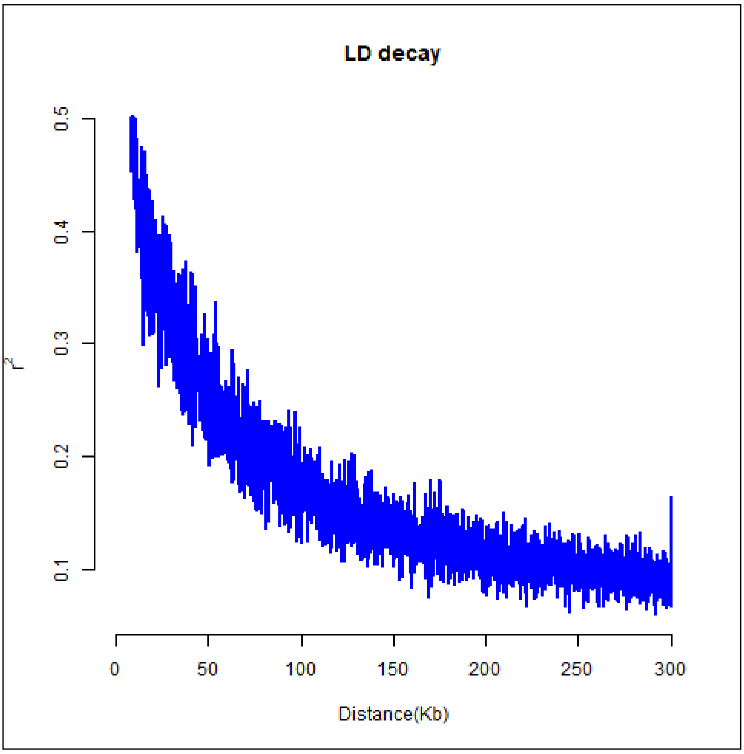


Figure 2. Linkage disequilibrium (LD) decay plot depicted from pairwise LD values (r^2) against genetic distance (Kb) between genomic markers across dromedary camel genome.

thigmotactic behavior and locomotor activity, and hyperactivity), immune response (lymphadenomegalia, and T-cell function), reproductive performance (infertility, abnormal embryo size, and embryonic/preweaning lethality), cell cycle, and skeletal structure (bone density and rib morphology) biomarkers in humans, mice and zebrafish (Informatics, 2014; Llano et al., 2014; Murter et al., 2019; Tirozzi et al., 2023; Ward et al., 2016; Zaqout & Kaindl, 2022).

Four (*ZCCHC8*, *RSRC2*, *KNTC1*, and *U6*) and seven (*TENM2*, *LYN*, *RPS20*, *SNORD54*, *MOS*, *KCNV2*, and *PUM3*) additional genes differentially regulate width and perimeter/girth measurements, respectively. *ZCCHC8*, *RSRC2*, *KNTC1*, and *U6* genes are implicated in the prevalence and incidence rates of a vast number of neoplastic processes, decreased reproductive performance, narrow eye opening, motor neuron diseases, retinitis pigmentosa, poikiloderma with neutropenia, and recessive intellectual disability in humans and mice (Gable et al., 2019; Informatics, 2014; Mroczek & Dziembowski, 2013; Sondka et al., 2018; Wu et al., 2019).

Besides, those genes that are specifically associated with perimeter/girth measurements of dromedary camels in our study, are widely recognized for their

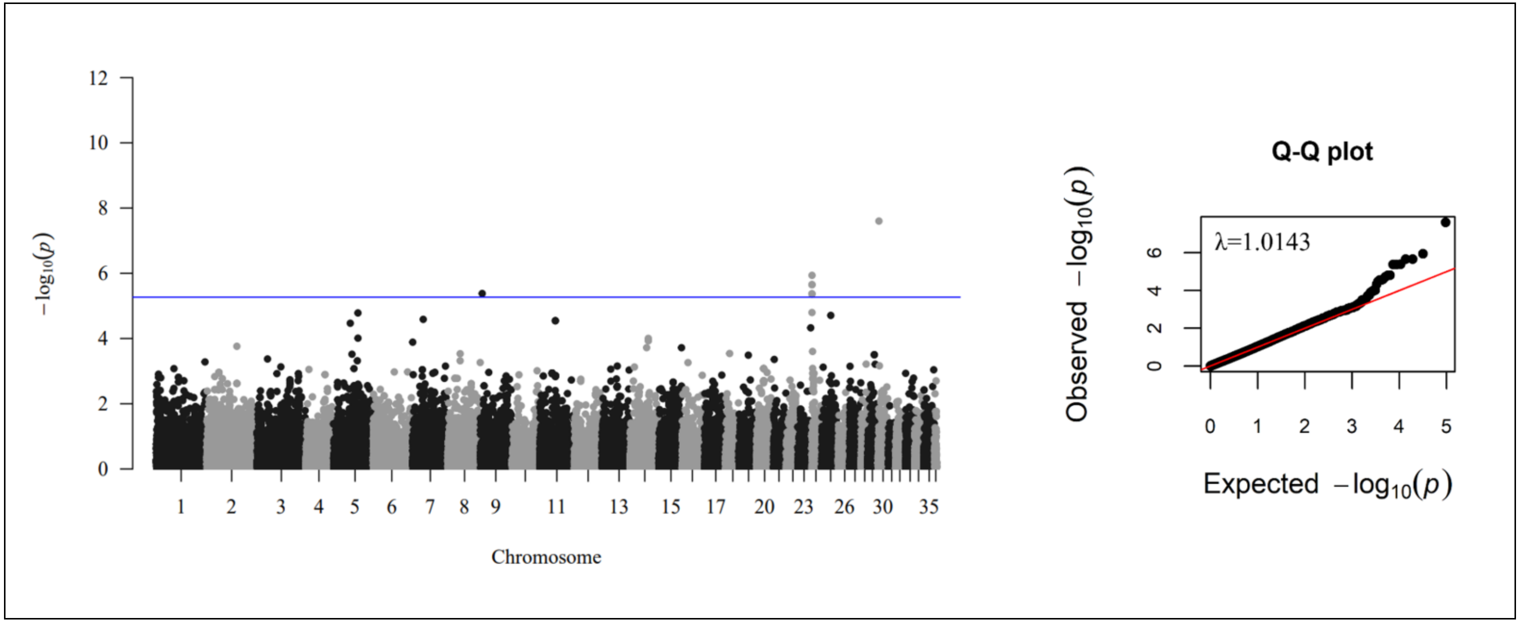


Figure 3. Manhattan and Q-Q plots displaying the results of the genome-wide association study for zoometrical trait 'Length' in dromedary camels. Negative log10 *P*-values (y-axis) of the associations between SNPs and length phenotypes are plotted against the genomic location of each SNP marker (x-axis). Blue line represents the threshold of genome-wide significance after correction for multiple testing (*q*-value= 0.05).

Table 2. Genome- and chromosome-wide significant associations between SNP markers and zoometrical traits in dromedary camels.

Level of significance	Trait	Chr[1]	rs[2]	Pos[3]	A1[4]	MAF[5]	β±SE[6]	P-value	q-value[7]	PVE[8]	Candidate gene(s) name(s)
Genome-wide	Length	9	AX-337955994	4135877	A	0.158	-3.573±0.865	2.348×10^{-05}	0.029	0.124	*POU2F2, ZNF574, GRIK5*
		24	AX-338053157	1257593	A	0.125	-3.761±0.818	2.394×10^{-05}	0.029	0.150	
		24	AX-338106016	1337164	A	0.138	-3.763±0.772	1.504×10^{-05}	0.026	0.165	
		24	AX-338015631	1382174	A	0.217	-3.033±0.634	2.389×10^{-05}	0.029	0.160	
		24	AX-338015633	1401421	A	0.138	-3.763±0.772	1.504×10^{-05}	0.026	0.165	
		24	AX-338053174	1421441	A	0.225	-3.232±0.624	9.484×10^{-06}	0.026	0.182	
		30	AX-338029294	2519875	A	0.025	-10.050±1.784	7.554×10^{-07}	0.001	0.209	
Chromosome-wide	Length	5	AX-337969319	41408799	A	0.496	2.375±0.543	1.113×10^{-04}	0.041	0.137	
		5	AX-337970609	60230516	G	0.292	-2.664±0.609	6.431×10^{-05}	0.040	0.137	*SPAG16*
		9	AX-337955994	4135877	A	0.158	-3.573±0.865	2.348×10^{-05}	0.008	0.124	*POU2F2, ZNF574, GRIK5*
		11	AX-338007414	38938407	A	0.017	-8.033±2.057	9.732×10^{-05}	0.030	0.112	*PCDH15*
		11	AX-338007417	38992975	A	0.017	-8.033±2.057	9.732×10^{-05}	0.030	0.112	*PCDH15*
		23	AX-338052835	32418534	A	0.358	-2.700±0.594	5.5×10^{-04}	0.043	0.146	*NFASC*
		24	AX-338053157	1257593	A	0.125	-3.761±0.818	2.394×10^{-05}	4.7×10^{-04}	0.149	
		24	AX-338106016	1337164	A	0.138	-3.763±0.772	1.504×10^{-05}	4.1×10^{-04}	0.165	
		24	AX-338084880	1345978	G	0.259	-2.530±0.590	6.294×10^{-05}	1.4×10^{-03}	0.132	
		24	AX-338015631	1382174	A	0.217	-3.033±0.634	2.389×10^{-05}	4.7×10^{-04}	0.160	
		24	AX-338015633	1401421	A	0.138	-3.763±0.772	1.504×10^{-05}	4.1×10^{-04}	0.165	
		24	AX-338053174	1421441	A	0.225	-3.232±0.772	9.484×10^{-06}	4.1×10^{-04}	0.182	
		24	AX-338015758	2769311	A	0.421	-1.924±0.531	5.325×10^{-04}	0.020	0.098	
		25	AX-338056852	23461775	A	0.042	-5.868±1.217	10×10^{-05}	0.020	0.162	*SAMD12*
		30	AX-338029294	2519875	A	0.025	-10.050±1.784	7.554×10^{-07}	1.783×10^{-05}	0.209	

Table 2. *Cont.*

Level of significance	Trait	Chr[1]	rs[2]	Pos[3]	A1[4]	MAF[5]	β±SE[6]	P-value	q-value[7]	PVE[8]	Candidate gene(s) name(s)
Chromosome-wide	Perimeter/girth	3	AX-337959884	90597288	A	0.038	7.662±1.715	5.288×10^{-05}	0.040	0.142	
		4	AX-337929795	47376072	A	0.087	-4.751±1.156	2.300×10^{-04}	0.045	0.123	*KCNV2*
		4	AX-337965078	47376072	A	0.087	-4.751±1.156	2.300×10^{-04}	0.045	0.123	*KCNV2*
		4	AX-338067469	47393983	G	0.209	-3.398±0.791	1.942×10^{-04}	0.045	0.133	*KCNV2*, *PUM3*
		18	AX-338039298	25972784	A	0.442	-3.123±0.650	4.558×10^{-05}	0.008	0.161	*PVRIG*, *STAG3*, *GAL3ST4*, *TRAPPC14*, *LAMTOR4*
		22	AX-338048863	9913664	G	0.158	-3.320±0.747	5.846×10^{-05}	0.008	0.141	*TENM2*
		22	AX-338084077	9922210	A	0.158	-3.115±0.774	4.105×10^{-04}	0.034	0.118	*TENM2*
		22	AX-338048865	9943037	G	0.158	-3.115±0.774	4.105×10^{-04}	0.034	0.118	*TENM2*
		29	AX-338064518	3727916	A	0.317	2.449±0.600	2.143×10^{-04}	0.047	0.122	*LYN*, *RPS20*, *SNORD54*, *MOS*
		29	AX-338064562	4248472	A	0.067	-4.675±1.243	4.403×10^{-04}	0.047	0.105	
		29	AX-338064566	4325706	G	0.138	-3.630±0.858	3.386×10^{-04}	0.047	0.130	
		35	AX-338075723	1644974	A	0.321	-3.096±0.731	8.224×10^{-05}	0.013	0.130	
	Width	18	AX-338039298	25972784	A	0.442	-1.671±0.365	1.500×10^{-04}	0.041	0.148	*PVRIG*, *STAG3*, *GAL3ST4*, *TRAPPC14*, *LAMTOR4*
		32	AX-338071659	18441303	G	0.129	-2.557±0.494	4.931×10^{-05}	0.005	0.182	*ZCCHC8*, *RSRC2*, *KNTC1*,*U6*

[1]Chr:chromosome; [2]rs:identifier code of the SNP; [3]Pos:position in baise pairs; [4]A1:minor allele; [5]MAF, minor allele frequency; [6]β±SE: allelic substitution effect ± standard error; [7]*q*-value: P-values corrected for multiple testing using a false discovery rate approach; [8]PVE: proportion of variance in phenotype explained by a given SNP.

implication on morpho-functional alterations at sensory-neural tissues and organs, neoplastic processes, immune structures, and pigmentation in humans and animal models. Concretely, *TENM2*, *KCNV2*, and *PUM3* genes are associated with abnormalities at retina ganglion, cone-rod distribution, eye size, visual cortex, superior colliculus, and lateral geniculate nucleus in humans, mice, and zebrafish (Thisse et al., 2001; Wissinger et al., 2011; Young et al., 2013), which are structures that play essential roles in normal visual processing and orienting motor responses, visuospatial attention, and perceptual decision-making. *LYN* gene is related to a wide range of neoplastic processes in humans (Sondka et al., 2018) and immune dysfunctions in mice (Lamagna et al., 2013; Verhagen et al., 2009). In addition, abnormal pigmentations at the skin, epidermis, ear, and tail, as well as decreased exploratory behaviour, are phenotypes associated to genomic variability in *RPS20* gene in mice (Informatics, 2014; McGowan et al., 2008).

Therefore, the association of this gene with perimeter/girth measurements in dromedary camels provides further evidence to support the correlations between leadership behaviour, body morphometrics, and coat colour in dromedary camels (Iglesias Pastrana et al., 2021). *MOS* gene, however, is mostly associated to reduced reproductive performance and cell cycle alterations in mice (Choi et al., 1996; College et al., 1994).

In regards the phenotypic variability for length measurements, it was associated with other seven candidate genes (*PCDH15*, *NFASC*, *SAMD12*, *SPAG16*, *POU2F2*, *ZNF574*, and *GRIK5*). *PCDH15*, *NFASC*, *SAMD12*, *POU2F2*, and *GRIK5* genes are reported to be generally linked with decreased general behaviour activity, quality of musculoskeletal movement and balance (proprioception), visual and hearing capacity, and immune function, as well as increased prevalence of neurodevelopmental disorders with central and peripheral motor dysfunction (i.e., hemorrhagic brain, abnormal synaptic transmission and postsynaptic currents, syndromic intellectual disability, and increased startle reflex and thermal nociceptive threshold) in humans, mice, rats, and zebrafish (Ahmed et al., 2008; Alagramam et al., 2001; Cen et al., 2018; Corcoran et al., 2004; Goodman & Zallocchi, 2017; Koromina et al., 2019; Pillai et al., 2009; Twigger et al., 2002; Unlu et al., 2019). A missense variant in *PCDH15* gene is also responsible for the unexpectedly low number of homozygous haplotype carriers for two different Holstein haplotypes that are related to insemination success and neonatal survival in cattle (Häfliger et al., 2022). On the other hand, *SPAG16* gene is listed as associated with decreased reproductive general performance (Escalier, 2006; Sun et al., 2023; Zhang et al., 2007) and increased prevalence of ciliary dyskinesia (PCD), a X-linked disorder that mainly affects respiratory tissues (Andjelkovic et al., 2018), in humans, mice, and cattle. *ZNF574* gene is a hub gene of adipose tissue metabolism in cattle (Wang et al., 2022) and is differentially regulated in many humans tumors (Berg et al., 2010; De Wilde et al., 2018; Zhang, Wu, & Huang, 2022).

Hereditary motor neuron disease and osteodysplasia widely condition locomotor performance in dromedary camels

Twenty-four SNPs at the chromosome-wide level of significance were found to be significantly associated with biomechanical traits in dromedary camels (Table 3). Eleven candidate genes were involved in the dromedary camel's biomechanics.

MIR187, *FBXO8*, and *TTC28* genes regulate phenotypic variation at both displacement and spatial position measurements in dromedary camels. Altered expression of *MIR187*, *FBXO8*, and *TTC28* genes has been correlated with diverse human malignancy phenotypes, as well as in regulation processes of inflammation, cell stemness, insulin secretion, and embryonic development, in humans and mice (Lasorsa et al., 2022; Lin et al., 2016; Tonne et al., 2013). Furthermore, the downregulation of *MIR187* gene is linked to intellectual disability and temporal lobe epilepsy in humans and animal models (Cattani et al., 2016; Ünalp et al., 2022), and *FBXO8* gene is implicated in motor neuron degeneration in amyotrophic lateral sclerosis in humans (Cronin et al., 2008). *TTC28* gene is additionally suggested for its functional role in developmental dysplasia (i.e., abnormal pelvic girdle bone and vertebrae morphology, and short tibia), decreased bone mineral density, increased heart weight, and decreased body length in mice (Informatics, 2014), and increased feed conservation ratio in pig (Borowska et al., 2017).

Phenotypic variation for acceleration-related traits in dromedaries was found to be controlled by six different genes (*PRSS56*, *CHRND*, *CHRNG*, *EIF4E2*, *EFHD1*, and *GRID1*). Loss of *PRSS56* gene function contributes to impaired visual acuity in humans and mice (Paylakhi et al., 2018). *CHRND* and *CHRNG* gene mutations cause severe congenital myasthenic and multiple pterygium syndrome/fetal akinesia in humans, mice, zebrafish, and dogs (Blakey et al., 2017; Bonanno et al., 2020; Etard et al., 2005; Vogt et al., 2008; Vogt et al., 2012). Various mutant mice models for *EIF4E2* gene served to unraveling the role of this gene in the regulation of synaptic plasticity and autism spectrum disorder-associated behaviors (Wiebe et al., 2020), and Sun et al. (2020) and Zhang et al. (2020) founded that this gene was also associated with the response to exercise in buffalo and protects the heart against hypoxia in zebrafish, respectively. Similarly, mutant mice and wildtype (AB line) zebrafish were used to unravel the functional role of *EFHD1* gene in axonal morphogenesis, cardiac mitoflash activation, protection of cardiomyocytes from ischemia, and brain general development and function (Eberhardt et al., 2022; Ulisse et al., 2020; Wasilewska et al., 2019). *GRID1* gene variants in humans are associated with schizophrenia, bipolar disorder, intellectual disability, and spastic paraplegia (Benamer et al., 2018; Ung et al., 2022), whilst mice lacking this gene suffer from sensorineural hearing loss (De Luca et al., 2022).

Table 3. Chromosome-wide significant associations between SNP markers and biomechanical traits in dromedary camels.

Level of significance	Trait	Chr[1]	rs[2]	Pos[3]	A1[4]	MAF[5]	β±SE[6]	P-value	q-value[7]	PVE[8]	Candidate gene(s) name(s)
Chromosome-wide	Acceleration	1	AX-338095659	49067023	A	0.013	-0.038±0.008	5.235×10^{-05}	0.041	0.142	
		5	AX-337973020	90882617	G	0.042	-0.020±0.004	1×10^{-04}	0.036	0.131	*PRRS56*, *CHRND*, *CHRNG*, *EIF4E2*, *EFHD1*
		5	AX-337973023	90898605	A	0.042	-0.020±0.004	1×10^{-04}	0.036	0.131	*CHRND*, *CHRNG*, *EIF4E2*, *EFHD1*
		11	AX-338008807	63080477	A	0.39	-0.008±0.002	8.187×10^{-05}	0.022	0.134	*GRID1*
		11	AX-338008810	63089184	A	0.383	-0.009±0.002	5.122×10^{-05}	0.022	0.143	*GRID1*
		27	AX-338085966	8630370	A	0.108	-0.012±0.003	2.413×10^{-04}	0.028	0.116	
		27	AX-338106557	8630370	A	0.108	-0.012±0.003	2.413×10^{-04}	0.028	0.116	
	Displacement	15	AX-338029686	44613389	A	0.067	0.047±0.009	6.037×10^{-05}	0.008	0.172	
		24	AX-338053796	7360225	A	0.062	0.037±0.008	1×10^{-04}	0.021	0.131	*MIR187*
		31	AX-338069903	13185060	A	0.154	0.028±0.007	2.691×10^{-04}	0.022	0.117	*FBXO8*
		31	AX-338069905	13196723	G	0.154	0.028±0.007	2.691×10^{-04}	0.022	0.117	*FBXO8*
		32	AX-338107240	5642595	G	0.1	0.037±0.008	7.053×10^{-04}	0.042	0.138	*TTC28*
		32	AX-338107243	5686300	G	0.1	0.036±0.008	7.774×10^{-04}	0.042	0.130	*TTC28*
	Spatial position	5	AX-337931137	14592645	G	0.033	0.102±0.021	2.022×10^{-04}	0.028	0.160	*U6*
		5	AX-337967736	14777622	A	0.033	0.102±0.021	2.022×10^{-04}	0.028	0.160	
		15	AX-338029686	44613389	A	0.067	0.069±0.014	9.997×10^{-05}	0.018	0.162	
		24	AX-338053796	7360225	A	0.062	0.054±0.013	2.020×10^{-04}	0.035	0.124	*MIR187*
		31	AX-338069903	13185060	A	0.154	0.042±0.010	2.777×10^{-04}	0.024	0.115	*FBXO8*
		31	AX-338069905	13196723	G	0.154	0.042±0.010	2.777×10^{-04}	0.024	0.115	*FBXO8*
		32	AX-338107240	5642595	G	0.1	0.057±0.012	4.865×10^{-04}	0.035	0.147	*TTC28*
		32	AX-338107243	5686300	G	0.1	0.05±0.012	6.632×10^{-04}	0.035	0.133	*TTC28*
	Velocity	9	AX-337998299	60922008	G	0.183	-0.015±0.003	7.342×10^{-05}	0.037	0.136	
		20	AX-338043118	1522955	A	0.312	-0.013±0.003	1.587×10^{-04}	0.030	0.130	*MYLK4*
		20	AX-338005638	1522955	A	0.314	-0.013±0.003	1.848×10^{-04}	0.030	0.126	*MYLK4*

[1]Chr:chromosome; [2]rs:identifier code of the SNP; [3]Pos:position in baise pairs; [4]A1:minor allele; [5]MAF, minor allele frequency; [6]β±SE: allelic substitution effect ± standard error; [7]*q*-value: P-values corrected for multiple testing using a false discovery rate approach; [8]PVE: proportion of variance in phenotype explained by a given SNP.

Besides, *MYLK4* gen is controlling velocity traits in dromedary camels. *MYLK4* gene polymorphisms have been linked to skeletal muscle metabolism and hypertrophic cardiomyopathy in mice (Huang et al., 2016; Sakakibara et al., 2021); with growth and meat tenderness traits cattle (Aytekin et al., 2020; Won et al., 2023), goat (Shi et al., 2020) and pig (Fontanesi et al., 2014); with energy metabolism in muscle in Chinese perch (Wu et al., 2021); and with milk production traits in water buffalo (Du et al., 2019).

Embryonic neurogenesis and neurodegeneration shape the behavioural patterns and processes of dromedary camels

Behavioural traits in dromedaries were associated with nine SNPs at genome-wide level (Figure 4 and Table 4) and fifty-five SNPs at chromosome-wide level of significance (Table 4). Novel thirty-eight candidate genes were identified as modulating factors of behavioural phenotypes in dromedary camels.

CACNA1E gen was associated with phenotypic variability for both general cognition and intelligence-linked traits. Polymorphisms in this gen are linked to impaired glucose metabolism, abnormal motor capabilities/coordination/movement/nociception, and increased fear/depression/anxiety-related behaviours in mice and rats (Huang et al., 2019; Rijkers et al., 2010; Smith et al., 2018). Eleven other genes (*MZT1*, *BORA*, *DIS3*, *PIBF1*, *KLF5*, *KLF12*, *GPC5*, *ABCC4*, *ERCC5*, *DST*, and *CACNA1E*) were explicative of the phenotypic variability encountered in our study sample for intelligence traits. *MZT1*, *BORA*, *DIS3*, *PIBF1*, and *KLF5* were mapped in a human patient with syndromic intellectual disability and autism spectrum disorder (Cosemans et al., 2018). A homozygous haplotype-related loss-of-function variant has been also identified in bovine *DIS3*, most likely causing embryonic lethality (Häfliger, Seefried, & Drögemüller, 2021); and mutations in humans *DIS3* engrosses the list of risk factors for multiple myeloma (Boyle et al., 2020). *PIBF1* additionally regulates embryonic development and litter size in mice and sheep (Tao et al., 2021), and the incidence of alterations in neural tube closure/morphology and Joubert syndrome (varying degrees of physical, mental, and visual impairments) in animal models such as mice and frog (Informatics, 2014; Ott et al., 2019). *KLF5* and *KLF12* mutant and wild-type mice are biased for the prognosis of cardiovascular diseases given their differential inner capabilities of structural remodeling of the heart and blood vessels (Shindo et al., 2002; Takeda et al., 2010), and the severity of clinical pancreatic cancer (He et al., 2019), respectively. *GPC5* and *ABCC4* genes mutations have been confirmed to be functionally implicated in skeletal and growth defects, neural tube closure defects, and predisposition to nephrotic syndrome in humans, pigs, frogs and zebrafish (Bassuk et al., 2013; de Pontual et al., 2011; Ma et al., 2020; Okamoto et al., 2011). Further shreds of evidence ascertained that non-synonymous mutations in *ABCC4* gene ascribe to reproductive traits in cattle, buffalo, and pig (Li et

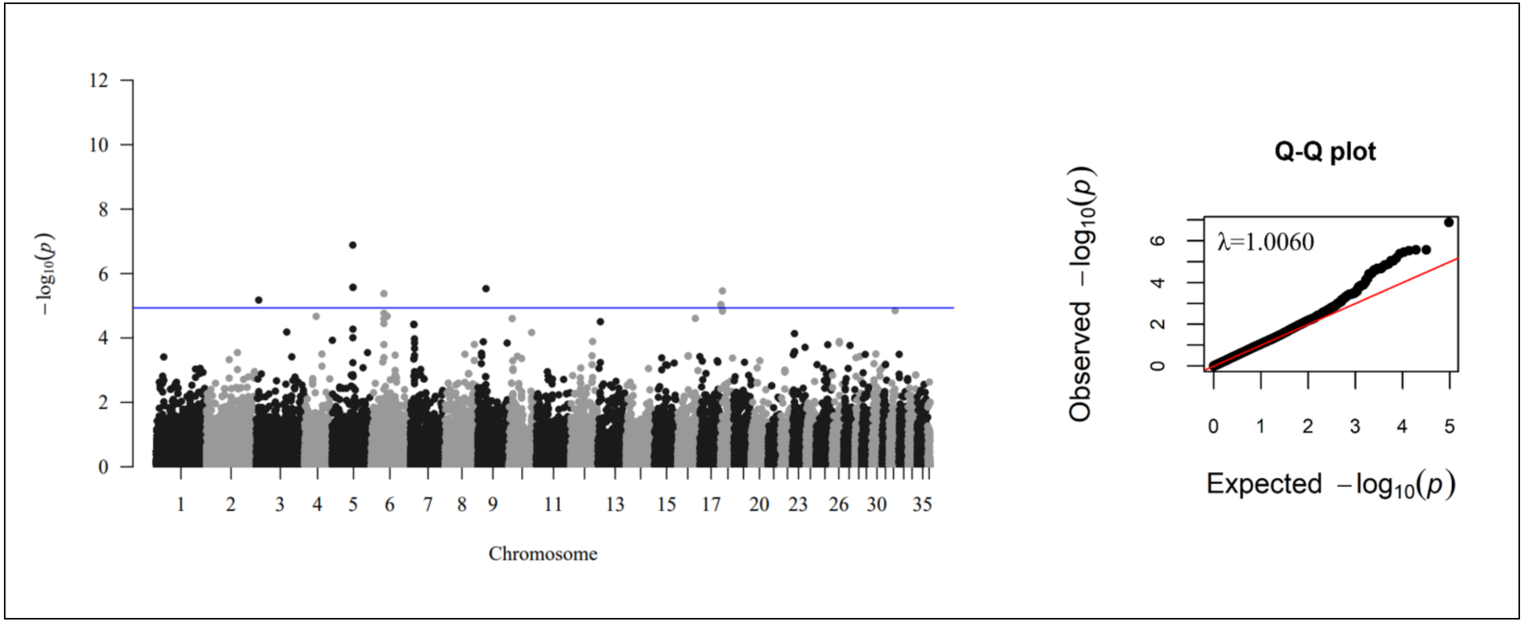


Figure 4. Manhattan and Q-Q plots displaying the results of the genome-wide association study for behavioural trait 'Intelligent Quotient' in dromedary camels. Negative log10 *P*-values (y-axis) of the associations between SNPs and length phenotypes are plotted against the genomic location of each SNP marker (x-axis). Blue line represents the threshold of genome-wide significance after correction for multiple testing (*q*-value= 0.05).

Table 4. Genome- and chromosome-wide significant associations between SNP markers and behavioural traits in dromedary camels.

Level of significance	Trait	Chr[1]	rs[2]	Pos[3]	A1[4]	MAF[5]	β±SE[6]	P-value	q-value[7]	PVE[8]	Candidate gene(s) name(s)
Genome-wide	Intelligent Quotient (IQ)	3	AX-337923932	6407091	A	0.121	5.127±1.086	4.104×10^{-05}	0.045	0.156	
		5	AX-337932262	51633138	A	0.013	17.266±3.077	4.985×10^{-06}	0.006	0.207	
		5	AX-337969986	52106921	A	0.029	10.963±2.178	6.011×10^{-05}	0.033	0.174	
		5	AX-338099603	52118548	A	0.029	10.963±2.178	6.011×10^{-05}	0.033	0.174	
		6	AX-337937069	31702577	G	0.108	5.687±1.126	0.002	0.033	0.175	*TRAV3*, *TRAV4*
		9	AX-337995041	20323326	A	0.067	7.204±1.421	3.877×10^{-05}	0.033	0.176	*ZNF536*
		18	AX-337999935	956822	A	0.188	4.542±0.947	0.001	0.050	0.160	
		18	AX-338037583	956822	A	0.188	4.542±0.947	0.001	0.050	0.160	
		18	AX-338000259	4973535	A	0.029	10.985±2.216	0.001	0.033	0.170	
Chromosome-wide	General cognition	21	AX-338010585	24771582	A	0.321	0.300±0.074	1.957×10^{-04}	0.025	0.119	
		21	AX-338105438	27637855	G	0.125	0.428±0.108	3.642×10^{-04}	0.026	0.114	*CACNA1E*
		21	AX-338048273	27655130	G	0.132	0.448±0.109	2.253×10^{-04}	0.025	0.122	*CACNA1E*
		29	AX-338028298	16938208	A	0.017	-1.087±0.271	2.135×10^{-04}	0.028	0.118	
		29	AX-338028299	16947732	G	0.017	-1.087±0.271	2.135×10^{-04}	0.028	0.118	
	Intelligence	14	AX-337984883	24522730	G	0.225	0.352±0.078	1.730×10^{-04}	0.013	0.145	
		14	AX-338022409	24548084	G	0.225	0.352±0.078	1.730×10^{-04}	0.013	0.145	
		14	AX-338022418	24602982	A	0.174	0.351±0.090	1.178×10^{-03}	0.050	0.110	
		14	AX-338023712	40665048	G	0.237	0.300±0.080	4.363×10^{-04}	0.013	0.106	*MZT1*, *BORA*, *DIS3*, *PIBF1*
		14	AX-338023714	40683674	G	0.239	0.300±0.080	4.117×10^{-04}	0.013	0.107	*BORA*, *DIS3*, *PIBF1*
		14	AX-338023716	40683674	A	0.229	0.284±0.080	8.542×10^{-04}	0.021	0.095	*BORA*, *DIS3*, *PIBF1*
		14	AX-338023725	40782683	G	0.287	0.281±0.071	2.879×10^{-04}	0.013	0.115	*PIBF1*
		14	AX-338078325	40827573	A	0.225	0.295±0.080	6.477×10^{-04}	0.013	0.100	*PIBF1*, *KLF5*
		14	AX-338023734	40865525	A	0.233	0.277±0.077	8.875×10^{-04}	0.013	0.097	*PIBF1*, *KLF5*
		14	AX-338023736	40904517	A	0.221	0.276±0.084	1.977×10^{-03}	0.026	0.082	*KLF5*
		14	AX-337986232	41370829	A	0.483	-0.275±0.066	1.415×10^{-04}	0.013	0.126	*KLF12*
		14	AX-338024712	53034349	A	0.033	0.760±0.201	4.319×10^{-04}	0.022	0.106	

Table 4. *Cont.*

Level of significance	Trait	Chr[1]	rs[2]	Pos[3]	A1[4]	MAF[5]	β±SE[6]	P-value	q-value[7]	PVE[8]	Candidate gene(s) name(s)
Chromosome-wide	Intelligence	14	AX-337987348	54869550	G	0.055	0.571±0.150	7.353×10^{-04}	0.038	0.108	*GPC5*
		14	AX-337987380	55173735	A	0.329	-0.300±0.064	1.748×10^{-04}	0.013	0.152	*GPC5*
		14	AX-338024922	55211008	G	0.2	-0.333±0.082	2.175×10^{-04}	0.014	0.120	*GPC5*
		14	AX-338024929	55258723	A	0.042	0.600±0.176	1.290×10^{-03}	0.050	0.087	*GPC5*
		14	AX-337987579	57425357	A	0.171	0.304±0.085	8.570×10^{-04}	0.050	0.095	*ABCC4*
		14	AX-338025572	62777326	A	0.217	0.280±0.078	8.255×10^{-04}	0.050	0.095	*ERCC5*
		20	AX-338008708	40202723	A	0.161	-0.392±0.083	8.085×10^{-05}	0.012	0.157	*DST*
		21	AX-338010585	24771582	A	0.321	0.272±0.071	4.640×10^{-04}	0.045	0.107	
		21	AX-338105438	27637855	G	0.125	0.458±0.010	2.656×10^{-04}	0.013	0.152	*CACNA1E*
		21	AX-338048273	27655130	G	0.132	0.468±0.010	2.021×10^{-04}	0.013	0.156	*CACNA1E*
	Intelligent Quotient (IQ)	3	AX-337923932	6407091	A	0.121	5.127±1.086	4.104×10^{-05}	0.020	0.156	
		4	AX-337963860	28991717	A	0.037	9.061±1.943	2.700×10^{-03}	0.033	0.153	*TEX10*, *INVS*
		5	AX-337966467	1049490	A	0.437	3.094±0.850	2.9×10^{-04}	0.048	0.010	*PTPN18*
		5	AX-337932262	51633138	A	0.013	17.266±3.077	4.985×10^{-06}	0.001	0.207	
		5	AX-337969963	51800375	G	0.079	5.625±1.467	2.5×10^{-04}	0.048	0.109	
		5	AX-337969978	52001303	G	0.037	8.440±1.956	2.3×10^{-04}	0.032	0.134	*UBE2E3*
		5	AX-337969986	52106921	A	0.029	10.963±2.178	6.011×10^{-05}	0.002	0.174	
		5	AX-338099603	52118548	A	0.029	10.963±2.178	6.011×10^{-05}	0.002	0.174	
		6	AX-338098301	31617037	A	0.185	3.870±0.976	4.367×10^{-04}	0.049	0.115	*SALL2*, *OR10G3*, *OR10G2*, *OR4E2*, *OR4E1*
		6	AX-338069531	31635047	G	0.216	3.832±0.844	7.181×10^{-05}	0.010	0.146	*OR10G3*, *OR10G2*, *OR4E2*, *OR4E1*, *TRAV3*, *TRAV4*
		6	AX-337937067	31691628	G	0.259	3.883±0.856	1.441×10^{-03}	0.010	0.146	*OR4E1*, *TRAV3*, *TRAV4*
		6	AX-337937069	31702577	G	0.108	5.687±1.126	2.5×10^{-03}	0.010	0.175	*TRAV3*, *TRAV4*
		6	AX-337975833	31712105	A	0.267	3.731±0.846	1.688×10^{-03}	0.012	0.140	*TRAV3*, *TRAV4*

Table 4. *Cont.*

Level of significance	Trait	Chr[1]	rs[2]	Pos[3]	A1[4]	MAF[5]	β±SE[6]	P-value	q-value[7]	PVE[8]	Candidate gene(s) name(s)
Chromosome -wide	Intelligent Quotient (IQ)	6	AX-337976385	38911834	G	0.05	7.893±1.728	1.256×10^{-03}	0.010	0.148	*SCFD1*
		6	AX-338069617	38963797	A	0.05	7.893±1.728	1.256×10^{-03}	0.010	0.148	*COCH*, *STRN3*
		6	AX-337976391	39058843	G	0.05	7.893±1.728	1.256×10^{-03}	0.010	0.148	*STRN3*, *U6*, *AP4S1*
		7	AX-337942930	8701842	A	0.271	4.424±1.072	1.216×10^{-04}	0.028	0.124	*PUS7*, *U1*, *SRPK2*
		7	AX-337981374	8739948	G	0.271	4.424±1.072	1.216×10^{-04}	0.028	0.124	*PUS7*, *U1*, *SRPK2*
		7	AX-337981376	8752290	A	0.271	4.424±1.072	1.216×10^{-04}	0.028	0.124	*PUS7*, *U1*, *SRPK2*
		9	AX-337995041	20323326	A	0.067	7.204±1.421	3.877×10^{-06}	0.005	0.176	*ZNF536*
		10	AX-337999835	8752356	A	0.017	12.506±2.788	2.5×10^{-04}	0.042	0.143	
		16	AX-338033076	44513833	A	0.017	12.547±2.842	1.021×10^{-04}	0.027	0.140	*ATP2A3*, *ZZEF1*
		18	AX-337999935	956822	A	0.188	4.542±0.947	1.577×10^{-03}	0.002	0.160	
		18	AX-338037583	956822	A	0.188	4.542±0.947	1.577×10^{-03}	0.002	0.160	
		18	AX-338000259	4973535	A	0.029	10.985±2.216	8.442×10^{-04}	0.002	0.170	
		18	AX-338037909	4981762	G	0.034	8.685±1.9	5.542×10^{-04}	0.002	0.150	
		18	AX-338104223	5033615	A	0.033	8.728±1.9	5.125×10^{-04}	0.002	0.150	
		32	AX-338107363	15037248	A	0.013	16.120±3.353	1.404×10^{-03}	0.007	0.161	*PXN*, *U4*, *SIRT4*, *PLA2G1B*, *MSI1*

[1]Chr:chromosome; [2]rs:identifier code of the SNP; [3]Pos:position in baise pairs; [4]A1:minor allele; [5]MAF, minor allele frequency; [6]β±SE: allelic substitution effect ± standard error; [7]*q*-value: P-values corrected for multiple testing using a false discovery rate approach; [8]PVE: proportion of variance in phenotype explained by a given SNP.

al., 2018), and resistance to paratuberculosis in cattle (Sanchez et al., 2020). Heritable disorders resulting from mutations in the *ERCC5* gene include both cancer and neurodegenerative processes (intracranial malformations and cerebro-oculo-facio-skeletal syndrome) in humans and mice (Kvarnung et al., 2018; Zhu et al., 2012). What's more, *DST* gene has been reported to be implicated in hereditary sensory and autonomic neuropathies in humans and mice (Ferrier et al., 2014).

Lastly, the intelligent quotient was found to be regulated by twenty-seven genes. Such genes play significant roles in the self-renewal, early embryo development, and reprogramming of embryonic stem cells in mice (Ding et al., 2015), and predisposition to intellectual disability in rats (*TEX10*) (Twigger et al., 2002); prevalence and incidence of cardiovascular-renal-hepatic-pancreatic dysplasia in zebrafish, mice and humans (*INVS* and *PTPN18*) (Informatics, 2014; Otto et al., 2003; Simons et al., 2005); human and mice senescence and premature aging, which in turn can be implicated in the development of age-related neurodegenerative processes (*UBE2E3*) (Plafker et al., 2018); incidence of recessive ocular coloboma and neural tube defects in humans and mice (*SALL2*) (Böhm et al., 2008; Kelberman et al., 2014); olfaction (*OR10G2*, *OR10G3*¸*OR4E2*, and *OR4E1*) (Lif Holgerson et al., 2023) and protection against caries (*TRAV4*) in humans (Briseño-Ruiz et al., 2013); increased risk of motor system dysfunctions (i.e., amyotrophic lateral sclerosis and benign hereditary chorea) and several autoimmune diseases in *Drosophila*, humans and rats (*SCFD1*) (Borg et al., 2023; Li et al., 2021; Twigger et al., 2002); high prevalence of progressive cochleo-vestibular dysfunction (reduced linear vestibular evoked potential and sensorineural hearing loss) in humans, mice and rats (*COCH*) (Informatics, 2014; Twigger et al., 2002; Usami et al., 2003); thigmotaxis, hyperactivity, vertical activity, brain-lung-thyroid syndrome, severe intellectual disability, mild fever-sensitive seizure, developmental delay, spastic paraplegia, muscular atrophy, cardiovascular failure, microcephaly, and short stature, in humans and animal models (*STRN3*, *AP4S1*, *PUS7*, *ATP2A3*, *ZZEF1*, and *PXN*) (De Brouwer et al., 2018; Hardies et al., 2015; Hossain et al., 2022; Informatics, 2014; Lenaerts et al., 2021; Ruzicka et al., 2019); regulation of neuronal differentiation and pathogenesis of Alzheimer disease in humans, mice and zebrafish (*ZNF536*, *U1*, and *SRPK2*) (Bai, 2018; Hong et al., 2012; Qin et al., 2009); muscle function, energy and redox metabolism during exercise in mice (*SIRT4*) (Han et al., 2019); incidence of diet-induced obesity and risk of diabetes and atherosclerosis in humans and mice (*PLA2G1B*) (Hollie et al., 2014); and incidence of abnormalities in neurocranium morphology, size and vascular perfusion in mice and rats (*MSI1*) (Informatics, 2014; Twigger et al., 2002).

Conclusions

Interindividual phenotypic variability for zoometrics, biomechanics and behaviour-related traits in dromedary camels is controlled by determinants of polygenic nature and that are located in multiple chromosomes. A total of 124 SNPs, located within 70 different candidate genes responsible for the synthesis of biological products that are mainly involved in the control of several neurodevelopmental processes and sensory perception, have been identified as significantly associated with such functional traits. These results enrich the empirical understanding of the genomic features of early domestication and modern selection in dromedary camels, and will inform future, sustainable breeding and conservation programs for this animal species. Concretely, the combination of genome-selective breeding and proper subagruppation of congeners depending on the similarity for phenotypic characteristics (assortative natural behaviour) at human-controlled environments, will largely support the efforts to preserve camel's health and welfare.

Author contributions: C.I.P, F.J.N.G., E.C. and J.V.D.B. conceived the project and designed the study. C.I.P., F.J.N.G. and J.V.D.B. carried out the phenotypic data collection. M.M., M.A.M.M. and E.C. completed the DNA extractions. C.I.P., M.M. and M.A.M.M. conducted the statistical analyses. C.I.P. and F.J.N.G. wrote the manuscript. All authors contributed to the editing and refinement of the final manuscript.

Funding: The present research was carried out in the financing framework of the international project CA.RA.VA.N - "Toward a Camel Transnational Value Chain" (Reference APCIN-2016-00011-00-00) and during the covering period of a predoctoral contract (FPU Fellowship) funded by the Spanish Ministry of Science and Innovation and a Ramón y Cajal Post-Doctoral Contract with the reference MCIN/AEI/10.13039/501100011033 and the European Union "NextGenerationEU"/PRTR.

Data availability statement: Data subject to third party restrictions. The data that support the findings of this study are available from Animal Breeding Consulting S.L. Restrictions apply to the availability of these data, which were used under license for this study.

Acknowledgments: The authors would also like to thank 'Aires Africanos' Eco-tourism Company, Oasis Park Fuerteventura, and 'Camelus' Camellos de Almería, for their direct technical help and assistance.

Conflicts of interest: The authors declare no conflict of interest.

References

Abdel-Aziem, S. H., Abdel-Kader, H. A., Alam, S. S., & Othman, O. E. (2015). Detection of MspI polymorphism and the single nucleotide polymorphism (SNP) of GH gene in camel breeds reared in Egypt. *African Journal of Biotechnology*, 14(9), 752-757.

Abri, M. A. A., & Faye, B. (2019). Genetic improvement in dromedary camels: challenges and opportunities. *Frontiers in genetics*, 10, 167.

Ahmed, Z. M., Riazuddin, S., Aye, S., Ali, R. A., Venselaar, H., Anwar, S., Belyantseva, P.P., Qasim, M., Riazuddin, S., & Friedman, T. B. (2008). Gene structure and mutant alleles of *PCDH15*: nonsyndromic deafness *DFNB23* and type 1 Usher syndrome. *Human genetics*, 124, 215-223.

Al-Sharif, M., Radwan, H., Hendam, B., & Ateya, A. (2022). DNA polymorphisms of *FGFBP1*, leptin, κ-casein, and αs1-casein genes and their association with reproductive performance in dromedary she-camels. *Theriogenology*, 178, 18-29.

Alagramam, K. N., Murcia, C. L., Kwon, H. Y., Pawlowski, K. S., Wright, C. G., & Woychik, R. P. (2001). The mouse Ames waltzer hearing-loss mutant is caused by mutation of *Pcdh15*, a novel protocadherin gene. *Nature genetics*, 27(1), 99-102.

Alhaddad, H., & Alhajeri, B. H. (2019). Cdrom archive: a gateway to study camel phenotypes. *Frontiers in genetics*, 10, 48.

Almathen, F., Elbir, H., Bahbahani, H., Mwacharo, J., & Hanotte, O. (2018). Polymorphisms in *MC1R* and *ASIP* genes are associated with coat color variation in the Arabian camel. *Journal of Heredity*, 109(6), 700-706.

Andjelkovic, M., Minic, P., Vreca, M., Stojiljkovic, M., Skakic, A., Sovtic, A., Rodic, M., Skodric-Trifunovic, V., Maric, N., Visekruna, J., Spasovski, V., & Pavlovic, S. (2018). Genomic profiling supports the diagnosis of primary ciliary dyskinesia and reveals novel candidate genes and genetic variants. *PloS one*, 13(10), e0205422.

Aytekin, İ., Bayraktar, M., Sakar, Ç. M., & Ünal, İ. (2020). Association between MYLK4 gene polymorphism and growth traits at different age stages in Anatolian black cattle. *Animal biotechnology*, 31(6), 555-560.

Bai, B. (2018). *U1* snRNP alteration and neuronal cell cycle reentry in Alzheimer disease. *Frontiers in Aging Neuroscience*, 10, 75.

Bassuk, A. G., Muthuswamy, L. B., Boland, R., Smith, T. L., Hulstrand, A. M., Northrup, H., Hakeman, M., Dierdorff, J.M., Yung, C.K., Long, A., Brouillette, R.B., Au, K.S., Gurnett, C., Houston, D.W., Cornell, R.A., & Manak, J.R. (2013). Copy number variation analysis implicates the cell polarity gene glypican 5 as a human spina bifida candidate gene. *Human molecular genetics*, 22(6), 1097-1111.

Benamer, N., Marti, F., Lujan, R., Hepp, R., Aubier, T. G., Dupin, A., Frébourg, G., Pons, S., Maskos, U., Faure, P., Hay, Y.A., Lambolez, B., & Tricoire, L. (2018). *GluD1*, linked to schizophrenia, controls the burst firing of dopamine neurons. *Molecular psychiatry*, 23(3), 691-700.

Berg, M., Ågesen, T. H., Thiis-Evensen, E., Merok, M. A., Teixeira, M. R., Vatn, M. H., Nesbakken, A., Skotheim, R.I., & Lothe, R. A. (2010). Distinct high resolution genome profiles of early onset and late onset colorectal cancer integrated with gene expression data identify candidate susceptibility loci. *Molecular cancer*, 9(1), 1-14.

Bitaraf Sani, M., Zare Harofte, J., Banabazi, M. H., Esmaeilkhanian, S., Shafei Naderi, A., Salim, N., Teimoori, A., Bitaraf, A., Zadehrahmani, M., Burger, P.A., Landi, V., Silawi, M., Sheshdeh, A.T., & Faghihi, M.A. (2021). Genomic prediction for growth using a low-density SNP panel in dromedary camels. *Scientific reports*, 11(1), 1-14.

Bitaraf Sani, M., Zare Harofte, J., Banabazi, M. H., Faraz, A., Esmaeilkhanian, S., Naderi, A. S., Salim, N., Teimoori, A., Bitaraf, A., Zadehrahmani, M., Burger, P.A., Asadzadeh, N., Silawi, M., Sheshdeh, A.T., Nazari, B.M., Faghihi, M.A., & Roudbari, Z. (2022). Identification of candidate genes for pigmentation in camels using genotyping-by-sequencing. *Animals*, 12(9), 1095.

Blakey, T. J., Michaels, J. R., Guo, L. T., Hodshon, A. J., & Shelton, G. D. (2017). Congenital myasthenic syndrome in a mixed breed dog. *Frontiers in Veterinary Science*, 4, 173.

Böhm, J., Buck, A., Borozdin, W., Mannan, A. U., Matysiak-Scholze, U., Adham, I., Schulz-Schaeffer, W., Floss, T., Wurst, W., Kohlhase, J., & Barrionuevo, F. (2008). *Sall1*, *sall2*, and *sall4* are required for neural tube closure in mice. *The American journal of pathology*, 173(5), 1455-1463.

Bonanno, C., Rodolico, C., Töpf, A., Foti, F. M., Liu, W.-W., Beeson, D., Toscano, A., & Lochmüller, H. (2020). Severe congenital myasthenic syndrome associated with novel biallelic mutation of the *CHRND* gene. *Neuromuscular Disorders*, 30(4), 336-339.

Borg, R., Purkiss, A., Cacciottolo, R., Herrera, P., & Cauchi, R. J. (2023). Loss of amyotrophic lateral sclerosis risk factor *SCFD1* causes motor dysfunction in *Drosophila*. *Neurobiology of Aging*, 126, 67-76.

Borowska, A., Reyer, H., Wimmers, K., Varley, P. F., & Szwaczkowski, T. (2017). Detection of pig genome regions determining production traits using an information theory approach. *Livestock Science*, 205, 31-35.

Boyle, E. M., Ashby, C., Tytarenko, R. G., Deshpande, S., Wang, H., Wang, Y., Rosenthal, A., Sawyer, J., Tian, E., Flynt, E., Hoering, A., Johnson, S.K., Rutherford, M.W., Wardell, C.P., Bauer, M.A., Dumontet, C., Facon, T., Thanendrarajan, S., Schinke, C.D., Zangari, M., van Rhee, F., Barlogie, B., Cairns, D., Jackson, G., Thakurta, A., Davies, F.E., Morgan, G.J., & Walker, B.A. (2020). *BRAF* and *DIS3* mutations associate with adverse outcome in a long-term follow-up of patients with multiple myeloma. *Clinical Cancer Research*, 26(10), 2422-2432.

Briseño-Ruiz, J., Shimizu, T., Deeley, K., Dizak, P. M., Ruff, T. D., Faraco, I. M., Poletta, F.A., Brancher, J.A., Pecharki, G.D., Küchler, E.C., Tannure, P.N., Lips, A., Vieira, T.C.S., Patir, A., Koruyucu, M., Mereb, J.C., Resick, J.M., Brandon, C.A., Letra, A., Silva, R.M., Cooper, M.E., Seymen, F., Costa, M.C., Granjeiro, J.M., Trevilatto, P.C., Orioli, I.M., Castilla, E.E., Marazita, M.K., & Alexandre R. Vieira (2013). Role of *TRAV* locus in low caries experience. *Human genetics*, 132, 1015-1025.

Burger, P. A., Ciani, E., & Faye, B. (2019). Old World camels in a modern world–a balancing act between conservation and genetic improvement. *Animal Genetics*, 50(6), 598-612.

Cattani, A. A., Allene, C., Seifert, V., Rosenow, F., Henshall, D. C., & Freiman, T. M. (2016). Involvement of micro RNAs in epileptogenesis. *Epilepsia*, 57(7), 1015-1026.

Cen, Z., Jiang, Z., Chen, Y., Zheng, X., Xie, F., Yang, X., Lu, X., Ouyang, Z., Wu, H., Chen, S., Yin, H., Qiu, X., Wang, S., Ding, M., Tang, Y., Yu, F., Li, C., Wang, T., Ishiura, H., Tsuji, S., Jiao, C., Liu, C., Xiao, J., & Wei Luo (2018). Intronic pentanucleotide TTTCA repeat insertion in the *SAMD12* gene causes familial cortical myoclonic tremor with epilepsy type 1. *Brain*, 141(8), 2280-2288.

Choi, T., Fukasawa, K., Zhou, R., Tessarollo, L., Borror, K., Resau, J., & Vande Woude, G. F. (1996). The Mos/mitogen-activated protein kinase (*MAPK*) pathway regulates the size and degradation of the first polar body in maturing mouse oocytes. *Proceedings of the National Academy of Sciences*, 93(14), 7032-7035.

Colledge, W., Carlton, M., Udy, G., & Evans, M. (1994). Disruption of c-mos causes parthenogenetic development of unfertilized mouse eggs. *Nature*, 370(6484), 65-68.

Corcoran, L. M., Koentgen, F., Dietrich, W., Veale, M., & Humbert, P. O. (2004). All known in vivo functions of the *Oct-2* transcription factor require the C-terminal protein domain. *The Journal of Immunology*, 172(5), 2962-2969.

Cosemans, N., Vandenhove, L., Maljaars, J., Van Esch, H., Devriendt, K., Baldwin, A., Fryns, J.P., Noens, I., & Peeters, H. (2018). *ZNF462* and *KLF12* are disrupted by a de novo translocation in a patient with syndromic intellectual disability and autism spectrum disorder. *European Journal of Medical Genetics*, 61(7), 376-383.

Cronin, S., Berger, S., Ding, J., Schymick, J. C., Washecka, N., Hernandez, D. G., Greenway, M.J., Bradley, D.G., Traynor, B.J., & Hardiman, O. (2008). A genome-wide association study of sporadic *ALS* in a homogenous Irish population. *Human molecular genetics*, 17(5), 768-774.

De Brouwer, A. P., Abou Jamra, R., Körtel, N., Soyris, C., Polla, D. L., Safra, M., Zisso, A., Powell, C.A., Rebelo-Guiomar, P., Dinges, N., Morin, V., Stock, M., Hussain, M., Shahzad, M., Riazuddin, S., Ahmed, Z.M., Pfundt, R., Schwarz, F., de Boer, L., Reis, A., Grozeva, D., Raymond, F.L., Riazuddin, S., Koolen, D.A., Minczuk, M., Roignant, J.Y., van Bokhoven, H., & Schwartz, S., (2018). Variants in *PUS7* cause intellectual disability with speech delay, microcephaly, short stature, and aggressive behavior. *The American Journal of Human Genetics*, 103(6), 1045-1052.

De Luca, P., Scarpa, A., Ralli, M., Tassone, D., Cassandro, C., Simone, M., de Campora, L., & Camaioni, A. (2022). Immune-Mediated Association Between Celiac Disease and Sensorineural Hearing Loss: A Systematic Narrative Review. *The Turkish Journal of Gastroenterology*, 33(4), 273.

de Pontual, L., Yao, E., Callier, P., Faivre, L., Drouin, V., Cariou, S., Haeringen, A.V., Geneviève, D., Goldenberg, A., Oufadem, M., Manouvrier, S., Munnich, A., Vidigal, J.A., Vekemans, M., Lyonnet, S., Henrion-Caude, A., Ventura, A., & Amiel, J. (2011). Germline deletion of the miR-17∼ 92 cluster causes skeletal and growth defects in humans. *Nature genetics*, 43(10), 1026-1030.

De Wilde, B., Beckers, A., Lindner, S., Kristina, A., De Preter, K., Depuydt, P., Mestdagh, P., Sante, T., Lefever, S., Hertwig, F., Peng, Z., Shi, L.M., Lee, S., Vandermarliere, E., Martens, L., Menten, B., Schramm, A., Fischer, M., Schulte, J., Vandesompele, J., & Speleman, F., (2018). The mutational landscape of *MYCN*, *Lin28b* and *ALKF1174L* driven murine neuroblastoma mimics human disease. *Oncotarget*, 9(9), 8334.

Ding, J., Huang, X., Shao, N., Zhou, H., Lee, D.-F., Faiola, F., Fidalgo, M., Guallar, D., Saunders, A., Shliaha, P.V., Wang, H., Waghray, A., Papatsenko, D., Sánchez-Priego, C., Li, D., Yuan, Y., Lemischka, I.R., Shen, L., Kelley, K., Deng, H., Shen, X., & Wang, J. (2015). *Tex10* coordinates epigenetic control of super-enhancer activity in pluripotency and reprogramming. *Cell stem cell*, 16(6), 653-668.

Du, C., Deng, T., Zhou, Y., Ye, T., Zhou, Z., Zhang, S., Shao, B., Wei, P., Sun, H., Khan, F.A., Yang, L., & Hua, G. (2019). Systematic analyses for candidate genes of milk production traits in water buffalo (*Bubalus Bubalis*). *Animal Genetics*, 50(3), 207-216.

Eberhardt, D. R., Lee, S. H., Yin, X., Balynas, A. M., Rekate, E. C., Kraiss, J. N., Lang, M.J., Walsh, M.A., Streiff, M.E., Corbin, A.C., Li, Y., Funai, K., Sachse, F.B., & Chaudhuri, D. (2022). *EFHD1* ablation inhibits cardiac mitoflash activation and protects cardiomyocytes from ischemia. *Journal of Molecular and Cellular Cardiology*, 167, 1-14.

Escalier, D. (2006). Knockout mouse models of sperm flagellum anomalies. *Human Reproduction Update*, 12(4), 449-461.

Etard, C., Behra, M., Ertzer, R., Fischer, N., Jesuthasan, S., Blader, P., Geisler, R., & Strähle, U. (2005). Mutation in the δ-subunit of the nAChR suppresses the muscle defects caused by lack of Dystrophin. *Developmental dynamics: an official publication of the American Association of Anatomists, 234(4), 1016-1025.*

Faye, B. (2015). Role, distribution and perspective of camel breeding in the third millennium economies. *Emirates Journal of Food and Agriculture*, 318-327.

Ferrier, A., Sato, T., De Repentigny, Y., Gibeault, S., Bhanot, K., O'Meara, R. W., Lynch-Godrei, A., Kornfeld, S.F., Young, K.G., & Kothary, R. (2014). Transgenic expression of neuronal dystonin isoform 2 partially rescues the disease phenotype of the dystonia musculorum mouse model of hereditary sensory autonomic neuropathy VI. *Human molecular genetics*, 23(10), 2694-2710.

Fitak, R. R., Mohandesan, E., Corander, J., Yadamsuren, A., Chuluunbat, B., Abdelhadi, O., Raziq, A., Nagy, P., Walzer, C., Faye, B., & Burger, P.A. (2020). Genomic signatures of domestication in Old World camels. *Communications biology*, 3(1), 316.

Fontanesi, L., Schiavo, G., Galimberti, G., Calò, D., & Russo, V. (2014). A genome wide association study for average daily gain in Italian Large White pigs. *Journal of animal science*, 92(4), 1385-1394.

Gable, D. L., Gaysinskaya, V., Atik, C. C., Talbot, C. C., Kang, B., Stanley, S. E., Pugh, E.W., Amat-Codina, N., Schenk, K.M., Arcasoy, M.O., Brayton, C., Florea, L., & Armanios, M., (2019). *ZCCHC8*, the nuclear exosome targeting component, is mutated in familial pulmonary fibrosis and is required for telomerase RNA maturation. *Genes & development*, 33(19-20), 1381-1396.

González, F. J. N., Vidal, J. J., Jurado, J. M. L., McLean, A. K., & Bermejo, J. V. D. (2019). Dumb or smart asses? Donkey's (*Equus asinus*) cognitive capabilities share the heritability and variation patterns of human's (*Homo sapiens*) cognitive capabilities. *Journal of Veterinary Behavior*, 33, 63-74.

Goodman, L., & Zallocchi, M. (2017). Integrin α8 and Pcdh15 act as a complex to regulate cilia biogenesis in sensory cells. *Journal of cell science*, 130(21), 3698-3712.

Häfliger, I. M., Seefried, F. R., & Drögemüller, C. (2021). Reverse Genetic Screen for Deleterious Recessive Variants in the Local Simmental Cattle Population of Switzerland. *Animals*, 11(12), 3535.

Häfliger, I. M., Spengeler, M., Seefried, F. R., & Drögemüller, C. (2022). Four novel candidate causal variants for deficient homozygous haplotypes in holstein cattle. *Scientific reports*, 12(1), 5435.

Han, Y., Zhou, S., Coetzee, S., & Chen, A. (2019). *SIRT4* and its roles in energy and redox metabolism in health, disease and during exercise. *Frontiers in Physiology*, 10, 1006.

Hansen Wheat, C., Fitzpatrick, J. L., Rogell, B., & Temrin, H. (2019). Behavioural correlations of the domestication syndrome are decoupled in modern dog breeds. *Nature communications*, 10(1), 2422.

Hardies, K., May, P., Djémié, T., Tarta-Arsene, O., Deconinck, T., Craiu, D., AR working group of the EuroEPINOMICS RES Consortium, Helbig, I., Suls, A., Balling, R., Weckhuysen, S., de Jonghe, P., Hirst, J., Afawi, Z., Barisic, N., Baulac, S., Caglayan, H., Depienne, C., de Kovel, C.G.F., Dimova, P., Guerrero-López, R., Guerrini, R., Hjalgrim, H., Hoffman-Zacharska, D., Jahn, J., Klein, K.M., Koeleman, B.P.C., Leguern, E., Lehesjoki, A.E., Lemke, J., Lerche, H., Marini, C., Muhle, H., Rosenow, F., Serratosa, J.M., Møller, R.S., Stephani, U., Striano, P., Talvik, T., von Spiczak, S., Weber, Y., & Zara, F. (2015). Recessive loss-of-function mutations in *AP4S1* cause mild fever-sensitive seizures, developmental delay and spastic paraplegia through loss of AP-4 complex assembly. *Human molecular genetic*s, 24(8), 2218-2227.

Hayes, B. J., Bowman, P. J., Chamberlain, A. J., & Goddard, M. E. (2009). Invited review: Genomic selection in dairy cattle: Progress and challenges. *Journal of dairy science*, 92(2), 433-443.

He, Z., Guo, X., Tian, S., Zhu, C., Chen, S., Yu, C., Jiang, J., & Sun, C. (2019). MicroRNA-137 reduces stemness features of pancreatic cancer cells by targeting *KLF12*. *Journal of Experimental & Clinical Cancer Research*, 38, 1-16.

Hollie, N. I., Konaniah, E. S., Goodin, C., & Hui, D. Y. (2014). Group 1B phospholipase A2 inactivation suppresses atherosclerosis and metabolic diseases in LDL receptor-deficient mice. *Atherosclerosis*, 234(2), 377-380.

Hong, Y., Chan, C. B., Kwon, I.-S., Li, X., Song, M., Lee, H.P., Liu, X., Sompol, P., Jing, P., Lee, H.G., Yu, S. P., & Ye, K. (2012). *SRPK2* phosphorylates tau and mediates the cognitive defects in Alzheimer's disease. *Journal of Neuroscience*, 32(48), 17262-17272.

Hossain, M. B., Islam, M. K., Adhikary, A., Rahaman, A., & Islam, M. Z. (2022). Bioinformatics Approach to Identify Significant Biomarkers, Drug Targets Shared Between Parkinson's Disease and Bipolar Disorder: A Pilot Study. *Bioinformatics and Biology Insights*, 16, 11779322221079232.

Huang, C., Yang, X., Zeng, B., Zeng, L., Gong, X., Zhou, C., Xia, J., Lian, B., Qin, Y., Yan, L., Liu, L., & Xie, P. (2019). Proteomic analysis of olfactory bulb suggests *CACNA1E* as a promoter of *CREB* signaling in microbiota-induced depression. *Journal of proteomics*, 194, 132-147.

Huang, W., Kazmierczak, K., Zhou, Z., Aguiar-Pulido, V., Narasimhan, G., & Szczesna-Cordary, D. (2016). Gene expression patterns in transgenic mouse models of hypertrophic cardiomyopathy caused by mutations in myosin regulatory light chain. *Archives of biochemistry and biophysics*, 601, 121-132.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Arando Arbulu, A., & Delgado Bermejo, J. V. (2021). The Youngest, the Heaviest and/or the Darkest? Selection Potentialities and Determinants of Leadership in Canarian Dromedary Camels. *Animals*, 11(10), 2886.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Camacho Vallejo, M. E., & Delgado Bermejo, J. V. (2022). Bayesian Linear Regression and Natural Logarithmic Correction for Digital Image-Based Extraction of Linear and Tridimensional Zoometrics in Dromedary Camels. *Mathematics*, 10(19), 3453.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Nogales Baena, S., & Delgado Bermejo, J. V. (2020). Camel Genetic Resources Conservation through Tourism: A Key Sociocultural Approach of Camelback Leisure Riding. *Animals*, 10(9), 1703.

Informatics, M. G. (2014). The International Mouse Phenotyping Consortium (IMPC). Obtaining and Loading Phenotype Annotations from the International Mouse Phenotyping Consortium (IMPC) Database, Database Release.

Ishag, I., Reissmann, M., Eltaher, H., & Ahmed, M. (2013). Polymorphisms of Tyrosinase gene (Exon 1) and its impact on coat color and phenotypic measurements of Sudanese Camel Breeds. *Scientific Journal of Animal Science*, 2(5), 109-115.

Janicke, T., Marie-Orleach, L., Aubier, T. G., Perrier, C., & Morrow, E. H. (2019). Assortative mating in animals and its role for speciation. *The American Naturalist*, 194(6), 865-875.

Karimi, O., Burger, P., Javanmard, A., Roudbari, Z., Mohajer, M., Asadzadeh, N., Harofteh, J.Z., Kazemi, A., & Naderi, A. (2023). A genome-wide association study of morphometric traits in dromedaries. *Veterinary Medicine and Science*, 9(4), 1781.

Kelberman, D., Islam, L., Lakowski, J., Bacchelli, C., Chanudet, E., Lescai, F., Patel, A., Stupka, E., Buck, A., Wolf, S., Beales, P.L., Jacques, T.S., Bitner-Glindzicz, M., Liasis, A., Lehmann, O.J., Kohlhase, J., Nischal, K.K., & Sowden, J.C. (2014). Mutation of *SALL2* causes recessive ocular coloboma in humans and mice. *Human molecular genetics*, 23(10), 2511-2526.

König, S., Simianer, H., & Willam, A. (2009). Economic evaluation of genomic breeding programs. *Journal of dairy science*, 92(1), 382-391.

Koromina, M., Flitton, M., Blockley, A., Mellor, I. R., & Knight, H. M. (2019). Damaging coding variants within kainate receptor channel genes are enriched in individuals with schizophrenia, autism and intellectual disabilities. *Scientific reports*, 9(1), 19215.

Kvarnung, M., Taylan, F., Nilsson, D., Anderlid, B. M., Malmgren, H., Lagerstedt-Robinson, K., Holmberg, E., Burstedt, M., Nordenskjöld, M., Nordgren, A., & Lundberg, E.S. (2018). Genomic screening in rare disorders: New mutations and phenotypes, highlighting *ALG14* as a novel cause of severe intellectual disability. *Clinical Genetics*, 94(6), 528-537.

Lamagna, C., Scapini, P., van Ziffle, J. A., DeFranco, A. L., & Lowell, C. A. (2013). Hyperactivated *MyD88* signaling in dendritic cells, through specific deletion of Lyn kinase, causes severe autoimmunity and inflammation. *Proceedings of the National Academy of Sciences*, 110(35), E3311-E3320.

Lasorsa, V. A., Montella, A., Cantalupo, S., Tirelli, M., de Torres, C., Aveic, S., Tonini, G.P., Ioalscon, A., & Capasso, M. (2022). Somatic mutations enriched in cis-regulatory elements affect genes involved in embryonic development and immune system response in neuroblastoma. *Cancer research*, 82(7), 1193-1207.

Lenaerts, L., Reynhout, S., Verbinnen, I., Laumonnier, F., Toutain, A., Bonnet-Brilhault, F., Hoorne, Y., Joss, S., Chassevent, A.K., Smith-Hicks, C., Loeys, B., Joset, P., Steindl, K., Rauch, A., Mehta, S.J., Chung, W.K., Devriendt, K., Holder, S.E., Jewett, T., Baldwin, L.M., Wilson, W.G., Towner, S., Srivastava, S., Johnson, H.F., Daumer-Haas, C., Baethmann, M., Ruiz, A., Gabau, E., Jain, V., Varghese, V., Al-Beshri, A., Fulton, S., Wechsberg, O., Orenstein, N., Prescott, K., Childs, A.M., Faivre, L., Moutton, S., Sullivan , J.A., Shashi, V., Koudijs, S.M., Heijligers, M., Kivuva, E., McTague, A., Male, A., van Ierland, Y., Plecko, B., Maystadt, I., Hamid, R., Hannig, V.L., Houge, G., & Janssens, V. (2021). The broad phenotypic spectrum of *PPP2R1A*-related neurodevelopmental disorders correlates with the degree of biochemical dysfunction. *Genetics in Medicine*, 23(2), 352-362.

Li, C. Y., Yang, T. M., Ou, R. W., Wei, Q. Q., & Shang, H. F. (2021). Genome-wide genetic links between amyotrophic lateral sclerosis and autoimmune diseases. *BMC medicine*, 19, 1-11.

Li, J., Liu, J., Liu, S., Plastow, G., Zhang, C., Wang, Z., Campanile, G., Salzano, A., Gasparrini, B., Hua, G., Liang, A., & Yang, L. (2018). Integrating RNA-seq and GWAS reveals novel genetic mutations for buffalo reproductive traits. *Animal reproduction science*, 197, 290-295.

Lif Holgerson, P., Hasslöf, P., Esberg, A., Haworth, S., Domellöf, M., West, C. E., & Johansson, I. (2023). Genetic Preference for Sweet Taste in Mothers Associates with Mother-Child Preference and Intake. *Nutrients*, 15(11), 2565.

Lin, S.-C., Kao, S.-Y., Chang, J. C.-Y., Liu, Y.-C., Yu, E.-H., Tseng, S.-H., Liu, C.H., & Chang, K.-W. (2016). Up-regulation of miR-187 modulates the advances of oral carcinoma by targeting *BARX2* tumor suppressor. *Oncotarget*, 7(38), 61355.

Llano, E., Gomez-H, L., García-Tuñón, I., Sánchez-Martín, M., Caburet, S., Barbero, J. L., Schimenti, J.C., Veitia, R.A., & Pendas, A. M. (2014). *STAG3* is a strong candidate gene for male infertility. *Human molecular genetics*, 23(13), 3421-3431.

Ma, C., Khederzadeh, S., Adeola, A. C., Han, X.-M., Xie, H.-B., & Zhang, Y.-P. (2020). Whole genome resequencing reveals an association of *ABCC4* variants with preaxial polydactyly in pigs. *BMC genomics*, 21, 1-13.

Macri, M., Luigi-Sierra, M. G., Guan, D., Delgado, J. V., Alvarez, J. F., Amills, M., & Martínez, A. M. (2023). Univariate and multivariate genome-wide association studies for hematological traits in Murciano-Granadina goats. *Animal Genetics*.

McGowan, K. A., Li, J. Z., Park, C. Y., Beaudry, V., Tabor, H. K., Sabnis, A. J., Zhang, W., Fuchs, H., Hrabé de Angelis, M., Myers, R.M., de Attardi, L., & Barsh, G.S. (2008). Ribosomal mutations cause p53-mediated dark skin and pleiotropic effects. *Nature genetics*, 40(8), 963-970.

McKay, S. D., Schnabel, R. D., Murdoch, B. M., Matukumalli, L. K., Aerts, J., Coppieters, W., Crews, D., Dias Neto, E.D., Gill, C.A., Gao, C., Mannen, H., Stothard, P., Wang, Z., van Tassell, C.P., Williams, J.L., Taylor, J.F., & Moore, S.S., (2007). Whole genome linkage disequilibrium maps in cattle. *BMC genetics*, 8(1), 1-12.

Mroczek, S., & Dziembowski, A. (2013). *U6* RNA biogenesis and disease association. *Wiley Interdisciplinary Reviews: RNA*, 4(5), 581-592.

Murter, B., Pan, X., Ophir, E., Alteber, Z., Azulay, M., Sen, R., Levy, O., Dassa, L., Vaknin, I., Fridman-Kfir, T., Salomon, R., Ravet, A., Tam, A., Levin, D., Vaknin, Y., Tatirovsky, E., Machlenkin, A., Pardoll, D., & Ganguly, S. (2019). Mouse *PVRIG* has CD8+ T cell–specific coinhibitory functions and dampens antitumor immunity. *Cancer immunology research*, 7(2), 244-256.

Nowier, A. M., El-Metwaly, H. A., & Ramadan, S. I. (2020). Genetic variability of tyrosinase gene in Egyptian camel breeds and its association with udder and body measurements traits in Maghrebi camel breed. *Gene Reports*, 18, 100569.

Okamoto, K., Tokunaga, K., Doi, K., Fujita, T., Suzuki, H., Katoh, T., Watanabe, T., Nishida, N., Mabuchi, A., Takahashi, A., Kubo, M., Maeda, S., Nakamura, Y., Noiri, E. (2011). Common variation in *GPC5* is associated with acquired nephrotic syndrome. *Nature genetics*, 43(5), 459-463.

Ott, T., Kaufmann, L., Granzow, M., Hinderhofer, K., Bartram, C. R., Theiß, S., Seitz, A., Paramasivam, N., Schulz, A., Moog, U., Blum, M., & Evers, C.M. (2019). The frog *Xenopus* as a model to study Joubert syndrome: the case of a human patient with compound heterozygous variants in *PIBF1*. *Frontiers in physiology*, 10, 134.

Otto, E. A., Schermer, B., Obara, T., O'Toole, J. F., Hiller, K. S., Mueller, A. M., Ruf, R.G., Hoefele, J., Beekmann, F., Landau, D., Foreman, J.W., Goodship, J.A., Strachan, T., Kispert, A., Wolf, M.T., Gagnadoux, M.F., Nivet, H., Antignac, C., Walz, G., Drummond, I.A., Benzing, T., & Hildebrandt, F. (2003). Mutations in *INVS* encoding inversin cause nephronophthisis type 2, linking renal cystic disease to the function of primary cilia and left-right axis determination. *Nature genetics*, 34(4), 413-420.

Pastrana, C., González, F., Osman, T., Ciani, E., & Bermejo, J. (2023). Curve estimation regression analysis to identify the model that best fits camel biomechanics applications for selective breeding. Proceedings of The 6th Conference of the International Society of Camelid Research and Development (ISOCARD)-The Role of Camel in Food Security and Economic Development.

Pastrana, C. I., González, F. J. N., Ciani, E., Ariza, A. G., & Bermejo, J. V. D. (2021). A tool for functional selection of leisure camels: Behaviour breeding criteria may ensure long-term sustainability of a European unique breed. *Research in Veterinary Science*, 140, 142-152.

Paylakhi, S., Labelle-Dumais, C., Tolman, N. G., Sellarole, M. A., Seymens, Y., Saunders, J., Lakosha, H., de Vries, W.N., Orr, A.C., Topilko, P., John, S.W.M., & Nair, S. (2018). Müller glia-derived *PRSS56* is required to sustain ocular axial growth and prevent refractive error. *PLoS genetics*, 14(3), e1007244.

Pillai, A. M., Thaxton, C., Pribisko, A. L., Cheng, J. G., Dupree, J. L., & Bhat, M. A. (2009). Spatiotemporal ablation of myelinating glia-specific neurofascin (NfascNF155) in mice reveals gradual loss of paranodal axoglial junctions and concomitant disorganization of axonal domains. *Journal of neuroscience research*, 87(8), 1773-1793.

Plafker, K. S., Zyla, K., Berry, W., & Plafker, S. M. (2018). Loss of the ubiquitin conjugating enzyme *UBE2E3* induces cellular senescence. *Redox Biology*, 17, 411-422.

Qin, Z., Ren, F., Xu, X., Ren, Y., Li, H., Wang, Y., Zhai, Y., & Chang, Z. (2009). *ZNF536*, a novel zinc finger protein specifically expressed in the brain, negatively regulates neuron differentiation by repressing retinoic acid-induced gene transcription. *Molecular and cellular biology*, 29(13), 3633-3643.

Rijkers, K., Mescheriakova, J., Majoie, M., Lemmens, E., van Wijk, X., Philippens, M., van Kranen-Mastenbroek, V., Schijns, O., Vles, J., & Hoogland, G. (2010). Polymorphisms in *CACNA1E* and Camk2d are associated with seizure susceptibility of Sprague–Dawley rats. *Epilepsy research*, 91(1), 28-34.

Rothschild, M. F. (2004). Porcine genomics delivers new tools and results: this little piggy did more than just go to market. *Genetics Research*, 83(1), 1-6.

Rúa, A. C. (2017). *Genética cuantitativa*: Editorial Síntesis.

Ruzicka, L., Howe, D. G., Ramachandran, S., Toro, S., Van Slyke, C. E., Bradford, Y. M., Eagle, A., Fashena, D., Frazer, K., Kalita, P., Mani, P., Martin, R., Moxon, S.T., Paddock, H., Pich, C., Schaper, K., Shao, X., Singer, A., & Westerfield, M. (2019). The Zebrafish Information Network: new support for non-coding genes, richer Gene Ontology annotations and the Alliance of Genome Resources. *Nucleic acids research*, 47(D1), D867-D873.

Sabahat, S., Nadeem, A., Brauning, R., Thomson, P. C., & Khatkar, M. S. (2022). Genome wide association study for growth in Pakistani dromedary camels using genotyping-by-sequencing. *Animal Bioscience*, 36(7), 1010.

Sakakibara, I., Yanagihara, Y., Himori, K., Yamada, T., Sakai, H., Sawada, Y., Takahashi, H., Saeki, N., Hirakawa, H., Yokoyama, A., Fukada, S.O., Sawasaki, T., & Imai, Y. (2021). Myofiber androgen receptor increases muscle strength mediated by a skeletal muscle splicing variant of *Mylk4*. *Iscience*, 24(4), 102303.

Sanchez, M.P., Guatteo, R., Davergne, A., Saout, J., Grohs, C., Deloche, M.C., Taussat, S., Fritz, S., Boussaha, M., Blanquefort, P., Delafosse, A., Joly, A., Schibler, L., Fourichon, C., & Boichard, D. (2020). Identification of the *ABCC4*, *IER3*, and *CBFA2T2* candidate genes for resistance to paratuberculosis from sequence-based GWAS in Holstein and Normande dairy cattle. *Genetics Selection Evolution*, 52(1), 1-17.

Shi, S.Y., Li, L.J., Zhang, Z.-J., Wang, E.Y., Wang, J., Xu, J.W., Liu, H.B., Wen, Y.F., He, H., Lei, C.Z., Chen, G., & Huang, Y.Z. (2020). Copy number variation of *MYLK4* gene and its growth traits of *Capra hircus* (goat). *Animal Biotechnology*, 31(6), 532-537.

Shim, H., Chasman, D. I., Smith, J. D., Mora, S., Ridker, P. M., Nickerson, D. A., Krauss, R.M., & Stephens, M. (2015). A multivariate genome-wide association analysis of 10 LDL subfractions, and their response to statin treatment, in 1868 Caucasians. *PLoS one*, 10(4), e0120758.

Shindo, T., Manabe, I., Fukushima, Y., Tobe, K., Aizawa, K., Miyamoto, S., Kawai-Kowase, K., Moriyama, N., Imai, Y., Kawakami, H., Nishimatsu, H., Ishikawa, T., Suzuki, T., Morita, H., Maemura, K., Sata, M., Hirata, Y., Komukai, M., Kagechika, H., Kadowaki, T., Kurabayashi, M., & Nagai, R. (2002). Krüppel-like zinc-finger transcription factor *KLF5*/*BTEB2* is a target for angiotensin II signaling and an essential regulator of cardiovascular remodeling. *Nature medicine*, 8(8), 856-863.

Simons, M., Gloy, J., Ganner, A., Bullerkotte, A., Bashkurov, M., Krönig, C., Schermer, B., Benzing, T., Cabello, O.A., Jenny, A., Mlodzik, M., Polok, B., Driever, W., Obara, T., & Walz, G. (2005). Inversin, the gene product mutated in nephronophthisis type II, functions as a molecular switch between Wnt signaling pathways. *Nature genetics*, 37(5), 537-543.

Smith, M. A., Katsouri, L., Virtue, S., Choudhury, A. I., Vidal-Puig, A., Ashford, M. L., & Withers, D. J. (2018). Calcium channel CaV2. 3 subunits regulate hepatic glucose production by modulating leptin-induced excitation of arcuate pro-opiomelanocortin neurons. *Cell reports*, 25(2), 278-287. e274.

Sondka, Z., Bamford, S., Cole, C. G., Ward, S. A., Dunham, I., & Forbes, S. A. (2018). The COSMIC Cancer Gene Census: describing genetic dysfunction across all human cancers. *Nature Reviews Cancer*, 18(11), 696-705.

Sun, T., Huang, G.Y., Wang, Z.H., Teng, S.H., Cao, Y.H., Sun, J.I., Hanig, Q., Chen, N.B., Lei, C.Z., & & Liao, Y.Y. (2020). Selection signatures of Fuzhong Buffalo based on whole-genome sequences. *BMC genomics*, 21, 1-10.

Sun, T., Pei, S., Liu, Y., Hanif, Q., Xu, H., Chen, N., Lei, C., & Yue, X. (2023). Whole genome sequencing of simmental cattle for SNP and CNV discovery. *BMC genomics*, 24(1), 179.

Takeda, N., Manabe, I., Uchino, Y., Eguchi, K., Matsumoto, S., Nishimura, S., Shindo, T., Sano, M., Otsu, K., Snider, P., Conway, S.J., & Nagai, R. (2010). Cardiac fibroblasts are essential for the adaptive response of the murine heart to pressure overload. *The Journal of clinical investigation*, 120(1), 254-265.

Tao, L., He, X., Wang, F., Pan, L., Wang, X., Gan, S., Di, R., & Chu, M.X. (2021). Identification of genes associated with litter size combining genomic approaches in Luzhong mutton sheep. *Animal Genetics*, 52(4), 545-549.

Thisse, B., Pflumio, S., Fürthauer, M., Loppin, B., Heyer, V., Degrave, A., & Charbonnier, X. (2001). Expression of the zebrafish genome during embryogenesis. *ZFIN direct data submission*.

Tirozzi, A., Quiccione, M. S., Cerletti, C., Donati, M. B., de Gaetano, G., Iacoviello, L., & Gialluisi, A. (2023). A Multi-Trait Association Analysis of Brain Disorders and Platelet Traits Identifies Novel Susceptibility Loci for Major Depression, Alzheimer's and Parkinson's Disease. *Cells*, 12(2), 245.

Tonne, J. M., Sakuma, T., Deeds, M. C., Munoz-Gomez, M., Barry, M. A., Kudva, Y. C., & Ikeda, Y. (2013). Global gene expression profiling of pancreatic islets in mice during streptozotocin-induced β-cell damage and pancreatic Glp-1 gene therapy. *Disease models & mechanisms*, 6(5), 1236-1245.

Twigger, S., Lu, J., Shimoyama, M., Chen, D., Pasko, D., Long, H., Ginster, H., Chen, C.F., Nigam, R., Kwitek, A., Eppig, H., Maltais, L., Maglott, D., Schuler, G., Jacob, H., & Tonellato, P.J. (2002). Rat Genome Database (RGD): mapping disease onto the genome. *Nucleic acids research*, 30(1), 125-128.

Ulisse, V., Dey, S., Rothbard, D. E., Zeevi, E., Gokhman, I., Dadosh, T., Minis, A., & Yaron, A. (2020). Regulation of axonal morphogenesis by the mitochondrial protein Efhd1. *Life Science Alliance*, 3(7).

Ünalp, A., Coskunpinar, E., Gunduz, K., Pekuz, S., Baysal, B. T., Edizer, S., Hayretdag, C., & Gudeloglu, E. (2022). Detection of deregulated miRNAs in childhood epileptic encephalopathies. *Journal of Molecular Neuroscience*, 72(6), 1234-1242.

Ung, D. C., Tricoire, L., Pietrancosta, N., Zlatanovic, A., Pode-Shakked, B., Raas-Rothschild, A., Elpeleg, O., Abu-Libdeh, B., Hamed, N., Papon, M.A., Marouillat, S., Thépault, R.A., Stevanin, G., Lambolez, B., Toutain, a., Hepp, R., & Laumonnier, F. (2022). *GRID1*/GluD1 homozygous variants linked to intellectual disability and spastic paraplegia impair mGlu1/5 receptor signaling and excitatory synapses. *medRxiv*, 2022-05.

Unlu, G., Gamazon, E. R., Qi, X., Levic, D. S., Bastarache, L., Denny, J. C., Roden, D.M., Mayzus, I., Breyer, M., Zhong, X., Konkashbaerv, A.I., Rzhetsky, A., Knapik, E.W., & Cox, N.J. (2019). *GRIK5* genetically regulated expression associated with eye and vascular phenomes: discovery through iteration among biobanks, electronic health records, and zebrafish. *The American Journal of Human Genetic*s, 104(3), 503-519.

Usami, S.-i., Takahashi, K., Yuge, I., Ohtsuka, A., Namba, A., Abe, S., Fransen, E., Patthy, L., Otting, G., & van Camp, G. (2003). Mutations in the *COCH* gene are a frequent cause of autosomal dominant progressive cochleo-vestibular dysfunction, but not of Meniere's disease. *European journal of human genetics*, 11(10), 744-748.

Verhagen, A. M., Wallace, M. E., Goradia, A., Jones, S. A., Croom, H. A., Metcalf, D., Collinge, J.E., Maxwell, M.J., Hibbs, M.L., Alexander, W.S., Hilton, D.J., Kile, B.T., & Starr, R. (2009). A kinase-dead allele of Lyn attenuates autoimmune disease normally associated with Lyn deficiency. *The Journal of Immunology*, 182(4), 2020-2029.

Vogt, J., Harrison, B. J., Spearman, H., Cossins, J., Vermeer, S., ten Cate, L. N., Morgan, N.V., Beeson, D., & Maher, E.R. (2008). Mutation analysis of *CHRNA1*, *CHRNB1*, *CHRND*, and *RAPSN* genes in multiple pterygium syndrome/fetal akinesia patients. *The American Journal of Human Genetics*, 82(1), 222-227.

Vogt, J., Morgan, N. V., Rehal, P., Faivre, L., Brueton, L. A., Becker, K., Fryns, J.P., Holder, S., Islam, L., Kivuva, E., Lynch, S.A., Touraine, R., Wilson, L.C., MacDonals, F., & Maher, E.R. (2012). *CHRNG* genotype–phenotype correlations in the multiple pterygium syndromes. *Journal of medical genetics*, 49(1), 21-26.

Wang, X., Wang, J., Raza, S. H. A., Deng, J., Ma, J., Qu, X., Yu, S., Zhang, D., Alshammari, A.M., Almohaimeed, H.M., & Zan, L. (2022). Identification of the hub genes related to adipose tissue metabolism of bovine. *Frontiers in Veterinary Science*, 9.

Ward, A., Hopkins, J., Mckay, M., Murray, S., & Jordan, P. W. (2016). Genetic interactions between the meiosis-specific cohesin components, *STAG3*, *REC8*, and *RAD21L*. *G3: Genes, Genomes, Genetics*, 6(6), 1713-1724.

Wasilewska, I., Gupta, R. K., Palchevska, O., & Kuźnicki, J. (2019). Identification of zebrafish calcium toolkit genes and their expression in the brain. *Genes*, 10(3), 230.

Webb, S. (1972). Locomotor evolution in camels. *Forma et function: An international journal of functional biology*.

Wiebe, S., Meng, X. Q., Kim, S.-H., Zhang, X., Lacaille, J.-C., Aguilar-Valles, A., & Sonenberg, N. (2020). The eIF4E homolog *4EHP* (eIF4E2) regulates hippocampal long-term depression and impacts social behavior. *Molecular autism*, 11, 1-16.

Wilkins, A. S., Wrangham, R. W., & Fitch, W. T. (2014). The “domestication syndrome” in mammals: a unified explanation based on neural crest cell behavior and genetics. *Genetics*, 197(3), 795-808.

Wissinger, B., Schaich, S., Baumann, B., Bonin, M., Jägle, H., Friedburg, C., Varsányi, B., Hoyng, C.B., Dollfus, H., Heckenlively, J.R., Rosenberg, T., Rudolph, G., Kellner, Y., Salati, R., Plomp, A., de Baere, E., Andrassi-Darida, M., Sauer, A., Wolf, C., Zobor, D., Bernd, A., Leroy, B.P., Enyedi, P., Cremers, F.P.M., Lorenz, B., Zrenner, E., & Kohl, S. (2011). Large deletions of the *KCNV2* gene are common in patients with cone dystrophy with supernormal rod response. *Human mutation*, 32(12), 1398-1406.

Won, K., Kim, D., Hwang, I., Lee, H.-K., & Oh, J.-D. (2023). Genome-wide association studies on collagen contents trait for meat quality in Hanwoo. *Journal of Animal Science and Technology*, 65(2), 311.

Wu, P., Chen, L., Cheng, J., Pan, Y., Zhu, X., Bao, L., Chu, W., & Zhang, J. (2021). The miRNA expression profile directly reflects the energy metabolic differences between slow and fast muscle with nutritional regulation of the Chinese perch (*Siniperca chuatsi*). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 259, 111003.

Wu, Y., Liu, W., Chen, J., Liu, S., Wang, M., Yang, L., Chen, C., Qi, M., Xu, Y., Qiao, Z., Yan, R., Kou, X., Zhao, Y., Shen, B., Yin, J., Wang, H., & Gao, Y. (2019). Nuclear exosome targeting complex core factor Zcchc8 regulates the degradation of *LINE1* RNA in early embryos and embryonic stem cells. *Cell Reports*, 29(8), 2461-2472. e2466.

Young, T. R., Bourke, M., Zhou, X., Oohashi, T., Sawatari, A., Fässler, R., & Leamey, C. A. (2013). Ten-m2 is required for the generation of binocular visual circuits. *Journal of Neuroscience*, 33(30), 12490-12509.

Zaqout, S., & Kaindl, A. M. (2022). Autosomal recessive primary microcephaly: not just a small brain. *Frontiers in Cell and Developmental Biology*, 9, 3635.

Zhang, C., Dong, S.-S., Xu, J.-Y., He, W.-M., & Yang, T.-L. (2019). PopLDdecay: a fast and effective tool for linkage disequilibrium decay analysis based on variant call format files. *Bioinformatics*, 35(10), 1786-1788.

Zhang, J., Wu, X., & Huang, L. (2022). *ZNF574* Promotes Ovarian Cancer Cell Proliferation and Migration through Regulating AKT and AMPK Signaling Pathways. *Annals of Clinical & Laboratory Science*, 52(4), 611-620.

Zhang, M., Sun, L., He, D., Chen, J., Dong, Z., Liang, H., Cao, Y., Cai, B., & & Yang, H. (2020). Mammalian-unique *eIF4E2* maintains GSK3β proline kinase activity to resist senescence against hypoxia. *bioRxiv*, 2020-10.

Zhang, Z., Zariwala, M. A., Mahadevan, M. M., Caballero-Campo, P., Shen, X., Escudier, E., Duriez, B., Bridoux, A.M., Leigh, M., Gerton, G.L., Kennedy, M., Amselem, S., Knowles, M.R., & Strauss, J.F. (2007). A heterozygous mutation disrupting the *SPAG16* gene results in biochemical instability of central apparatus components of the human sperm axoneme. *Biology of reproduction*, 77(5), 864-871.

Zhou, X., & Stephens, M. (2014). Efficient multivariate linear mixed model algorithms for genome-wide association studies. *Nature methods*, 11(4), 407-409.

Zhu, M.L., Wang, M., Cao, Z.G., He, J., Shi, T.Y., Xia, K.Q., Qiu, L.X., & Wei, Q.Y. (2012). Association between the *ERCC5* Asp1104His polymorphism and cancer risk: a meta-analysis. *PLoS One*, 7(7), e36293.

CHAPTER 6

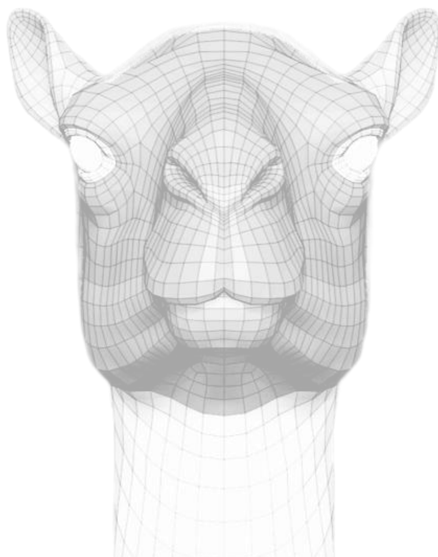
SOCIOCULTURAL DIMENSIONS OF CAMELBACK LEISURE RIDING TOURS

6.1 Camel genetic resources conservation through tourism: a key sociocultural approach of camelback leisure riding

Carlos Iglesias Pastrana[1], Francisco Javier Navas González[1], Elena Ciani[2], Sergio Nogales Baena[1] and Juan Vicente Delgado Bermejo[1]

[1]Department of Genetics, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain

[2]Department of Biosciences, Biotechnologies and Biopharmaceutics, Faculty of Veterinary Sciences, University of Bari 'Aldo Moro', 70121 Bari, Italy



Quality indicator information provided on the publication

Status of the manuscript: Published

Journal (year, volume, page(s)): *Animals* 2020, *10*, 1703

International database in which it is indexed: Journal of Citation Reports (JCR)

Thematic area in the reference database: Veterinary Sciences

Impact index of the journal in the year of the article's publication: 2.752

Rank/number of thematic area journals: 19/146 (Q1)

Abstract

Camels are exotic elements, which can be comprised within adventure travel companies promoting ecotourism activities. Such recreations contribute to sustainable livelihoods for local communities and educational empowerment towards nature and its conservation. At present, some local camel breeds' survival reduces to this animal-based leisure industry and its reliability to perform and promote customized services accurately. By conducting an on-site questionnaire to customers participating in camelback riding tours, we assessed the motivational factors affecting participation, satisfaction, and loyalty in this tourism segment that may have made it socially differentiated. The sixfold combination of staff performance, culture geography, diverse and humane close interaction, camel behavior and performance, sociotemporal context, and positive previous experience involves the elemental dimensions that explain customer satisfaction and return intention probability within this entertainment business. Customer knowledge is essential for stakeholders to build personalized riding experiences and align profits with environmental sustainability and biodiversity mainstream concerns into their everyday operations. In turn, domestic camel tourist rides could be managed as a viable path to nature conservation by helping endangered local breeds to avoid their functional devaluation and potential extinction.

Keywords

Animal-based tourism, camelback riding, quality service, customer satisfaction, return intention probability, biodiversity conservation

Introduction

Animal-based tourism is an emerging business around the world, which lets holidaymakers closely view or interact with animals. The interaction between animals and tourists may be the basis on which to support conservation and/or an educational purpose (Carr, 2009; Moorhouse et al., 2015). The animal species involved, the type of encounter, its surrounding, and animal welfare subjective perception play a pivotal role in the experience making potential or authenticity for visitors (Holopainen, 2012). Besides, certain species and naturalness leisure activities are commonly found to be iconic and/or unique for some destinations and often linked to the livelihoods of local communities (Stone, Lenao, & Moswete, 2019).

Tourists engage with a country or region's culture not only for its past heritage but for its practices in a living context (Robinson & Picard, 2006). The reconsideration of attractions as huge promotors for local communities' economic development and sustainable enhancement (Kiráľová, 2019), also requires that inhabitants undergo substantial cultural and social changes, both positive and negative, to adapt to the new demands derived from these touristic resources. The impacts occurring via tourism may lead to changes in societal structure and values in different traditional daily practices (Du Cros & McKercher, 2020). Additionally, tourists' daily decisions may impact animals and local residents in travel destinations. This, in turn, may imply foreign and local people attitudes towards animal welfare may evolve as a result of these animals or species used in the creation of tourism experiences being simply conceived as economic resources (García-Rosell & Hancock, 2020).

Increasing social awareness on animal welfare issues has made animal-human touristic encounters face harsh constant criticism and global concerns over the years about the wider impacts on animals' freedom violation (Schmidt-Burbach, Ronfot, & Srisangiam, 2015). For this reason, tourism companies involved in this leisure experiences have started to implement innovative techniques (behavioral/environmental enrichment, proper feeding and nursing). In other words, animal welfare has progressively become a critical criterion for tour operators when selecting their suppliers and aiming at satisfying tourists' demands, as the latter are more conscious about positive animal well-being support when choosing to book an animal-based tourism service (Shaheer, Carr, & Insch, 2019).

For camel-based tourism, research briefings on the social side and economic impact of this subsector worldwide are noticeably scarce. Donlon, Donlon, and Agrusa (2010) and Seifu, Angassa, and Boitumelo (2018) underlined the relevance of camel wrestling in Turkey and camel ecotourism in Botswana, respectively, and its potential as a heritage resource within this animal-based tourism enterprise. The investigation of the sociocultural attractions for foreign visitors of these animal-associated spectacles in Turkey was carried out by Çalıskan (2010). Instead, no comprehensive quantitative data regarding public perspective about camel-human leisure interactions, the most relevant factors that lead customers to make use of these activities and those potentially conditioning their general satisfaction and return intention probability, are available.

To the knowledge of the authors, the present paper constitutes the first holistic approach in this applied-research field, largely focusing on domestic camel rides in Spain. Originally from the nearest African coast, the one-humped camel (*Camelus dromedarius*) arrived in the Canary Islands around 1405 accompanying the first human expeditions of the European colonization of the islands (Mejías, 2014; Morera, 1991). Their rapid adaptation to the climate and orographic conditions of this emplacement led to the expansion of the camel herd throughout the archipelago, although its presence was and still is higher in the southern areas of Gran Canaria, Tenerife, and the whole insular territory of Fuerteventura and Lanzarote (Schulz, 2008; Schulz et al., 2010); less numerous and isolated herds could be found along the Iberian Peninsula, mainly in southern areas. After several decades of isolation and health-based importing restrictions from other geographically closed camel populations, dromedaries in Canary

Islands could differentiate themselves as a distinct breed through evolution and genetic drift (Wilson & Gutierrez, 2015).

For centuries, Canarian camels participated in multiple agricultural labors, military operations, and as beast of burden at short and long distances [16]. According to historical chronicles (Millares Cantero et al., 2011; Verneau et al., 1981), the opening of island ports to Atlantic traffic in the late 1800s led to the evolvement of an active tourism network that completely changed the functional destination of these animals in the islands a few decades later. The mechanization of agricultural works and transportation means from the last third of 20th century made its census suffer a dramatic reduction in rural areas (Iglesias et al., 2020a) and being this species progressively adapted to the transport of tourists instead (Mejías, 2014). Fortunately, tourism rise and expansion in the 1990s resulted in a population recovery. Since then, these animals have a cardinal role in the tourism industry, which is the principal income source for local camel breeders (Wilson & Gutierrez, 2015) apart from the European Union live animal market (Faye, 2013; Romero, Marrero, & Moreno, 2012). Other emerging but still minoritarian productive niches of this breed, which lack phenotypic characterization and selection programs, are milk, meat, and wool (Díaz Medina, 2017; MAPAMA, 2019).

The current census of this camel breed is estimated on 1200 individuals, and it is included in the Spanish Official Catalogue of Livestock as an endangered autochthonous breed since 2012 by the Order AAA/251/2012 of the Spanish Ministry of Agriculture, Food and Environment. As it constitutes the only Spanish and European traditional camel population, this distinctive breed deserves functional revaluation for selective breeding with conservation purposes (Iglesias et al., 2020a, 2020b, 2020c). With this objective, an in-depth assessment of camel tourism dimensions is fully required given its far-iconic tourism attractiveness.

The present research aims at identifying which are the most important quality service attributes or demand features that influence customer general satisfaction and return intention probability in camel-riding tourist walks. Comprehensive data gathering animal attributes (behavioral features, welfare status, and global performance), staff attitudes, tourist motivations, and overall satisfaction have been recorded. The applicative results are intended to drive such popular recreational ridings in the most sustainable way as possible, both for the welfare of the animals themselves and their long-term viability as an ecotourism alternative, fortifying avenues in camel production and biodiversity conservation strategies (Hall, 2010). Additionally, the exploration of consumer attitudes and preferences towards camel-riding experiences can provide insights to further reorientation and research on other leisure events such as educational activities and assisted therapy in which the camel is an element of the interactive experience.

Theoretical background

Riding camel conformation/performance and customer satisfaction

Camels are capable to travel long distances in the desert and other sandy areas on minimum energy expenditure even under extreme environmental conditions (Gebreyohanes & Assen, 2017). However, when used in recreational rides, these animals may have to walk on tarred, hard-surfaced grounds that can injure their soles and make the animal lame. It is, therefore, very important to provide additional cares to their feet and legs, since rideability or suitability as riding subjects in animals is notedly influenced by the rhythm and quality of the gaits, apart from personality traits (Graf, von Borstel, & Gauly, 2013).

In this sense, saddle camels are sought to be well-balanced, tough, energetic, and stable on their limbs so they are light and agile in its movements, and thus, the rider can find camel riding easy and feel comfortable, both at slow and fast gaits. Their bones are finer in comparison to those camels used as beasts of burden and their feet are medium-sized, large enough to support both their own weight and the rider's and small enough to move with agility on sandy soils. Although these conformational features may be desirable for the tasks that they are required to develop, animals lacking some of them can be also trained to become riding camels, with the inconvenience that they may offer a less comfortable interaction with the rider, especially over long journeys (Khan, Arshad, & Riaz, 2003).

Concerning comfort of sitting on camel's back, as their gravity center is supposed to be about 15 cm above and behind the elbow, it is preferable for the rider's position to be in front of the hump for better control over the animal. Furthermore, due to the particular style of walking of camels as an adaptation for sandy environments (Iglesias et al., 2020b), instead of trying to resist the camel swaying, it is preferable to keep the balance while rocking along with the camel movements, not against them. For novel riders, a position behind the hump is preferred since it could provide the rider with a higher sense of security (Khan et al., 2003). An alternative option may be using the more complex English saddle, iron-made and composed of a pair of lateral sitting platforms both with seatbelt.

In addition to the aforementioned physical features, riding camels may be indirectly selected considering the dimensions of their personality or for the psychological attributes being involved in the learning of the tasks that they are required to be engaged in, during training sessions and tourist walks (Iglesias, Navas, et al., 2020c). Effective training methods both inherited from tradition and backed by science in working animals, aligned with the camel's natural learning abilities, will allow for the most efficient way of physical, physiological, and psychological stresses withstanding. Hence, visitors would be provided with a worthwhile experience as a result of an outstanding suitable workout.

Tourism geography and culture

The territorial nature of tourism has become an object of study by social sciences for a wider understanding of the key geographical factors that operate in the territory when creating tourist development processes. It is indisputable that tourism is a spatial phenomenon as the set of activities or experiences it comprises cannot take place in the absence of physical space (Dunets et al., 2019), where a set of objects, both natural and cultural, acts as a tourist attraction. Territorial development patterns are based on the physical and regional geography and competitiveness and reflect special attributes of these resources around which tourism is built (Bejarano, 2009).

Although for architectural tourism, stakeholders focus development policies around the site or sites in question, rural or nature-based tourism may present a dispersing effect (Williams, 1998). At a geographical range, this last type of tourism comprises numerous relatively small-scaled sites where different rural lifestyle activities are offered (Roberts & Hall, 2001). However, some natural resources (i.e., plant or animal species or peculiar orography) are exclusive (autochthonous) of concrete places for pure ecological reasons. Such exclusive place-specific attractions might have the potential to increasingly improve destination attractiveness and bring economic support for nature conservation if well managed.

On the other hand, the symbolic and representational dimension of tourism or the notion of space as a product of a certain type of social practices provides a better comprehension of the processes of the social and cultural transformation of a community in its encounter with the tourist community (Pung, Gnoth, & Del Chiappa, 2020). In this perception of tourism as a force for social and cultural change, the tourist dynamic is subjected to the permanent search for new forms of organization of space and territorial configuration to preserve the cultural richness of destinations, while answering sustainability concerns and fulfilling the interests of the communities that inhabit these territories and traveler motivations (Williams, 1998). In the same context, tourism geography helps to integrate the processes of the social construction of spaces, social relations, mental perceptions and representations, experiences, and interests of both receiving communities and tourists in the exercise of ordered territorial planning of the tourist phenomena (Saarinen, Rogerson, & Hall, 2017).

Staff attitudes and quality service

Several research studies have inquired into the direct connection between employees' positive and negative behaviors and customers' overall satisfaction with service encounters (Dinu & Dinu, 2019). They all conclude that the higher the required standards staff attitudes and productivity reach, the more appropriate care and effort costumers will be served with. In this scene, companies must promote their employees' understanding of their role in business success through investing time, money, and effort on their development, engagement, and positivity. Such adequate training and proper resources' disposal will, in turn, be translated into the fulfilment of customers' needs and goals and also be reflected in staff manners towards the company, coworkers, and customers (Zhang et al., 2019). At last, consumers' assertive judgment may influence the financial growth and stability of the service company as their positive satisfaction leads to their trust and willingness in promoting the enterprise and its products to others as well. Moreover, consumer bolstering drives further opportunities when seeking for investors and suppliers, which will only embrace partnerships with business organizations that fairly succeed in customers' expectations attainment (Fornell et al., 2020).

Customer knowledge in domestic animal tourism

In the last decades, biological local resources (wild and domestic flora and fauna) have become major appealing subjects within ecotourism. The sustainability of ecotourism involves responsible traveling to natural areas, environmental sustainability, and social responsibility towards nature preservation (Fennell, 2020). These natural attractions act as direct financial support for nature self-sustaining and conservation and for some territories they represent a high percentage of the gross domestic product (Tuohino & Hynonen, 2001).

Specific consumers attempt to escape from massive destinations and get involved in activities that let them disconnect from their daily routine and enrich their environmental consciousness (Meleddu & Pulina, 2016). Some of these distractions promote close interactions with domestic animals in fenced pens or vast territories under controlled conditions (Bertella, 2014; Moorhouse et al., 2015), being tourists provided with exceptional and memorable experiences. They order for interactive encounters that allow them to satisfy a combination of social, recreational, and personal emotional needs at the same time they contribute to financial empowerment for local people. In the purchasing election, they prioritize those destinations and travel suppliers that are known to follow animal welfare's management standardized practices and nature sustainable exploitation's principles according to personal previous experience(s), previous experience(s) of others, and media promotion (Black & Crabtree, 2007; Sheppard & Fennell, 2019). The emotional capabilities of animals per se contribute to create an hedonic encounter, which improves experience memorability and then can add psycho-pedagogical values to the activity (Bertella, 2014).

Demographic structure compels all age groups and a uniform distribution of both genders. Regarding customer social profile within this tourism brand, they are generally medium and superior educated with high purchasing powers. This latter finding could explain their willingness to pay more for tourism companies with recognized financial promotion of environmental awareness, nature conservation, and locals' economic empowerment (Center for Responsible Travel, 2009).

Tourism and animal ethics

Tourists are increasingly offered nature experiences involving animals as the prime focus both ex situ or in the animal's natural habitat. In this context, camels are sometimes forced to perform in ways that are uncommon and improper for their species that rises environmental and social concerns. This situation has driven this entertainment industry to reassess its specific guidelines for an integrative sustainable approach not only aiming enjoyment but also emphasizing educational intentions and corresponding to animal rights (Sheppard & Fennell, 2019). New inquiries into the moral acceptability of animal use for human pleasure and the proper cares they need to be supplied with if used for recreation activities should be therefore addressed. In this regard, Hall and Brown (2006) state that the viability of tourism operations strongly depends on the extent in which animal welfare concerns are present within tourism industry.

Nonetheless, despite large literature can be consulted on the welfare of animals immersed in the major animal sector (laboratories and factory farming), respective work for animals used for entertainment purposes continues to be a minority. The small number of respective studies in this field are brief theoretical summaries and species-contextualized researches that use the concept of animal welfare in a general manner (Burns, 2004; Duffy & Moore, 2011; Orams, 2004; Wearing & Jobberns, 2010). Furthermore, since the maintenance of high levels of welfare markedly depends on animal species and also on idiosyncratic temperament features, complex ethological characterizations and animal welfare official regulations are widely available for many species but remains scarce for others (i.e., camels) (Iglesias Pastrana et al., 2020). In this scenario, until more objective data are available for practical use, it becomes crucial to take into account that not only forced works by trainers but also the disability of these and the riders to interpret animal behavior and/or needs and sometimes anthropomorphism attitudes (the misattribution of human traits, emotions, or intentions to nonhuman entities) are detrimental to optimal animal welfare (McLean & McGreevy, 2010).

Conclusively, the real impact of these activities thus is an emerging contemporary research topic within this specific consumption experience and tourism policies that needs further efforts (Fennell, 2015). In case of absence of a species-specific ethogram, environmental enrichment programs and well-being subjective appraisal of animals before, during and after participating in leisure activities can be regularly performed by multistep evaluation general protocols (de Mori et al., 2019). Ethical operations will be reached through management decisions, the impacts this industry has on animals minimized and the social reputation of these interactive experiences improved toward an ethics-focused oncoming in tourism planning (Fennell, 2019).

Material and methods

Study sample

Our animal sample comprises 8 dromedaries (6 males and 2 females; aged between 4 and 32 years), and the English type saddles were used for tourist rides. All the consumers that booked and enjoyed a camel ride with independence from their country of origin (Table 1) during the research period (1 July to 30 September 2019) were asked to voluntarily fulfil an on-site questionnaire.

Study area

The present empirical inquiry is based on the investigation of a particular case, which may be suitable for extrapolation to similar enterprises as they all share homogeneous framework elements and strategies, i.e., camel breeding in nationally protected arid and semiarid areas and their exploitation in touristic activities (Travis, 2011). Protected areas are a key part of programs to conserve biodiversity and ecosystems as they are conceived as large terrain extensions where multidisciplinary management strategies can be executed both for protecting natural resources (physiographic regions, biotic communities, genetic heritage, and unimpaired natural processes) and promoting education and recreation (Dudley et al., 2010).

Located in southwestern Spain (Andalusia Autonomous Community), Doñana National Park is a natural reserve that covers 54,252 ha, with a socioeconomic influence area of 200,601.86 ha. Due to its privileged geographical location between two continents and its proximity to the meeting point of the Atlantic Ocean and the Mediterranean Sea, this nature reserve represents the confluence of different ecosystems (marshes, shallow streams, and sand dunes) that make it to be classified as a single natural landscape. It is considered as the largest nature reserve in Europe and is declared as a World Heritage Site by United Nations Educational, Scientific and Cultural Organization (UNESCO) (UNESCO World Heritage Centre, 1994).

Dromedaries or one-humped camels were presumably introduced in this emplacement from the Canary Islands in 1829 by the Marquis of Molina as beasts of burden and finally disappeared for poaching practices by the 1950s after having escaped from herds to the wild (Chapman & Buck, 1893, 2019). Fortunately, domestic dromedaries have been progressively reintroduced in limited herds in this reserve intended to serve as an ecotourism icon.

With an estimated average of 250,000 visitors per year (2017 Summary Report of National Parks Network, Ministry for Ecological Transition and Demographic Challenge, Government of Spain), a total distribution area greater than other national parks where Canarian camels are raised (Teide National Park 18,990 ha; Timanfaya National Park 5107.50 ha) (Figure 1), the historical presence of these animals and its orographic and climatic characteristics, the Doñana National Park could become a potential location for camel breeding and thus contributing to the conservation of this threatened indigenous breed. What's more, Andalusia is one of the main tourist destinations in Spain (Tourism Statistics, National Statistics Institute), which may be a potential issue when appealing to customers to be involved in this entertaining recreation.

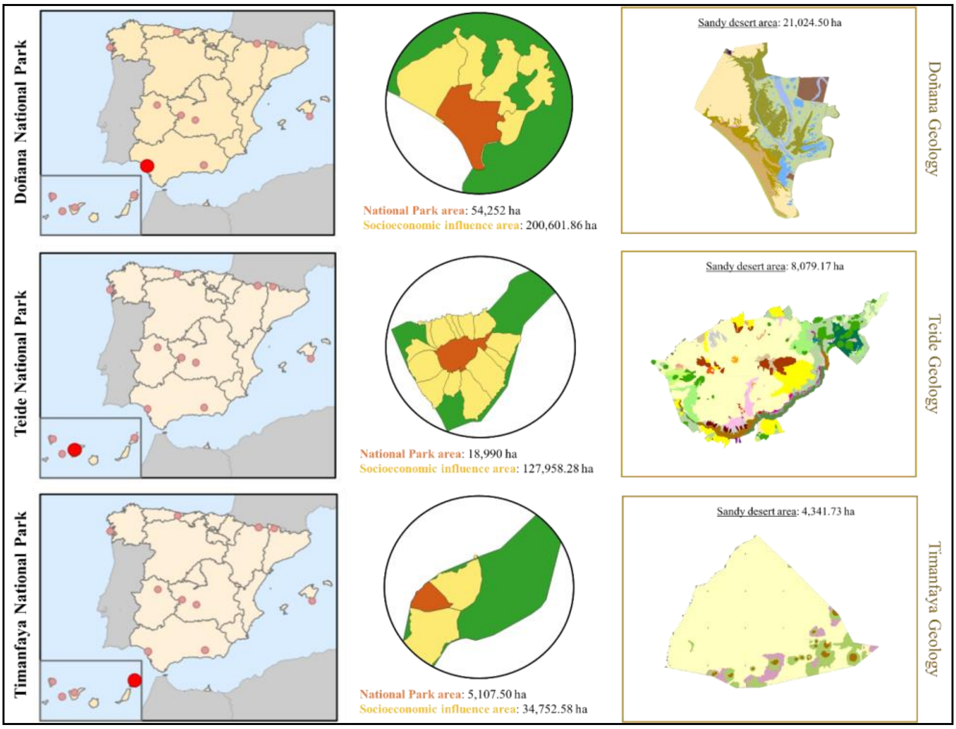


Figure 1. Quantum Geographical Information System (QGIS) maps displaying geographical location, surface, and geology of Doñana, Teide, and Timanfaya National Parks. Sandy desert area's extension within each National Park is light-yellow colored.

The knowledge of the sociocultural dimensions of this tourism alternative will allow, on the one hand, its value enhancement in Doñana National Park, the strengthening of the socioeconomic status in the area of socioeconomic influence of the park's natural and cultural values, and its constitution as a potential alternative economic niche for the conservation of Canarian camels. In the Canary Islands, where these activities are already part of the usual inventory of tourism companies and the camel is an identifying emblem within local sand landscapes, in addition to the aforementioned benefits, the results of this research will greatly facilitate the extent promotion and empowerment of these activities as a sustainable iconic tourist choice.

By conducting an on-site visitor questionnaire survey after the completion of the trip, we could assess visitors' profiles, their general satisfaction with these activities, and their return intention probability. The questionnaire was available in four languages (Spanish, English, French, and Portuguese), and it was designed through a deep review of consumer behavior researches in domestic animal tourism.

These written questionnaires were completed from 1 July to 30 September 2019, which is high season for southern Spain and thus, the business has higher demand. All the camel-riding consumers during the research period were asked to voluntarily fulfil the questionnaire. They all received basic training and guidance on the best practices for riding camels before the walk started.

The visitor survey was designed to collect multiple data. First of all, demographics (gender, age, and nationality), sociotemporal variables (month of visit and travel companions), other personal data of interest (study level, previous experience in camel riding, and personal perception of involved camels' well-being), and factors affecting the decision-making process in tourism customers when choosing a destination (interests, motivations, and business duties). Riders' overall satisfaction was assessed through the evaluation of staff performance, camel behavior/welfare, and service quality. Last, customer knowledge about camel functionalities, previous experience in camel-riding, and social awareness/agreement with the potential of such touristic rides in endangered breeds conservation and intention to return were considered. Staff performance appraisal includes language abilities, knowledge of camels and nature, manners, social abilities, and willingness to serve (Sigurðardóttir & Helgadóttir, 2015). Service quality was evaluated through the dynamic and varied nature of the ride, consumer perception on whether walk length is proper or not, and overall perceived quality. Relationship between price and quality-quantity can be inferred from global customer contentment on just mentioned characteristics (short, adequate, or long journey, and whether the user suggests some improvement or not), based on the relative importance of price in quality and value judgments for consumer's satisfaction and return intention probability (Zeithaml, 1988). For instance, Homburg, Hoyer, and Koschate (2005) reported that as satisfaction increases, the negative impact of the magnitude of a price increase is weakened.

According to literature, there is no single type of Likert scale that fits best to all the issues (Kline, 2008). For this reason, we used a mixed-scale approach to measure customer satisfaction and attitudes towards camel rides. The number of items within each scale was also variable depending on the characteristic being evaluated. Travel motivation, staff performance, and quality service were asked to be measured on a 10-point Likert scale. On the other hand, camel behavior and welfare as well as personal attitudes towards camel tourism and other functional niches were rated on a 5-point Likert scale. When evaluating services, atmosphere and expectations fulfilment in tourism, longer response scales are preferable since they will reflect reliable distinctions among individuals' responses and thus increase total valid score variance, measurement precision, and method validity (Coelho & Esteves, 2007; Simms et al., 2019). Contrastingly, for psychological constructs (i.e., personality traits and behavioral intentions or attitudes towards a certain topic), rating scales are preferred to be odd-numbered as they include a mid, neutral alternative that allows respondents to express a neutral opinion and minimize potential ambiguity between adjacent categories (Kline, 2008), which should preferably be avoided when evaluating behavior.

Data statistical analysis

General model: factors and variables considered

The questions included in the on-site visitor questionnaire survey were turn into the independent factors and dependent variables considered for the general model used in this study. Factors considered in the general model were organized in clusters, namely, customer and trip profile, decision-making motivating factors, staff performance, camel behavior, quality of riding route, previous experience, and customer impressions, whereas dependent variables were considered in the cluster of customer satisfaction and loyalty. Independent factors and dependent variables comprising each cluster are shown in Table 2.

Parametric assumptions testing and approach decision

Shapiro-Francia W' test (for $5 \leq n \leq 1000$ samples) was performed to study data distribution using the Shapiro-Francia normality routine of the Stata Version 15.0 software (StataCorp, 2017). Levene's test was performed to determine the homogeneity of variance across groups using the explore procedure of the descriptive statistics package in SPSS Statistics, Version 25.0, IBM Corp. (Corp., 2017). As provided parametric assumptions were grossly violated (Supplementary Table S1) and the strong subdivision occurring when testing for the effect of multiple factors may condition results, a Bayesian approach was followed to avoid power and precision loss in a relatively small data sample context as suggested by Hox et al. (2014) and Lee and Song (2004).

Relationship between factors and variables

Once parametric assumptions had been tested and as a previous step to simple linear regression, potential multicollinearity and factor redundancy problems were discarded using Bayesian inference for Pearson correlations. Bayesian inference for Pearson correlations was performed to identify the relationship between variable pairs to detect and discard a multicollinearity issue between redundant factors (generalized Pearson correlation coefficient over 0.8 across variable pairs (Signori, 2019) using the Pearson correlation task from the Bayesian statistics procedure in SPSS Statistics, Version 25.0, IBM Corp. (Corp., 2017).

Multifactorial dimensionality reduction

Multifactorial dimensionality reduction can help to identify meaningful capturing the information (variability) for specific sets of factors within a dataset. One of the reference methods to perform dimensionality reduction effectively is principal component analysis (PCA). Kaiser-Meyer-Olkin (KMO) test of sampling adequacy and Bartlett's test of sphericity was computed to establish the validity of the data set. Bartlett's test of sphericity was performed to determine whether variables are unrelated and therefore unsuitable for structure detection. Initial and extraction communalities were assessed to determine which variables should be maintained or discarded from PCA. The cumulative proportion of variance criterion was finally employed to determine the number of components to extract. Cronbach alpha statistic was used to determine the reliability and validity of the reduced variable set. All statistical tests referred above were performed using SPSS Statistics for Windows statistical software, Version 25.0, IBM Corp. (Corp., 2017). Component loadings lower than |0.5| were ruled out provided their confounding nature. Varimax with Kaiser normalization rotated component was performed to reduce the number of factors to be included in our general model (Fernández Álvarez et al., 2020), as it identifies which of all the factors considered are able to capture the maximum fraction possible of the variability in the dataset (significantly loaded factors ≥ 0.5).

Bayesian linear regression modelling for customer general satisfaction and return intention probability

Once meaningful variability capturing factors had been identified (significantly loaded factors for each of the six dimensions identified by PCA), we built two separate simple linear regression predictive models comprising those factors holding a significant linear relationship with dependent variables of customer general satisfaction and return intention probability in regards to camel tourist walks (dependent variables), respectively. To this aim, the Linear Regression package from the Bayesian statistics task of SPSS Statistics for Windows, Version 25.0, IBM Corp. (Corp., 2017) was used. A full description of the algorithms used by SPSS to perform Bayesian Inference on Multiple Linear Regression Models in this study can be found in the public document IBM SPSS Statistics Algorithms Version 25.0. by IBM Corp. (Corp., 2017). The Bayesian Linear Regression test routine of the Linear Regression and related package of the Stata Version 16.0 software process was used to compute posterior distribution statistics for each factor included in each model for each dependent variable.

Model validity

Acceptance rate, efficiency, and Monte Carlo standard error (MCSE) were used to determine the validity of the Bayesian methods implemented. The acceptance rate is the proportion of proposed values of β that were included in our final Markov chain Monte Carlo (MCMC) sample. The asymptotically optimal acceptance rate is 0.234 under quite general conditions (Roberts, Gelman, & Gilks, 1997). Efficiency describes mixing properties of the Markov chain. High efficiency means good mixing (low autocorrelation) in the MCMC sample, and low efficiency means bad mixing (high autocorrelation) in the MCMC sample. An efficient Metropolis–Hastings (MH) sampler has an AR between 15% and 50% (Roberts & Rosenthal, 2001) and low autocorrelation and thus relatively large effective sample size (ESS) for all model parameters. The Monte Carlo standard error (MCSE) is an approximation of the error in estimating the true posterior mean.

Bayesian statistics predictive accuracy of the model (Kaplan & Depaoli, 2012) can be estimated through posterior predictive checking (Gelman et al., 2013). The posterior predictive p values (PPP values), as defined in Appendix C of Lee and Song (2003), were computed as a goodness of fit measure for the model being tested, with a value around 0.5 indicating a plausible good-fitting model and values toward the extremes of 0 or 1 indicating that the model is not plausible. This is because the PPP values is the proportion of time during an MCMC run that a chosen test statistic, generated from a distribution predicted by the model, is higher than the test statistic generated from the distribution of the actual input data.

The marginal likelihood, also known as the evidence, or model evidence, is the denominator of the Bayes equation. Log marginal likelihood was performed to determine the performance of data fit implementing a penalty as model complexity increases (Aydin et al. 2014). The model reporting the highest log marginal likelihood is precisely the model that is the best sequential predictor of the data tested according to the log scoring rule (Chickering & Heckerman, 1996). A difference of 0.01 between two log-likelihood values is considered to be the same model. A difference of more than 3 log likelihood units (considered as "strong evidence against competing model") can be used as threshold for accepting a more parameter-rich model (Aydin et al., 2014). A positive log likelihood means that the likelihood is larger than 1. This is possible because the log likelihood is not itself the probability of observing the data, but just proportional to it (Edwards, 1992).

The ability to explain or capture the variability observed in the data set being studied (AIC and AICc) and the predictive potential (BIC) of the model designed for the data being modeled were computed as well (Clyde et al., 2019; Drton & Plummer, 2017; Karangeli et al., 2011). In statistics, the Bayesian information criterion (BIC), Schwarz information criterion (SIC), Schwarz Bayesian criterion (SBC), or Schwarz Bayesian information criterion (SBIC) is a criterion for model selection among a finite set of models; the model with the lowest BIC is preferred. BIC is defined as—2 times the approximated log marginal likelihood (multiplied by—2 for historical reasons given most goodness-of-fit statistics are on the deviance scale). It is calculated as—$2L_m + m\ln n$, where n is the sample size, L_m is the maximized log-likelihood of the model, and m is the number of parameters in the model. The index takes into account both the statistical goodness of fit and the number of parameters that have to be estimated to achieve this particular degree of fit, by imposing a penalty for increasing the number of parameters (Clyde et al., 2019; Drton & Plummer, 2017). Using BIC, we can approximate the Bayes factor between two models by their R-squared and the numbers of predictors used in the models, when we have large sample of data, which makes the comparison more effective. Additionally, mean square error was computed to measure how close a regression line is to a set of points, that is how good a certain model fits the data being observed and to calculate the minimum mean-square error (MMSE).

Results

Respondents sample

The total number of respondents was 131 (55 males and 76 females), that is the total number of camel-riding consumers during the research period (1 July to 30 September 2019). Customer qualitative profile (age, nationality, study level, and travel companions) is represented in Figure 2. Table 1 compiles quantitative demographics of camelback riding customers.

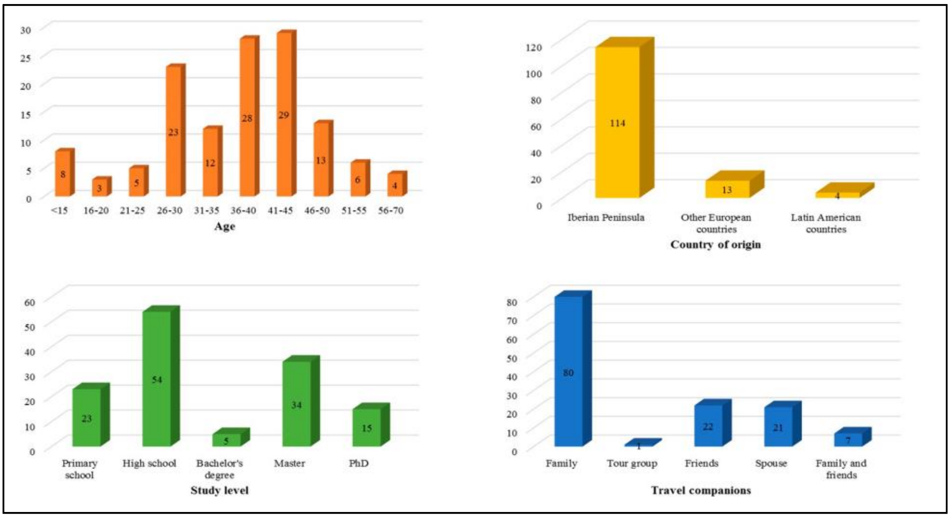


Figure 2. Outputs from camelback riding customer's qualitative profile frequency analysis.

Table 1. Camelback riding customer's demographics.

Country of origin		Number of visitors
Iberian Peninsula	Northern provinces	33
	Middle provinces	34
	Southern provinces	46
	Balearic Islands	1
Other European countries	Denmark	3
	France	2
	Germany	5
	Italy	3
Latin American countries	Argentina	1
	Cuba	1
	Honduras	1
	Venezuela	1

Descriptive statistical analysis

A summary of the descriptive statistics for the variables and potential conditioning factors of customer general satisfaction and return intention probability in regards to camel tourist walks is included in Table 2. In regards to user complacency on walk overall quality, 62% of respondents were satisfied and highly satisfied.

Table 2. Summary of descriptive statistics of factors and variables of customer's general satisfaction and return intention probability in regards to camel tourist walks.

Clusters	General Model Factors and Dependent Variables	Mean	SEM	Median	Mode	SD	CV	Variance	IQR	Min	Max	Percentile 25	Percentile 75
Customer and trip profile	Month of visit	8.33	0.12	8.00	8.00	1.33	15.93	1.76	8.00	2.00	10.00	8.00	9.00
	Sex	1.59	0.04	2.00	2.00	0.49	31.07	0.25	1.00	1.00	2.00	1.00	2.00
	Age	5.73	0.19	6.00	7.00	2.12	37.05	4.51	9.00	1.00	10.00	4.00	7.00
	Country origin	1.15	0.04	1.00	1.00	0.44	37.83	0.19	2.00	1.00	3.00	1.00	1.00
	Study level	3.73	0.12	3.00	3.00	1.38	37.02	1.91	6.00	1.00	7.00	3.00	5.00
	Travel companion	2.05	0.12	1.00	1.00	1.40	68.44	1.97	5.00	1.00	6.00	1.00	3.00
Decision-making motivating factors	Camel knowledge	7.09	0.32	8.00	10.00	3.18	44.78	10.08	9.00	1.00	10.00	5.00	10.00
	Environmental knowledge	7.62	0.25	8.00	10.00	2.40	31.51	5.77	9.00	1.00	10.00	5.75	10.00
	Andalusian culture	7.28	0.27	8.00	8.00	2.44	33.50	5.95	9.00	1.00	10.00	6.00	9.00
	Andalusian friends/relatives	6.46	0.45	8.00	10.00	3.74	57.85	13.96	9.00	1.00	10.00	1.75	10.00
	Special event in Andalusia	5.49	0.51	6.00	1.00	3.58	65.26	12.84	9.00	1.00	10.00	1.00	9.00
	Conference/meeting	3.87	0.60	1.00	1.00	3.74	96.54	13.96	9.00	1.00	10.00	1.00	8.00

Table 2. *Cont.*

Clusters	General Model Factors and Dependent Variables	Mean	SEM	Median	Mode	SD	CV	Variance	IQR	Min	Max	Percentile 25	Percentile 75
Decision-making motivating factors	Education/research	4.76	0.52	5.00	1.00	3.54	74.39	12.54	9.00	1.00	10.00	1.00	8.00
	Business	3.14	0.53	1.00	1.00	3.17	101.05	10.07	9.00	1.00	10.00	1.00	5.00
	Holidays	9.41	0.17	10.00	10.00	1.82	19.30	3.30	9.00	1.00	10.00	10.00	10.00
Staff performance	Language abilities	9.48	0.08	10.00	10.00	0.94	9.96	0.89	5.00	5.00	10.00	9.00	10.00
	Camel knowledge	9.75	0.07	10.00	10.00	0.74	7.59	0.55	6.00	4.00	10.00	10.00	10.00
	Nature knowledge	9.49	0.10	10.00	10.00	1.15	12.09	1.32	7.00	3.00	10.00	9.00	10.00
	Manners	9.80	0.05	10.00	10.00	0.61	6.19	0.37	4.00	6.00	10.00	10.00	10.00
	Social skills	9.70	0.08	10.00	10.00	0.91	9.36	0.83	8.00	2.00	10.00	10.00	10.00
	Willingness to serve	9.77	0.08	10.00	10.00	0.92	9.39	0.84	9.00	1.00	10.00	10.00	10.00
Camel behavior	Unfocused/Distracted	1.46	0.09	1.00	1.00	0.86	58.90	0.74	4.00	1.00	5.00	1.00	2.00
	Calm/Awaiting	4.24	0.11	5.00	5.00	1.25	29.53	1.57	4.00	1.00	5.00	4.00	5.00
	Mistrustful	1.31	0.09	1.00	1.00	0.79	60.23	0.62	4.00	1.00	5.00	1.00	1.00
	Fearful	1.22	0.08	1.00	1.00	0.67	55.16	0.45	4.00	1.00	5.00	1.00	1.00
	Depressed	1.12	0.06	1.00	1.00	0.54	47.95	0.29	4.00	1.00	5.00	1.00	1.00

Table 2. *Cont.*

Clusters	General Model Factors and Dependent Variables	Mean	SEM	Median	Mode	SD	CV	Variance	IQR	Min	Max	Percentile 25	Percentile 75
Camel behavior	Curious	2.93	0.14	3.00	3.00	1.25	42.76	1.57	4.00	1.00	5.00	2.00	4.00
	Surprised	1.52	0.10	1.00	1.00	0.84	55.07	0.70	4.00	1.00	5.00	1.00	2.00
	Rejection	1.11	0.04	1.00	1.00	0.39	34.77	0.15	2.00	1.00	3.00	1.00	1.00
	Indifferent/Irresponsive	1.48	0.11	1.00	1.00	0.95	64.46	0.91	4.00	1.00	5.00	1.00	2.00
	Cautious	3.05	0.16	3.00	3.00	1.43	46.95	2.05	4.00	1.00	5.00	2.00	4.00
	Nervous	1.37	0.09	1.00	1.00	0.76	55.69	0.58	3.00	1.00	4.00	1.00	1.00
Quality of riding route	Secure	9.75	0.05	10.00	10.00	0.58	5.99	0.34	3.00	7.00	10.00	10.00	10.00
	Interesting	9.21	0.10	10.00	10.00	1.08	11.77	1.18	5.00	5.00	10.00	9.00	10.00
	Varied	8.53	0.15	9.00	10.00	1.57	18.39	2.46	8.00	2.00	10.00	7.25	10.00
	Appropriately long	8.87	0.17	10.00	10.00	1.77	20.00	3.15	9.00	1.00	10.00	8.00	10.00
	Walk overall quality	3.02	0.10	4.00	4.00	1.15	38.08	1.32	3.00	1.00	4.00	2.00	4.00
Previous experience	Previous experience	1.66	0.04	2.00	2.00	0.48	28.73	0.23	1.00	1.00	2.00	1.00	2.00
	When did previous experience take place?	9.62	1.07	9.50	10.00	6.91	71.83	47.75	26.00	1.00	27.00	3.75	15.00

Table 2. *Cont.*

Clusters	General Model Factors and Dependent Variables	Mean	SEM	Median	Mode	SD	CV	Variance	IQR	Min	Max	Percentile 25	Percentile 75
Previous experienc e	Comparison between experiences	4.05	0.18	4.00	5.00	1.11	27.36	1.23	4.00	1.00	5.00	3.00	5.00
	Did you receive previous training before the walk?	1.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00	1.00	1.00	1.00	1.00
Customer impressio ns	Personal impression on involved camels' welfare	2.50	0.05	3.00	3.00	0.59	23.48	0.35	2.00	1.00	3.00	2.00	3.00
	Do you think this tourism activity has wide impacts on camel health and welfare?	3.13	0.10	3.00	4.00	1.12	35.75	1.25	4.00	1.00	5.00	2.00	4.00

Table 2. *Cont.*

Clusters	General Model Factors and Dependent Variables	Mean	SEM	Median	Mode	SD	CV	Variance	IQR	Min	Max	Percentile 25	Percentile 75
Customer impressions	Personal impression on camel riding as a sustainable tourism activity	4.45	0.07	5.00	5.00	0.77	17.24	0.59	4.00	1.00	5.00	4.00	5.00
	Easiness of camel-back riding	3.02	0.08	3.00	3.00	0.92	30.40	0.84	3.00	1.00	4.00	3.00	4.00
	Comfortability of camel-back riding	2.53	0.07	3.00	3.00	0.66	25.97	0.43	2.00	1.00	3.00	2.00	3.00
	Familiarity towards the uses of camels in the world	2.15	0.11	2.00	1.00	1.06	49.16	1.12	4.00	1.00	5.00	1.00	3.00

Table 2. *Cont.*

Clusters	General Model Factors and Dependent Variables	Mean	SEM	Median	Mode	SD	CV	Variance	IQR	Min	Max	Percentile 25	Percentile 75
Customer impressions	What do you think camels are raised for?	7.71	0.56	5.00	5.00	6.17	80.05	38.09	26.00	1.00	27.00	3.00	10.00
	Consciousness about the usefulness of such activities in endangered camels breeding and conservation	3.30	0.11	3.00	3.00	1.26	38.30	1.60	4.00	1.00	5.00	2.00	4.00
	Walk length	1.79	0.04	2.00	2.00	0.41	22.96	0.17	1.00	1.00	2.00	2.00	2.00
Customer satisfaction and loyalty	General satisfaction	2.36	0.06	2.00	2.00	0.67	28.43	0.45	4.00	1.00	5.00	2.00	3.00
	Return intention probability	3.98	0.09	4.00	4.00	0.98	24.60	0.96	4.00	1.00	5.00	4.00	5.00

Dimensionality reduction

Table 3 and Table 4 show a summary of general model clusters and the factors that each of them comprised, Varimax with Kaiser normalization rotated component loadings for each of these factors, eigenvalues, and percentage of variability in the dataset that is explained by each resulting principal component dimension.

Considering the factors of the general model clustered together on each principal component dimension, we determine the existence of the following factor dimensions: Principal Component Dimension 1 (PC1) or staff performance and trust-based camel-human partnership, Principal Component Dimension 2 (PC2) or sociospatial motivating factors, Principal Component Dimension 3 (PC3) or diverse and humane close interaction, Principal Component Dimension 4 (PC4) or camel behavior and performance, Principal Component Dimension 5 (PC5) or sociotemporal context, and Principal Component Dimension 6 (PC6) or camelback riding previous experience.

Varimax with Kaiser normalization rotated component loadings determined Principal Component Dimension 1 (PC1) or staff performance and trust-based camel-human partnership comprised the factors of language abilities, staff's camel knowledge, nature knowledge, manners, social skills, and willingness to serve; Principal Component Dimension 2 (PC2) or socio-spatial motivating factors comprised the factors of customers' camel knowledge, environmental knowledge, Andalusian culture, Andalusian friends/relatives, special event in Andalusia, conference/meeting, education/research, or business; Principal Component Dimension 3 (PC3) or diverse and humane close interaction comprised the factors of route being varied and adequately long, personal impression on involved camels' welfare, and familiarity towards worldwide camel uses; Principal Component Dimension 4 (PC4) or camel behavior and performance involved the factors of camel being unfocused/distracted, fearful, surprised or rejective, and the knowledge of customers about functional niches of camels worldwide; Principal Component Dimension 5 (PC5) or sociotemporal context comprised the factors of month of the visit, animal involved in the touristic rides, travel companion, and the knowledge of customers about functional niches of camels worldwide; Principal Component Dimension 6 (PC6) or camelback riding previous experience which was constituted by previous experience and time to previous experience of camel rides.

Table 3. Summary of general model clusters and factors that each cluster comprised and Varimax with Kaiser normalization rotated component loadings for each of these factors.

Clusters	General Model Factors	PC1	PC2	PC3	PC4	PC5	PC6
Customer and trip profile	Month of visit	-0.003	0.322	-0.200	0.433	0.670	-0.411
	Animal	-0.064	0.191	-0.193	0.464	0.796	-0.293
	Sex	-0.096	0.270	-0.106	-0.137	-0.026	0.070
	Age	-0.082	0.120	0.026	-0.336	-0.160	-0.211
	Country of origin	0.061	-0.339	0.076	0.319	-0.056	0.178
	Study level	0.043	-0.003	0.091	-0.335	-0.299	0.094
	Travel companion	0.017	-0.061	0.148	-0.414	-0.766	0.270
Decision-making motivating factors	Customers' camel knowledge	0.260	0.743	-0.104	-0.090	-0.007	0.113
	Environmental knowledge	0.050	0.767	-0.049	-0.142	-0.086	0.198
	Andalusian culture	0.009	0.808	-0.089	-0.192	-0.185	0.114
	Andalusian friends/relatives	-0.009	0.695	-0.034	-0.328	-0.077	0.116
	Special event in Andalusia	-0.002	0.789	-0.091	-0.169	-0.058	0.037
	Conference/meeting	0.020	0.865	-0.136	-0.009	-0.019	0.084
	Education/research	0.023	0.872	-0.108	0.019	-0.033	0.046
	Business	0.034	0.802	-0.114	0.227	-0.131	0.142
	Holidays	0.422	0.419	-0.127	-0.020	0.208	-0.188
Staff performance	Language abilities	1.171	-0.054	-0.067	-0.065	-0.032	-0.080
	Staff's camel knowledge	1.172	-0.052	-0.060	-0.064	-0.026	-0.078
	Nature knowledge	0.881	-0.048	-0.034	0.026	-0.040	0.003
	Manners	1.171	-0.060	-0.069	-0.069	-0.032	-0.077
	Social skills	1.171	-0.061	-0.059	-0.066	-0.032	-0.079
	Willingness to serve	1.172	-0.061	-0.058	-0.063	-0.033	-0.079
Camel behavior	Unfocused/Distracted	0.082	-0.081	-0.015	0.571	-0.406	-0.203
	Calm/Awaiting	0.270	-0.097	0.338	0.047	0.049	-0.308
	Mistrustful	-1.168	0.067	0.068	0.066	0.029	0.075
	Fearful	0.016	0.106	-0.004	0.707	-0.500	-0.137
	Depressed	0.007	-0.091	0.032	0.454	-0.273	-0.094
	Curious	0.048	0.052	0.030	0.412	-0.068	-0.028
	Surprised	0.026	0.303	-0.048	0.694	-0.499	-0.112
	Rejection	0.025	0.177	-0.011	0.700	-0.499	-0.055
	Indifferent/Irresponsive	-0.036	-0.304	0.048	0.134	-0.222	-0.139
	Cautious	0.058	0.220	-0.091	-0.135	0.287	0.189
	Nervous	-0.004	0.063	-0.025	0.393	-0.229	0.000

Table 3. *Cont.*

Clusters	General Model Factors	PC1	PC2	PC3	PC4	PC5	PC6
Quality of riding route	Secure	-0.018	0.278	0.275	-0.140	0.328	-0.176
	Interesting	0.430	0.172	0.406	0.143	0.196	0.131
	Varied	0.085	0.154	1.247	0.107	0.186	0.013
	Appropriately long	0.046	0.118	0.970	0.065	0.057	-0.031
Preivous experience	Previous experience	0.225	-0.160	-0.196	0.423	0.358	0.843
	When did previous experience take place?	-0.189	0.175	0.138	-0.367	-0.313	-0.707
Customer impressions	Personal impression on involved camels' welfare	0.102	0.235	0.663	0.027	0.009	0.268
	Personal impression on camel riding as a sustainable tourism activity	0.047	0.345	0.410	-0.008	-0.113	-0.003
	Easiness of camel-back riding	0.067	0.149	0.469	0.086	-0.146	0.186
	Comfortability of camel-back riding	0.224	-0.056	0.277	-0.001	-0.022	0.257
	Familiarity towards the uses of camels in the world	0.039	0.260	-0.647	-0.084	0.035	0.164
	What do you think camels are raised for?	0.033	0.338	-0.056	0.671	-0.506	0.017
	Do you think this tourism activity has wide impacts on camel health and welfare?	0.131	0.374	-0.095	0.055	0.236	0.170
	Consciousness about the usefulness of such activities in endangered camels breeding and conservation	-0.169	0.428	0.151	-0.073	0.052	-0.153
	Walk length	-0.020	-0.081	0.314	0.099	0.341	0.064
Cronbach's alpha (0.99)		0.873	0.845	0.741	0.779	0.744	0.705
Variability accounted for (based on total eigenvalues) (35.49%)		9.650	6.808	6.214	4.749	4.441	3.630

PC: Principal components dimensions. Grey shaded cells indicate significantly loaded factors (factor loading > |0.50|) for interpretation, hence variables clustered together per each principal component dimension.

Relationship between factors and variables

Supplementary Table S2 summarizes the estimated sample Pearson correlation coefficient and the Bayes factors. For almost all variable pairs, the estimated Pearson correlation coefficient reaches values from −0.46 to 0.91, and the corresponding Bayes factor was always > 1. These values indicate that the factors and variables considered in this study provide significant evidence in favor of a moderate to strong linear correlation.

Table 4. Bayes factor model summary of model testing for customer general satisfaction and return intention probability in regards to camel tourist walks.

	Parameters	PC1	PC2	PC3	PC4	PC5	PC6
Customer general satisfaction	Sum of Squares	10.289	13.200	15.996	11.157	19.040	3.329
	df	19	27	20	35	40	5
	Mean Square	0.542	0.489	0.800	0.319	0.476	0.666
	F	1.727	N/A	2.523	0.743	1.076	1.597
	Sig.	0.064	N/A	0.003	0.810	0.384	0.187
	R Square	0.401	1.000	0.433	0.419	0.365	0.190
	Adj. R Square	0.169	1.000	0.262	-0.145	0.026	0.071
	Bayes Factor	0.000	N/A	0.200	0.000	0.000	0.017
Return intention probability	Sum of Squares	12.166	22.000	29.862	42.923	45.291	11.418
	df	19	27	20	35	40	5
	Mean Square	0.640	0.815	1.493	1.226	1.132	2.284
	F	0.701	N/A	1.645	1.470	1.331	2.738
	Sig.	0.800	N/A	0.067	0.125	0.142	0.035
	R Square	0.210	1.000	0.326	0.582	0.412	0.287
	Adj. R Square	-0.090	1.000	0.128	0.186	0.102	0.182
	Bayes Factor	0.000	N/A	0.000	0.000	0.000	0.150

PC: Principal components dimensions. Grey shaded cells indicate significantly loaded factors (factor loading > |0.50|) for interpretation, hence variables clustered together per each principal component dimension.

Reduced linear models: Bayesian linear regression modelling for customer general satisfaction and return intention probability

Determination coefficient or percentage of variance captured and significance for each of the models comprising the variables significantly loading on each of the six principal component dimensions are provided in Table 4. Table 4 also suggests model comprising significantly loading factors in dimension 3 and model comprising significantly loading factors in dimension 6, which significantly explain and predict for customer general satisfaction and return intention probability, respectively, than others comprising just the intercept. The rest of the dimensions did not report a significant result for any of the variable clusters previously determined by principal component analysis, revealing the relationship with them, and the dependent variables may be other than linear, hence a direct predictive simple relationship cannot be determined, then were not considered in reduced linear models for customer general satisfaction and return intention probability.

Predictors in model comprising variables in dimension 3 were able to capture 43.3% of the variability of customer general satisfaction. Contrastingly, predictors in the model comprising variables in dimension 6 were able to capture 28.7% of the variability in return intention probability. The 95% credibility interval shows that there is a 95% probability that these regression coefficients in the population lie within the corresponding intervals. When 0 is not contained in the credibility interval, a significant effect for such factor is detected.

Model validity

The posterior predictive *p* values (PPP values) for both models were around 0.5. This value indicates moderately plausible good-fitting models. Similarly, the difference of one log-likelihood unit and BIC can be considered as evidence of model for return intention probability better predictive ability. The summary of the results for the parameters of validity of both models is reported in Supplementary Table S3 and Table S4. When R^2, AIC, AICc, and BIC criterion were compared between models, the model for customer general satisfaction presented a slight ability to capture variability as suggested by R^2 values.

Discussion

Theoretical and managerial implications

Camel-riding experiential consumption in southern Spain was evaluated through the identification of decision-making, customer general satisfaction and return intention probability potentially influencing factors. This animal-close experience is an outdoor exotic adventure that includes physical challenging, cultural exchange, and activities in nature, with relatively high levels of sensory stimulation (Sanford, Jong, & Pottinger, 2016). Tourists parties (mainly adult relatives and friends) from foreign countries and national regions where camels are not traditionally reared nor its functional niches are well known (Figure 2 and Table 1), tempted to visit faraway destinations for different reasons (cultural and natural heritage, leisure iconic activities, and/or professional/business goals) (Dileep, 2019), are finally involved in such activities in these places where camels are reared and act as a potential tourism attraction (PC2, Table 3).

This finding addresses the fact that camelback riding may not be a major vacation preference to consumers when planning their holidays and tour agencies may not include this entertaining recreation in their tour guides and proposals; as supported by Figure 2, with only one tour group being sampled. Contextually, tourism operators and stakeholders have a central role when revalorizing camel rides to make them become an adjacent constructive element within the cultural heritage that makeup the local tourist space within a sustainable framework.

With a mild climate and a wide variety of sceneries, southern Spain is one of the most popular places as a tourist destination in this country both for national and international citizens. These circumstances, strongly linked with the fact that camels are progressively being raised in this region for its oroclimatic peculiarities (sandy landscapes of southwestern areas), constitute a huge opportunity for their functional revalorization as leisure animals lastly aiming the conservation of the autochthonous endangered Canarian camel, the only genetic resource of such nature in Spain and Europe (Ramón, 2016).

As a key part of this conservation strategy, the enhancement of wide-audience environmental education programs financially supported by competent authorities and which contemplates camels in its academical content could not only help to enrich consumer profile by generating interests towards these animals in the youngers (Figure 2) but also help tourism enterprises to experience higher demand for such type of entertainment. Within this initiative, individuals directly involved in this sector and with proven experience in the daily management of these animals should be the leaders. Therefore, interested users will be provided with empirical knowledge and skills concerning camel handling prior to the walk and be trained to manage any incidence that may occur during the journey, intending to make it as enjoyable as possible. In fact, staff performance (general attitudes and derived service quality) and trust-based animal-human relationships (fearless, focused, and trusted camel) are service characteristics that affect customer satisfaction, according to our results (PC1, Table 3). Likewise, a mistrustful camel may be the result of a poor training workout, hence an indirect, negative judgment of previous staff performance and fair estimate of user satisfaction itself (O'Brien, 2005).

The intrinsic characteristics of the walk most valued by riders are its diversity, their perception towards the adequate length of the ride, and overall quality (PC3, Table 3). Since user complacency was high in this regard (62% of respondents were satisfied and highly satisfied), longer excursions could be a better option for the camel and provide further emotional support for riders than shorter jaunts only if taking prolonged breaks on multiple occasions throughout the journey, generally tied in with hydrating the camel, even though guides are quick to ensure guests that the camels can last great lengths without water for its particular physiological adaptations (Ouajd & Kamel, 2009). Instead, the indirect estimation of respondents' perception about pricing shows this factor is not as relevant as lengthiness sensory stimulation during the journey when explaining customer satisfaction. Zeithaml (1988) proposes that price functions as a surrogate for quality when no more intrinsic cues are available, which is not applicable in this particular case.

In the same dimension (PC3), the well-being of the camels involved according to subjective criteria and the consumer's familiarization with camel functional niches (in our case, the vast majority (74%) were not at all or not very familiar with this item) influenced and predicted for the general perception and satisfaction (PC3, Tables 3 and

4) (Moorhouse et al., 2015). Our results suggest that the more familiarized users are with camel functionalities, the more criticism they develop when evaluating the impact of these activities on camel welfare and the fulfillment of personal expectations. To avoid falling into unfounded evaluations as well as to provide unfamiliarized consumers with objective information with a proven scientific basis in this regard, herdsmen and animal welfare legislative authorities are responsible for the elaboration and dissemination of codes of good practice for these activities, promoting adequate training sessions for camels, and encouraging consumers' coaching prior to carrying out the activity.

Although some breeders might abuse or neglect camels for their conception as trade tools for their own benefit, most of the animal owners fortunately realize that well-reared and healthy animals are the best working ones (Johan Lagerkvist et al., 2011). Here, customers are fundamental when judging owners' attitudes and handling practices towards the camels to decide whether or not it is convenient to ride the camel/s and recommend the same trekking company to other travelers looking for a cruelty-free camel-riding experience. Ultimately, the overall performance of the activity will be satisfactory, both in terms of impact on animal welfare and overall consumer satisfaction (de Mori et al., 2019).

In the same frame-analytic scenario, the variables integrating the fourth dimension (PC4, Table 3) might reinforce the abovementioned customer facet. When camel functional niches are well known for consumers, these may be more likely to judge camels for behavioral features that involve mistrust, fear, or rejection as they are factors with derogatory effects on the performance and quality of the route and, therefore, consumer satisfaction.

These undesired behavior traits not only could be derived from poor habit training and idiosyncratic components but also affect camel performance by overstraining practices and improper-fitting saddles. Given that these activities are concentrated in a short period of time and the number of animals involved is limited, since it is an endangered species and, in the particular case of Doñana, in process of functional reintroduction, the animals may be susceptible to cumulative fatigue and tiredness as the business takes advantage of this high season as much as it can because it is the most economically fruitful time for their self-financing and maintenance for the rest of the year. Besides, due to the fact that is an activity preferable to experience accompanied, it is most common for camels to support two riders on its back (PC5, Table 3). However, like those that offer camel riding rely on tourists to make money and finally supply what the tourists demand, they must be conscious about increasing global concerns on animal welfare because unhappy tourists that feel the animals are being treated badly or not getting enough rest will not be engaged in these activities and influence enforcement opportunities, by reporting poor practice when it occurs.

In this sense, considering that Andalusia continues to be a tourist preference and the Doñana National Park receives visitors during the rest of the year, this overburdening fatigue can be avoided by proper fairly constant training and physical stimulation as long as camel rides and camel-close interactions could become an alternative for other recreational experiences with transversal education purposes and serve as a therapeutic resource for social groups with special needs (Parish-Plass, 2013). According to this statement, Majchrzak et al. (2015) maintained that these activities are not a stressful experience for animals and could be a form of environmental enrichment based on cortisol levels in saliva. Such evidence provides a further criterion to promote these activities and thus, enhance their potential to become a sustainable business supporting camel farms' long-term viability, regional economic growth, and natural resources conservation, by not standing for unethical practices and having a policy on tourism to be able to justify the options they offer.

Last, the combination or co-occurrence of all considered sociocultural dimensions of camel rides in this pioneer research approach would not only affect satisfaction but also return intention probability. With large added value, positive previous experiences seemed to be a conditioning and predicting factor for tourists when seeking for further involvement in this emerging exotic tourism attraction (PC6, Tables 3 and 4).

Limitations and future research approaches

Despite this study offers an all-round and overall view of camelback riding as emerging tourist experiences with a large potential to contribute to sustainable socioeconomic development and natural resources conservation, we discuss possibilities for future research within this academic field. First, despite of the fact that pricing is not presumably influencing customer satisfaction and return intention probability, the categorical inclusion of users' profession would help to improve the knowledge of the socioeconomic level of camel riding consumers. In addition, we will be able to test whether a new experiential dimension, including variables already considered (sex, age, country of origin, and study level) and the new one proposed, appears on the scene. Income levels could be a potential factor conditioning users' expenditure in destinations where camel rides are offered, in such a manner that tourists cannot spend more money than which they have already spent in secondary activities, as camelback tourist rides actually are. Further guidance would be provided for stakeholders when aiming to implement strategic actions (i.e., competitive but affordable prices).

Within the same framework, it would also be interesting to investigate the different sources of information from which consumers had learned about the places where camel rides were available as tourism attractions and whether prior to booking they had knowledge about the welfare and general care of the animals in a specific location. Findings will enable us to identify weak points in the value chain of this touristic alternative and propose multivariate sources to meet its specific needs and goals as well as distribute the latest product information.

A third consideration is the potential utility of an ethological and biomechanical characterization of the camel breed. The first one is a useful tool to empirically evaluate the real impact of tourist rides in camel welfare and general health status by comparing behavioral features that camels show during rides and natural behavioral patterns. In this regard, investigate if ridden camel behavior whether is sexually dimorphic could also provide valuable information. Regarding kinetics assessment, it allows to correlate camel physical performance and constitution with customer satisfaction, as camels with greater lightness and agility are expected to put up with a strict sports practice and reach the desired performance during riding walks. This functional appraisal (Iglesias et al., 2020a, 2020b, 2020c) and the results of the customer satisfaction surveys will be traced for each animal to identify which physical attributes and personality traits would be the most appropriate for pleasant customer experience. Age must be an influencing factor to being considered in this regard so as to ultimately estimate camel's useful life to remain in service for this purpose. Therefore, new selection criteria will be embraced aiming for the genetic improvement and conservation of Canarian camel, mostly relegated to tourism and leisure activities.

Different types of camel saddles would also be a good opportunity to inference consumer perception on the easiness and comfortability of camel riding and managerial implications on camel well-being.

Last, the replication of this research proposal in other geographical locations where Canarian camels are present, such as the Canary Islands, may give greater validity to our findings and make results more likely to be generally applied to the whole endangered population.

Conclusions

This paper presents a pioneer systematic approach of the sociocultural dimensions that surround camel tourism, particularly camelback riding tours. This exotic leisure activity attracts flocks of tourists seeking for traversing sandy environments on the back of these animals in caravans while supporting their positive welfare at the time of encountering. Essentially, the diverse social and cultural determinants that potentially contribute to creating this experience can be summarized as follows: staff performance, culture geography, diverse and humane close interaction, camel behavior and performance, sociotemporal context, and positive previous experience. The resultant specific-consumer knowledge assessment not only supplies the dire need for further practical research of animal-based tourist experiences but also capacitates involved stakeholders to refine their abilities to successfully meet and satisfy customer's expectations according to the current social concerns, travel decision-making criteria, demands, and sustainability issues within this adventure enterprise. Tourism companies will, in turn, gain customer loyalty and fortify revenue opportunities. Contextually, this empirical marketing segmentation sheds light on the potential functional reintroduction of Canarian camels in national-protected areas out-of-the-archipelago that reunite geological and orographic conditions for these species' survival, thus contributing to the long-term viability of this autochthonous endangered breed and avoid its extinction.

Supplementary materials: The following are available online at http://www.mdpi.com/2076-2615/10/9/1703/s1, Table S1: Normality testing for customer general satisfaction and return intention probability in regards to camel tourist walks, Table S2: Bayesian inference and Pearson correlation outputs' summary for factors and variables of customer general satisfaction and return intention probability in regards to camel tourist walks, Table S3: Bayesian estimates of linear regression coefficients and model validity parameters for explanatory and predictive model comprising significantly loading factors in Dimension 3 for Customer General Satisfaction in regards to camel tourist walks, Table S4: Bayesian estimates of linear regression coefficients and model validity parameters for explanatory and predictive model comprising significantly loading factors in Dimension 6 for the Return Intention Probability in regards to camel tourist walks.

Author contributions: Conceptualization, F.J.N.G. and E.C.; data curation, C.I.P. and F.J.N.G.; formal analysis, C.I.P. and F.J.N.G.; funding acquisition, J.V.D.B.; investigation, C.I.P., F.J.N.G. and S.N.B.; methodology, C.I.P. and F.J.N.G.; project administration, E.C. and J.V.D.B.; resources, J.V.D.B.; software, F.J.N.G.; supervision, F.J.N.G. and J.V.D.B.; validation, F.J.N.G. and J.V.D.B.; visualization, E.C.; writing-original draft, C.I.P. and F.J.N.G.; writing—review and editing, C.I.P., F.J.N.G., E.C., S.N.B. and J.V.D.B. All authors have read and agree to the published version of the manuscript.

Funding: The present research was carried out in the financing framework of the international project CA.RA.VA.N—"Toward a Camel Transnational Value Chain" (Reference APCIN-2016-00011-00-00) and during the covering period of a predoctoral contract (Submodality 2.2 "Predoctoral research staff") funded by University of Cordoba, Spain.

Acknowledgments: The authors would like to thank "Aires Africanos" Eco-tourism Company for its direct technical help and assistance.

Conflicts of interest: The authors declare no conflict of interest. The founding sponsors had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; and in the decision to publish the results.

References

Aydin, Z., Marcussen, T., Ertekin, A. S., & Oxelman, B. (2014). Marginal likelihood estimate comparisons to obtain optimal species delimitations in Silene sect. Cryptoneurae (*Caryophyllaceae*). *PLoS ONE*, 9(9), e106990.

Bejarano, E. (2009). Una geografía del turismo para la comprensión de la territorialización turística. Proceedings of XII Encuentro de Geógrafos de América Latina "Caminando en una América Latina en transformación".

Bertella, G. (2014). The co-creation of animal-based tourism experience. *Tourism Recreation Research*, 39(1), 115-125.

Black, R., & Crabtree, A. (2007). *Quality assurance and certification in ecotourism* (Vol. 5): CABI Books.

Burns, P. M. (2004). Tourism planning: A third way? *Annals of Tourism Research*, 31(1), 24-43.

Çalışkan, V. (2010). Examining cultural tourism attractions for foreign visitors: the case of camel wrestling in Selcuk Ephesus. *Turizam*, 14(1), 22-40.

Carr, N. (2009). *Animals in the tourism and leisure experience*: Taylor & Francis.

Chapman, A., & Buck, W. J. (1893). *Wild Spain: Records of Sport with Rifle, Rod, and Gun, Natural History and Exploration (Vol. 1)*: Library of Alexandria.

Chapman, A., & Buck, W. J. (2019). *Unexplored Spain*: Good Press.

Chickering, D. M., & Heckerman, D. (1996). Efficient approximations for the marginal likelihood of incomplete data given a Bayesian network. Proceedings of the 12th international conference on Uncertainty in artificial intelligence.

Clyde, M., Cetinkaya-Rundel, M., Rundel, C., Banks, D., Chai, C., & Huang, L. (2019). Chapter 7. Bayesian Model Choice. In *An Introduction to Bayesian Thinking*: BookDown.

Coelho, P. S., & Esteves, S. P. (2007). The choice between a fivepoint and a ten-point scale in the framework of customer satisfaction measurement. *International Journal of Market Research*, 49(3), 313-339.

Corp., I. (2017). *IBM SPSS Statistics for Windows (Version 25.0)*. Armonk, NY: IBM Corp.

de Mori, B., Ferrante, L., Florio, D., Macchi, E., Pollastri, I., & Normando, S. (2019). A protocol for the ethical assessment of wild animal–Visitor interactions (AVIP) evaluating animal welfare, education, and conservation outcomes. *Animals*, 9(8), 487.

Díaz Medina, E. (2017). *Estudios sobre identificación, lactación y cría de dromedarios en la isla de Fuerteventura (Canarias)*. Tesis Doctoral: Universitat Autònoma de Barcelona (Barcelona, Spain).

Dileep, M. R. (2019). *Tourism, Transport and Travel Management*: Routledge.

Dinu, G., & Dinu, L. (2019). Measuring Customer Satisfaction of Tourist Services. Case study: President Hotel. *Ovidius University Annals, Economic Sciences Series*, 19(1), 421-426.

Donlon, J. G., Donlon, J. H., & Agrusa, J. (2010). Cultural tourism, camel wrestling, and the tourism 'bubble'in Turkey. *Anatolia*, 21(1), 29-39.

Drton, M., & Plummer, M. (2017). A Bayesian information criterion for singular models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 79(2), 323-380.

Du Cros, H., & McKercher, B. (2020). *Cultural tourism*: Routledge.

Dudley, N., Parrish, J. D., Redford, K. H., & Stolton, S. (2010). The revised IUCN protected area management categories: the debate and ways forward. *Oryx*, 44(4), 485-490.

Duffy, R., & Moore, L. (2011). Global regulations and local practices: The politics and governance of animal welfare in elephant tourism. *Journal of Sustainable Tourism*, 19(4-5), 589-604.

Dunets, A., Muhamedieva, A., Sycheva, I., Perepechkina, E., Vakhrushev, I., & Kulchytskiy, A. (2019). Spatial tourism planning: Using the model of functional and planning complexes. *Journal of Environmental Management and Tourism*, 10(4), 711-719.

Edwards, A. (1992). *Likelihood (expanded edition)*: Johns Hopkins University Press.

Faye, B. (2013). Camel meat in the world. *Camel meat and meat products*, 7-16.

Fennell, D. A. (2015). Ethics in tourism. In *Education for sustainability in tourism* (pp. 45-57): Springer.

Fennell, D. A. (2019). The future of ethics in tourism. In *The Future of Tourism* (pp. 155-177): Springer.

Fennell, D. A. (2020). *Ecotourism*: Routledge.

Fernández Álvarez, J., León Jurado, J. M., Navas González, F. J., Iglesias Pastrana, C., & Delgado Bermejo, J. V. (2020). Optimization and Validation of a Linear Appraisal Scoring System for Milk Production-Linked Zoometric Traits in Murciano-Granadina Dairy Goats and Bucks. *Applied Sciences*, 10(16), 5502.

Fornell, C., Morgeson, F. V., Hult, G. T. M., & VanAmburg, D. (2020). Satisfied Customers: An Asset Driving Financial Performance. In *The Reign of the Customer* (pp. 139-154): Springer.

García-Rosell, J.-C., & Hancock, P. Working animals, ethics and crithical theory. In *Animals and Business Ethics*: Springer.

Gebreyohanes, M., & Assen, A. (2017). Adaptation mechanisms of camels (*Camelus dromedarius*) for desert environment: a review. *Journal of Veterinary Science & Technology*, 8, 1-5.

Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., & Rubin, D. B. (2013). *Bayesian data analysis*: Chapman and Hall/CRC.

Graf, P., von Borstel, U. K., & Gauly, M. (2013). Importance of personality traits in horses to breeders and riders. *Journal of Veterinary Behavior*, 8(5), 316-325.

Hall, C. M. (2010). Tourism and biodiversity: more significant than climate change? *Journal of Heritage Tourism*, 5(4), 253-266.

Hall, D. R., & Brown, F. (2006). *Tourism and welfare: Ethics, responsibility and sustained well-being*: CABI Books.

Holopainen, I. (2012). *Animal encounters as experiences: Animal-based tourism in the travel magazine Matkalehti*: University of Helsinki.

Homburg, C., Hoyer, W. D., & Koschate, N. (2005). Customers' Reactions to Price Increases: Do Customer Satisfaction and Perceived Motive Fairness Matter? *Journal of the Academy of Marketing Science*, 33(1), 36-49.

Hox, J., Moerbeek, M., Kluytmans, A., & Van De Schoot, R. (2014). Analyzing indirect effects in cluster randomized trials. The effect of estimation method, number of groups and group sizes on accuracy and power. *Frontiers in psychology*, 5, 78.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S. and Delgado, J. V. (2020a). Zoometric characterization and body condition score in Canarian camel breed. *Archivos de zootecnia*, 69(265), 14-21.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S. and Delgado, J. V. (2020b). Biokinematics and applied thermography in the Canarian camel breed. *Archivos de zootecnia*, 69(265), 102-107.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S. and Delgado, J. V. (2020c). Ethological characterization of the Canarian camel breed. *Archivos de zootecnia*, 69(265), 108-115.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Barba Capote, C. J., & Delgado Bermejo, J. V. (2020). Effect of Research Impact on Emerging Camel Husbandry, Welfare and Social-Related Awareness. *Animals*, 10(5), 780.

Johan Lagerkvist, C., Hansson, H., Hess, S., & Hoffman, R. (2011). Provision of farm animal welfare: Integrating productivity and non-use values. *Applied Economic Perspectives and Policy*, 33(4), 484-509.

Kaplan, D., & Depaoli, S. (2012). Bayesian structural equation modeling. In *Handbook of Structural Equation Modeling* (Hoyle, R.H., Ed.): The Guilford Press.

Karangeli, M., Abas, Z., Koutroumanidis, T., Malesios, C., & Giannakopoulos, C. (2011). Comparison of Models for Describing the Lactation Curves of Chios Sheep Using Daily Records Obtained from an Automatic Milking System. Proceedings of the 5th International Conference on Information and Communication Technologies for Sustainable Agri-production and Environment (HAICTA).

Khan, B. B., Arshad, I., & Riaz, M. (2003). *Production and management of camels*: University of Agriculture, Faisalabad, Department of Livestock Management.

Kiráľová, A. (2019). Sustainable tourism marketing strategy: competitive advantage of destination. In *Sustainable Tourism: Breakthroughs in Research and Practice* (pp. 183-206): IGI Global.

Kline, R. B. (2008). *Becoming a behavioral science researcher: A guide to producing research that matters*: Guilford Press.

Lee, S.-Y., & Song, X.-Y. (2004). Evaluation of the Bayesian and maximum likelihood approaches in analyzing structural equation models with small sample sizes. *Multivariate behavioral research*, 39(4), 653-686.

Lee, S. Y., & Song, X. Y. (2003). Bayesian analysis of structural equation models with dichotomous variables. *Statistics in medicine*, 22(19), 3073-3088.

Majchrzak, Y. N., Mastromonaco, G. F., Korver, W., & Burness, G. (2015). Use of salivary cortisol to evaluate the influence of rides in dromedary camels. *General and comparative endocrinology*, 211, 123-130.

MAPAMA. Camello Canario. *Catálogo Oficial de Razas*. Available online: https://www.mapa.gob.es/es/ganaderia/temas/zootecnia/razas-ganaderas/razas/catalogo/peligro-extincion/otras-especies/camello-canario/default.aspx (accessed on 1 March 2020).

McLean, A. N., & McGreevy, P. D. (2010). Ethical equitation: Capping the price horses pay for human glory. *Journal of Veterinary Behavior*, 5(4), 203-209.

Mejías, J. M. M. (2014). Aproximación a la importancia histórica del camello en Canarias. Proceedings of the XX Coloquio de Historia Canario-Americana.

Meleddu, M., & Pulina, M. (2016). Evaluation of individuals' intention to pay a premium price for ecotourism: An exploratory study. *Journal of Behavioral and Experimental Economics*, 65, 67-78.

Millares Cantero, A., Millares Cantero, S., Quintana Navarro, F., & Suárez Bosa, M. (2011). *Historia Contemporánea de Canarias*: Obra Social de La Caja de Canarias.

Moorhouse, T. P., Dahlsjö, C. A., Baker, S. E., D'Cruze, N. C., & Macdonald, D. W. (2015). The customer isn't always right—conservation and animal welfare implications of the increasing demand for wildlife tourism. *PloS one*, 10(10).

Morera, M. (1991). La tradición del camello en Canarias. *Anuario de Estudios Atlánticos*, 1(37), 167-204.

O'Brien, C. E. (2005). *Horse Economics: A Personal Finance Guide for the Horse Owner*: Trafalgar Square Books.

Orams, M. (2004). Why dolphins may get ulcers: Considering the impacts of cetacean-based tourism in New Zealand. *Tourism in Marine Environments*, 1(1), 17-28.

Ouajd, S., & Kamel, B. (2009). Physiological particularities of dromedary (*Camelus dromedarius*) and experimental implications. *Scandinavian Journal of Laboratory Animal Sciences*, 36(1), 19-29.

Parish-Plass, N. (2013). *Animal-assisted psychotherapy: Theory, issues, and practice*: Purdue University Press.

Pung, J. M., Gnoth, J., & Del Chiappa, G. (2020). Tourist transformation: Towards a conceptual model. *Annals of Tourism Research*, 81, 102885.

Ramón, F. L. (2016). De los parques nacionales a la conservación de la biodiversidad. *Revista de administración pública*(200), 213-230.

Center for Responsible Travel. (2009). El mercado de productos de turismo responsable en América Latina y Nepal. In *SNV-Organización de Desarrollo de los Países Bajos*: University of Standford.

Roberts, G. O., Gelman, A., & Gilks, W. R. (1997). Weak convergence and optimal scaling of random walk Metropolis algorithms. *The annals of applied probability*, 7(1), 110-120.

Roberts, G. O., & Rosenthal, J. S. (2001). Optimal scaling for various Metropolis-Hastings algorithms. *Statistical Science*, 16(4), 351-367.

Roberts, L., & Hall, D. (2001). *Rural tourism and recreation: Principles to practice*: CABI Books.

Robinson, M., & Picard, D. (2006). *Tourism, culture and sustainable development*: Culture and Development Section, UNESCO.

Romero, C. G., Marrero, F. F., & Moreno, C. G. R. (2012). Razas: Raza camello canario. *AE-Revista Agroecológica de Divulgación*(7), 64.

Saarinen, J., Rogerson, C. M., & Hall, C. M. (2017). *Geographies of tourism development and planning*: Taylor & Francis.

Sanford, C. A., Jong, E. C., & Pottinger, P. S. (2016). *The Travel and Tropical Medicine Manual*: Elsevier Health Sciences.

Schmidt-Burbach, J., Ronfot, D., & Srisangiam, R. (2015). Asian elephant (*Elephas maximus*), pig-tailed macaque (*Macaca nemestrina*) and tiger (*Panthera tigris*) populations at tourism venues in Thailand and aspects of their welfare. *PloS one*, 10(9), e0139092.

Schulz, U. (2008). *El camello en Lanzarote*: Aderlan.

Schulz, U., Tupac-Yupanqui, I., Martínez, A., Méndez, S., Delgado, J. V., Gómez, M., Dunner, S., & Cañón, J. (2010). The Canarian camel: a traditional dromedary population. *Diversity*, 2(4), 561-571.

Seifu, E., Angassa, A., & Boitumelo, W. (2018). Community-based camel ecotourism in Botswana: Current status and future perspectives. *Journal of Camelid Science*, 11, 33-48.

Shaheer, I., Carr, N., & Insch, A. (2019). What are the reasons behind tourism boycotts? *Anatolia*, 30(2), 294-296.

Sheppard, V. A., & Fennell, D. A. (2019). Progress in tourism public sector policy: Toward an ethic for non-human animals. *Tourism Management*, 73, 134-142.

Signori, D. (2019). Multicollinearity. In *STAT 302*: Simon Fraser University.

Sigurðardóttir, I., & Helgadóttir, G. (2015). Riding high: Quality and customer satisfaction in equestrian tourism in Iceland. *Scandinavian Journal of Hospitality and Tourism*, 15(1-2), 105-121.

Simms, L. J., Zelazny, K., Williams, T. F., & Bernstein, L. (2019). Does the number of response options matter? Psychometric perspectives using personality questionnaire data. *Psychological assessment*, 31(4), 557.

StataCorp. (2017). *Stata Statistical Software (Version 15)*. College Station, TX.

Stone, M. T., Lenao, M., & Moswete, N. (2019). *Natural Resources, Tourism and Community Livelihoods in Southern Africa: Challenges of Sustainable Development*: Routledge.

Travis, A. S. (2011). *Planning for tourism, leisure and sustainability: International case studies*: CABI Books.

Tuohino, A., & Hynonen, A. (2001). Ecotourism—imagery and reality. Reflections on concepts and practices in Finnish rural tourism. *Nordia Geographical Publications*, 30(4), 21-34.

Verneau, R., Luis, J. A. D., Perera, M. J. L., & García, J. H. (1981). *Cinco años de estancia en las Islas Canarias*: Benchomo S.L.

UNESCO World Heritage Centre. *The Kingdom of Spain: Properties Inscribed on the World Heritage List*. Available online: https://whc.unesco.org/en/statesparties/es (accessed on 26 June 2020).

Wearing, S., & Jobberns, C. (2010). Ecotourism and the commodification of wildlife: Anima welfare and the ethics of zoos. In *Zoos and Tourism: Conservation, Education, Entertainment?* (Frost, W., Ed.): Channel View Publications.

Williams, S. (1998). *Tourism geography*: Psychology Press.

Wilson, R., & Gutierrez, C. (2015). The one-humped camel in the Canary Islands: History and present status. *Tropicultura*, 33(4).

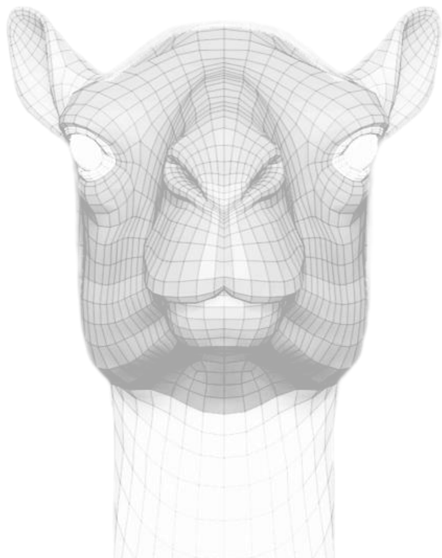
Zeithaml, V. A. (1988). Consumer perceptions of price, quality, and value: a means-end model and synthesis of evidence. *Journal of marketing*, 52(3), 2-22.

Zhang, L., Guo, X., Lei, Z., & Lim, M. K. (2019). Social network analysis of sustainable human resource management from the employee training's perspective. *Sustainability*, 11(2), 380.

6.2 A tool for functional selection of leisure camels: behaviour breeding criteria may ensure long-term sustainability of a European unique breed

Carlos Iglesias Pastrana[1], Francisco Javier Navas González[1,2], Elena Ciani[3], Antonio González Ariza[1] and Juan Vicente Delgado Bermejo[1]

[1]Department of Genetics, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain
[2]Andalusian Institute of Agricultural and Fisheries Research and Training (IFAPA), Alameda del Obispo, 14004 Cordoba, Spain
[3]Department of Biosciences, Biotechnologies and Biopharmaceutics, Faculty of Veterinary Sciences, University of Bari 'Aldo Moro', 70121 Bari, Italy



Quality indicator information provided on the publication

Status of the manuscript: Published

Journal (year, volume, page(s)): *Research in Veterinary Science* 2021, *140*, 142-152

International database in which it is indexed: Journal of Citation Reports (JCR)

Thematic area in the reference database: Veterinary Sciences

Impact index of the journal in the year of the article's publication: 2.554

Rank/number of thematic area journals: 35/145 (Q1)

Abstract

Livestock selection for desirable temperament traits still remains disregarded for minor productive species, such as camels. Despite dromedary camels from Canary Islands were at once polyvalent, current major functionality for this unique European recognised breed is limited to tourism-oriented interactive experiences. The conservation of this endemic breed implies the immediate enforcement of selective breeding programmes by including behavioural functional traits as genetic selection criteria. With this purpose, we evaluated the suitability of a practical proposal to qualitatively and quantitatively evaluate camel behaviour performance to be applied in breeding programmes for the improvement of camel personality dimensions. One-hundred thirty-one respondents enjoying a camelback leisure riding during high season in Southern Spain were asked to voluntarily fulfill an on-site questionnaire just after the tourist ride concluded. Eleven behaviour criteria were rated on a 5- point Likert-type scale by each respondent for the camel they had ridden on. Generalized Procrustes Analysis revealed that a general consensus between participants for dromedary behavioural features were reached, more substantial for those expressions reflecting agitation and/or indifference towards interaction with human. Moreover, the variability in animal behaviour patterns could be attributed to camel sex- and age-related differences. Mid- to long-term sustainability of Canarian camels may rely on the ability of involved stakeholders to adapt leisure opportunities to customer demands and expectations. Hence, those camel behavioural features with a conditioning potential of overall participants satisfaction, may become potential objective selection criteria candidates. Consequently, camel functional selective breeding may ensure camel breed preservation and sustainable protection based on leisure activities.

Keywords

Dromedary camel, leisure activities, behavioural response, customer subjective perception, selection criteria, endangered breed conservation

Introduction

Contemporary tourists frequently avoid massive destinations and leisure activities which do not let them disconnect from their daily routine (Meleddu & Pulina, 2016). Instead, travellers tend to decide on their visits to rural areas motivated by the desire to get involved in learning adventures that foster nature appreciation. These experiences are promoted when a positive contribution to the environment in which the tourist experience takes place can be developed (Xu & Chan, 2016). Such environmentally sound and culturally founded activities are grouply named in the literature as ecotourism or responsible nature- based tourism (Fennell, 2020). The varied elements, either biological and cultural, which they include even constitute local iconic emblems themselves (Anup, 2016).

Contextually, towering dunes, gravel plains and barren mountains from the Middle East (Breulmann et al., 2007; Daher, 2006), India (Sindhu & Singh, 2014), Africa (Seifu, Angassa, & Boitumelo, 2018) and Spain (Wilson & Gutierrez, 2015) attract thousands of local and foreign visitors tempted to discover the captivating beauty of these world's most inhospitable corners.

In this context, the particularities of the animals and plant species that survive in desert climates play a pivotal role in the configuration and attractiveness of these locations. For instance, camels are among the first things that come to mind when people think about deserts (Jones, 2012). For these reasons, travel agencies have customized guided tours to contemplate camel trekking, excursions and picture taking in their services list for those singular arid emplacements where domestic and basic desensitization-trained camels are bred (Edwards et al., 2010; Seifu et al., 2018; Wilson, 2013).

These camel-human close interactive encounters provide tourists turn into enjoyable and memorable experiences (Bulbeck, 2012; Campos et al., 2017) from which, if done responsibly, tour operators and locals may receive tangible profits and positive social reputation ensures proper care and sustainable conditions for the animals (Coria & Calfucura, 2012; Iglesias Pastrana et al., 2020).

Despite breeding goals in camels worldwide are mainly focused on production and conformation traits (Faye, 2014), their role as an income generator in the tourism industry has effectively resulted in the persistence and survival of local breeds in marginal geographies for decades (Wilson & Gutierrez, 2015).

This functional relegation originated in the last third of the twentieth century when camel domestic species were displaced from field labour by technified transportation means (Iglesias et al., 2020a). This functional relegation to a secondary position brought about the dramatic reduction of total census and the necessity for new niches to be explored.

The local dromedary camel breed (*C. dromedarius*) from Canary Islands (Spain), was historically and archetypically known because of its role as service animals (Schulz, 2008). The influx of the tourism industry in the archipelago (Wilson & Gutierrez, 2015) fortunately led to a population recovery around the 1990s. The influence was so noticeable that such functional niche continues to be the major income source for local breeders at present. Notwithstanding the aforementioned, no selective breeding for this functional purpose has ever been carried which promoted the consideration of the breed as endangered autochthonous livestock by the Spanish Ministry of Agriculture, Food and Environment (Order AAA/251/2012). Then, official census estimates evidenced the urging need for the support of national biocultural heritage's protection measures. Indeed, the

Canary camel breed is the only genetic resource of such nature currently extant in Spain, but which also spreads across the whole European continent (Schulz et al., 2010; Wilson & Gutierrez, 2015).

Since this local breed major functionality is leisure riding, close interaction to humans may greatly be shaped by the behavioural pat- terns displayed by camels. Consequently, such a large influence of camel behaviour may condition customer satisfaction and thus business loyalty.

To this aim, the objective of this paper is to use Generalized Procrustes Analysis to obtain a consensual configuration among behavioural descriptions of each camel participating in the touristic experiences through the testimonies of the tourists participating of the attraction. Furthermore, this analysis also allows to compare the proximity between the terms that are used by different participants/respondents to describe camels, which may standardize the levels to be considered within behaviour as breeding criteria, defining the patterns that participants/respondents may find desirable or undesirable.

In this scenario, the establishment of an organized breeding strategy for camel functional traits such as personality dimensions (Iglesias et al., 2020b) may assist cameleers in adapting or creating new niches (i.e., assisted therapy) matching the participants' expectations and attempting to stabilize its census and ensure its long-term viability.

Material and methods

Participants/Respondent sample

The number of participants/respondents was 131 (55 males, 76 females), which is the total number of camel-riding users during the research period (1st July to 30th September 2019). Figure 1 presents age distribution in the sample of participants/respondents.

Animal units and data compilation

A total of 8 dromedaries were involved in the experience (6 males and 2 females; aged between 4 and 32 years) as shown in Table 1. The animals were reared for tourist rides (English type saddles) in Southern Spain (Iglesias Pastrana et al., 2020). The sex ratio in the sample is justified by the general preference among camel breeders for males provided their enhanced physical working activities which may rely on a morpho-anatomical basis (Schulz, 2008).

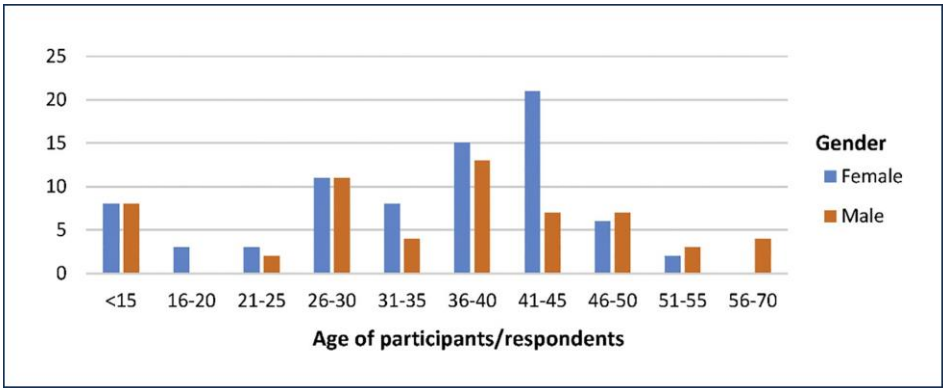


Figure 1. Age distribution in participant/respondent sample.

Table 1. Descriptive qualitative data of the study sample.

Animal ID	Sex	Age (years)	Coat colour
1	Male	4	Ashed
2	Male	4	Ashed
3	Female	5	Cinnamon
4	Female	5	White
5	Male	14	Cinnamon
6	Male	28	Blonde
7	Male	30	Blonde
8	Male	32	Roan

The selected dromedaries were trained by the same operator to discard the potential conditioning effects that may derive from the use of different trainers. The experiences were performed in a controlled environment in which the only potential fear-eliciting stimuli is the proximity and closed interaction with humans.

The intraherd domestication protocol used includes systematic desensitization practices three times per week during one complete year before a dromedary camel can be successfully engaged in interactive experiences with humans. The minimum age for camels to start desensitization is 4 years old.

Data collection was performed from 1st July to 30th September 2019, high season in Southern Spain, hence a time during which the business is in high demand. When organizing a tourist route, the business leader always seeks for at least two animals to get involved (caravan), since it is crucial for the camels to be accompanied by conspecifics given its gregariousness (Tefera, 2004).

Participants/respondents were provided with basic guidance on the best practices for handling and riding camels prior to the walk (Iglesias Pastrana et al., 2020). All the participants in camelback riding tours during the referred period (*n*=131) were asked to blindly evaluate the behavioural response of the camel which they had ride on.

Qualitative and quantitative behaviour assessment

Immediately after each experience had concluded, an on-site questionnaire was made to touristic ride participants. Mood descriptors used followed the premises in Navas et al. (2017) and Navas González et al. (2020).

Participants were asked to rate the behavioural overall patterns which the dromedary camel had displayed during the tourist experience following a 5-point Likert-type scale (Kline, 2008) for eleven behavioural criteria: distraction, calmness, mistrustfulness, scare, depression, curiosity, surprise, rejection, indifference, cautiousness and nervous- ness. All of these items are indirect indicators of fearfulness or the way in which the animals interact with potential fearful stimuli. Description of the behavioural criteria used was adapted from Navas González et al. (2018) and can be consulted in Supplementary Table S1.

Prior to fulfill the questionnaire, the meaning of the qualitative descriptors of behaviour were clarified by the herdsmanship, who had been previously tutorized by the leaders of this research design for ac- curate and unbiased results (Minero et al., 2009).

Data statistical analysis

Generalized Procrustes Analysis (GPA)

Generalized Procrustes Analysis (GPA) was used to reduce the scale effects and to obtain a consensus configuration among touristic ride participants (Dijksterhuis & Gower, 1991). Furthermore, it enabled the comparison between the behavioural terms used by different participants/respondents to describe the camels that they had ridden on.

The values used in the present research correspond to the average rating for each dromedary camel and touristic ride participant/respondent. The aim of generalized Procrustes analysis in the context of the present study is to transform the data to remove scaling effects (as some participants/respondents might use a wider scale) or position effects (some participants/respondents might tend to rate camels using the lowest or the highest end of the rating scales), to obtain a consensus configuration that will then be used in an external preference mapping. To perform the Generalized Procrustes Analysis we used the Generalized Procrustes Analysis package of Sensory data analysis routine of XLSTAT software, version 2018.5. Addinsoft, Paris, France (Addinsoft, 2018). As 131 participants responded to the surveys, we considered a number of 131 configurations. Each participant scored each of the eleven behavioural dimensions.

External preference mapping allows to relate the preferences shown by the participants/respondents to behavioural patterns of the dromedary camels used for touristic rides as a way to determine the dimensionality of animals as an element of human-animal interaction in a commercial framework.

The first step of the external preference mapping method developed in this study consisted in mapping the dromedary camels on the basis of their behavioural characteristics. This first visualization is on its basis a sensory map. By applying the PREFMAP method of XLSTAT software, version 2018.5. Addinsoft, Paris, France (Addinsoft, 2018), we modelled for each participant/respondent's (or group of participants/respondents) behavioural ratings of dromedary camels, with the aim to represent the participants/respondents on the sensory map.

Afterwards, two permutation tests were run to determine the percentage of variance explained by the consensus among participants/ respondents and to determine the number of dimensions to retain in the analysis. The first consensus test was performed to check if the consensus configuration is a true consensus. This permutation test allows determining whether the observed Rc value (Rc corresponds to the proportion of the original variance explained by the consensus configuration) is significantly higher than 95% of the results that are obtained when permuting the data. In our case 500 permutations were run to perform the consensus test. The second permutation test was used to verify how many dimensions should be retained to display the results.

Afterwards, unstandardized Principal Component Analysis (PCA) was run. Although the Generalized Procrustes Analysis already includes a rotation step for each configuration, for it to match the consensus configuration, the PCA corresponds to the optimal transformation of the consensus configuration under the usual PCA constraints. The PCA transformation is then applied to each configuration corresponding to each participant/respondent. Then, eigenvalues are calculated as they report the fraction of the variability which corresponds to each particular axe.

Results are then separated into the results corresponding to the consensus of each configuration (participants/respondents). The objects' coordinates of the consensus configuration are used later in a PREFMAP analysis as the coordinates of the products on the external preference map.

A combined selection index (ICO) was developed following the premises in Van Vleck (Van Vleck, 1993) to summarize the position in the rank for each of the two parameters to determine those behavioural features for which a higher consensus was reached. The combined index used (ICO) was as follows:

$$\mathrm{ICO} = \frac{\text{Position in the Rank Rank of F1 Correlation} * \text{W1} + \text{GCI position in the Rank} * \text{W2}}{2}$$

where W_1 is the weight for the position in the rank for correlation of dimension F1 in the initial consensus among participants/respondents for each of the behavioural features,

W_2 for the position in the rank for correlation of dimension F2 in the initial consensus among participants/ respondents for each of the behavioural features. The fraction of vari- ability explained by each of the dimensions was used to weight coefficients. Hence, W_1 was 0.9999 and W_2 was 0.0001. As a result, the behavioural features presenting greater ICO values were the ones for which a greater consensus was reached.

Effect of dromedary age, sex and coat colour on participant/respondent perception of behavioural features and level of satisfaction about the interactive experience

Bayesian One-way ANOVA procedure was used to detect differences between the mean for perception of behavioural features depending on the factors of sex and coat colour of and the level of satisfaction of the participant/respondent in regards the touristic camel ride using the Bayesian ANOVA task from the Bayesian statistics procedure (Corp, 2017a).

As age was a covariate, Bayesian inference Pearson correlation was used to characterize the posterior distribution of the linear correlation between dromedary age and perception of behavioural patterns by participants/respondents using the Pearson correlation task from the Bayesian statistics procedure (Corp, 2017a). The correlation methods used and discussed in this paper can be validly used even if we work with repeated measures as we tested independent data (Bakdash & Marusich, 2017).

When $r_{xy} = |1|$ this means that the dependent variable y is perfectly linearly correlated with the independent variable x, whereas a coefficient of $|0.8| < r_{xy} < |1|$, suggests a strong linear correlation; a coefficient of $|0.3| < r_{xy} < |0.6|$, suggests a moderate correlation; a coefficient of $0 < r_{xy} < |0.3|$, suggests a weak correlation (Profillidis & Botzoris, 2019).

In the sections below, we provide a detailed summary of the priors and posterior distributions used and reported by this study, respectively. A full description of the algorithms used by SPSS to perform Bayesian Inference on Multiple Linear Regression Models in this study can be found in the public document IBM SPSS Statistics Algorithms v. 25.0. by IBM Corp (2017b).

Although quadratic approximation has been reported to be computationally faster, in terms of discretization and computing the likelihood over all possible parameter combinations, than other approximations such as the Markov Chain Monte Carlo (MCMC) methods used in this study, for instance, when large number of parameters are being considered in a model. However, the use of this quadratic approach was not feasible given it assumes the posterior distribution follows a normal distribution. In the context of our data, this assumption cannot be presumed provided the gross violation reported for the distribution properties reported for previous testing.

Jeffrey-Zellner-Siow (JZS) mixture of g-priors

For the present analyses, the Jeffrey-Zellner-Siow (JZS) miXture of g- priors (Liang et al., 2008) was used. JZS prior is especially appropriate for Bayesian inference on linear regression analyses (Rouder et al., 2012) as it is a symmetric and centered at zero prior, hence positive and negative values of the slope parameters have a priori the same likelihood to occur. Furthermore, JZS prior is scale invariant, thus the resulting Bayes factor does not depend on the scale of both the dependent variable and factors or covariates. The procedure of defining a scaled prior for unstandardized coefficients (β_i) equals to the process of defining a prior for standardized coefficients (β_i*) (Rouder et al., 2012).

Third, the scale parameter γ is fixed to a constant by the user, which allows prior beliefs to be specified about the expected effect size. IBM Corp (2017b) algorithm guide reports that the algorithm of JZS prior for linear regression analyses, to compute the Bayes Factor uses the default value of $\gamma = 2\sqrt{\pi} = 3.5$, which reflects a prior belief of a medium effect size. Authors such as Rouder and Morey (2012) also report other theoretical advantages of the JZS prior, such as its consistency in model selection (the fact that the Bayes factor, goes to infinity as the number of observations N increases without bound favouring the data-generating model) or consistency in information (the Bayes factor for a certain effect goes to infinity as the proportion of explained variance or R Squared (R^2) increases to 1). Additionally, Bayes factors for JZS prior can be relatively easily highly precisely computed (Morey & Rouder, 2015).

Factor and covariate effects Bayesian modelling (FCEBM)

Being y_i any of the effects of any of the independent variables (covariates) considered in this study, then the posterior distribution of y_i in the context of the data D is:

$$p(y_i/D) = \sum_{i=20}^{i} p(\, y_i|M_i, D)\; p(M_i|D)$$

The aforementioned equation represents an average of the posterior distributions under each model, weighted by the corresponding posterior model probabilities. In the previous equation, the posterior predictive distribution of y_i given a particular model M_i is:

$$p(y_i|M_i D) = \int p(y_i|\beta_i, M_i, D) p(\beta_i|M_i D)\, d\beta_i$$

and the posterior probability of model M_i is given by

$$p(M_i|D) = \frac{p(D|M_i)p(M_i)}{\sum_{i=20}^{i} p\,(D|M_i)p(M_i)}$$

where

$$p(M_i|D) = \int p(D|\beta_i, M_i)p(\beta_i|M_i)\, d\beta_i$$

is the integrated likelihood of model M_i, β_i is the vector of parameters of model M_i, $p(\beta_i|M_i)$ is prior density of βi under model M_i, $p(D|\beta_i|M_i)$ is the likelihood, and $p(M_i)$ is the prior probability that M_i is the true model.

Although in the absence of other constraints, in a study comprising P potential covariates, the number of models (K), can be enormous ($K = 2^P$). Only a small number of these models will be sufficiently supported by the data, and as a result be selected by SPSS for each covariate.

Marginal posterior distributions of all unknowns were estimated using the Gibbs sampling algorithm.

Factors and covariate effect Bayesian interpretation (CEBI)

To interpret the effect of each particular covariate, the following steps were accomplished. The detection of the likelihood that a factor or covariate has an effect on each particular variable was computed through the posterior probability $p[\beta_i^* \neq 0/D]$. Kass & Raftery (1995) standard rules of thumb were considered to interpret this posterior probability (<50%: evidence against the effect, 50–75%: weak evidence for the effect, 75–95%: positive evidence, 95–99%: strong evidence, >99%: very strong evidence). These standard rules are com- parable to commonly used thresholds to define significance of evidence through Bayes factor (BF) found in literature.

Second, posterior distribution mean estimates are used to measure the magnitude of the effect of a particular factor and covariate. Con- textually, 95% Credibility Interval shows that there is a 95% probability that these regression coefficients (Posterior distribution mean value for each covariate and factor) in the population lie within the corresponding intervals. When 0 is not contained in the Credibility Interval, a significant effect for such factor is detected.

Convergence criterion

The rounds of iteration continued until a tolerance convergence criterion of 10^{-8} was reached as suggested in the literature (Arora, 2017). Once the convergence criterion was determined, initial parameters were set, and model fitting properties were evaluated. The maximum number of iteration rounds used for each analysis was 2000 as suggested in IBM SPSS. Statistics Algorithms version 25.0 by IBM Corp (2017b). This converge criterion was chosen as well given it has been used in Bayesian ANOVA and linear regression analyses in research contexts of limited sample sizes (Pizarro Inostroza et al., 2020).

Results

Table 2 summarizes the efficiency of each Generalized Procrustes Analysis transformation in terms of reduction of the total variability. Procrustes superimposition consists in three stages after 19 iterations. These stages comprise the three transformation steps of any ordinary Procrustes fit for two configurations of landmarks. This is the translation to a common centroid or center of gravity, scaling both configurations to the same centroid size, and orthogonal rotation to minimize summed squared distances between the corresponding landmarks (Goodall, 1991). Procrustes analysis involves finding the optimal superposition of two or more 'forms' via orthogonal, rotation, translation or transposition, and scaling (Theobald & Wuttke, 2006). Table 2 suggests that scaling both configurations to the same centroid size is the only efficient transformation method ($P < 0.001$). This may stem from the fact that it is through scaling that variables measured in different units, such as those in our study, are standardized. Hence, their relative repercussions can be determined.

Table 2. Generalized Procrustes Analysis transformation efficiency analysis.

Source	df	Sum of squares	Mean squares	F	Pr > F
Residuals after scaling	2730	3438.211	1.259		
Scaling	130	571.959	4.400	3.493	<0.0001
Residuals after rotation	2860	4010.170	1.402		
Rotation	7150	551.525	0.077	0.061	1.000
Residuals after translation	10,010	4561.695	0.456		
Translation	1430	247.740	0.173	0.138	1.000
Corrected Total	111.440	4809.435	0.420		

Figure 2 presents the residuals by dromedary camel (object) after the aforementioned transformations in Table 2. We can observe that the dromedary Camel ID4/Female has the smallest residual. This indicates that there is most probably a consensus between participants/respondents when evaluating Camel ID4/Female behavioural response. Contrastingly, dromedary Camel ID5/Male was the one for whom consensus between participants/respondents less likely existed. This may be indicative

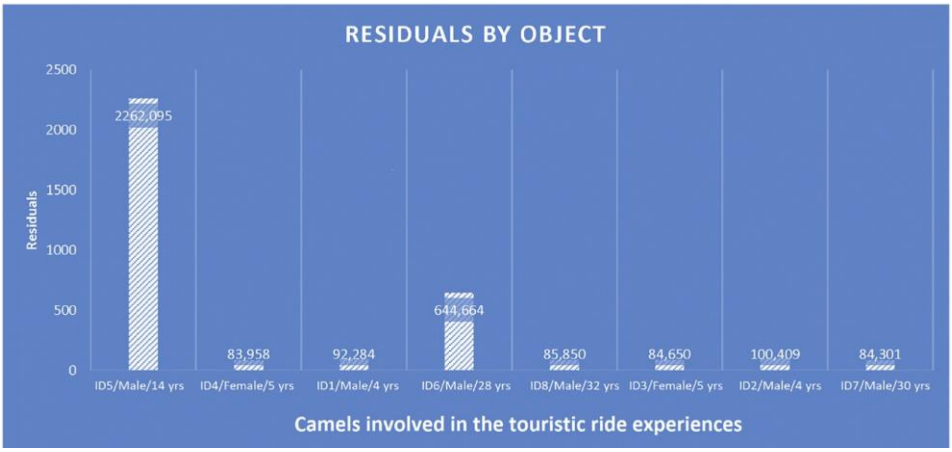


Figure 2. Residuals per dromedary camel involved in the touristic ride experiences (object).

of the behaviour patterns displayed by Camel ID4/ Female being the most stable and thus predictable, especially when compared to its opposite, Camel ID5/Male, who displayed a wider behavioural repertoire.

Figure 3 shows the residuals by participant/respondent (configuration) after the aforementioned transformations have been applied (Goodall, 1991). Thirty-four respondents presented the highest residual value of 57.659, which means that they gave rates that do not match the consensus. Apparently, she camels were those for which a rather stable behavioural repertoire was reported or for which customer appreciation identified a rather defined character.

Figure 4 presents scaling factors of the Generalized Procrustes Analysis transformations (Chapman, 1990). A factor lower than 1 indicates that the corresponding participant/respondent was using a wider scale than the others. If scaling factors are higher than 1, it is indicative of the respective participant/respondent not using the rating scale as widely as the other participants/respondents. Eighty-five participants/respondents used a wider scale than the rest of participants/respondents. This translates into more than half of the respondents being able to distinguish, thus to capture, higher levels of variability.

The proportion of the original variability explained by the consensus configuration was 27.02% (Figure 5). Table 3 shows that for the second dimension, the F value is below the 95th percentile. So we can conclude that two dimensions are enough.

The total of the variability of the consensus (100%; F1 99.99% and F2: 0.01%) is represented on the two axes (Figure 6). Results are almost identical when the variability is split across the participants/respondents. When residual variance is low (<1%), homogeneity within the group of respondents is reported. Each respondent's residual

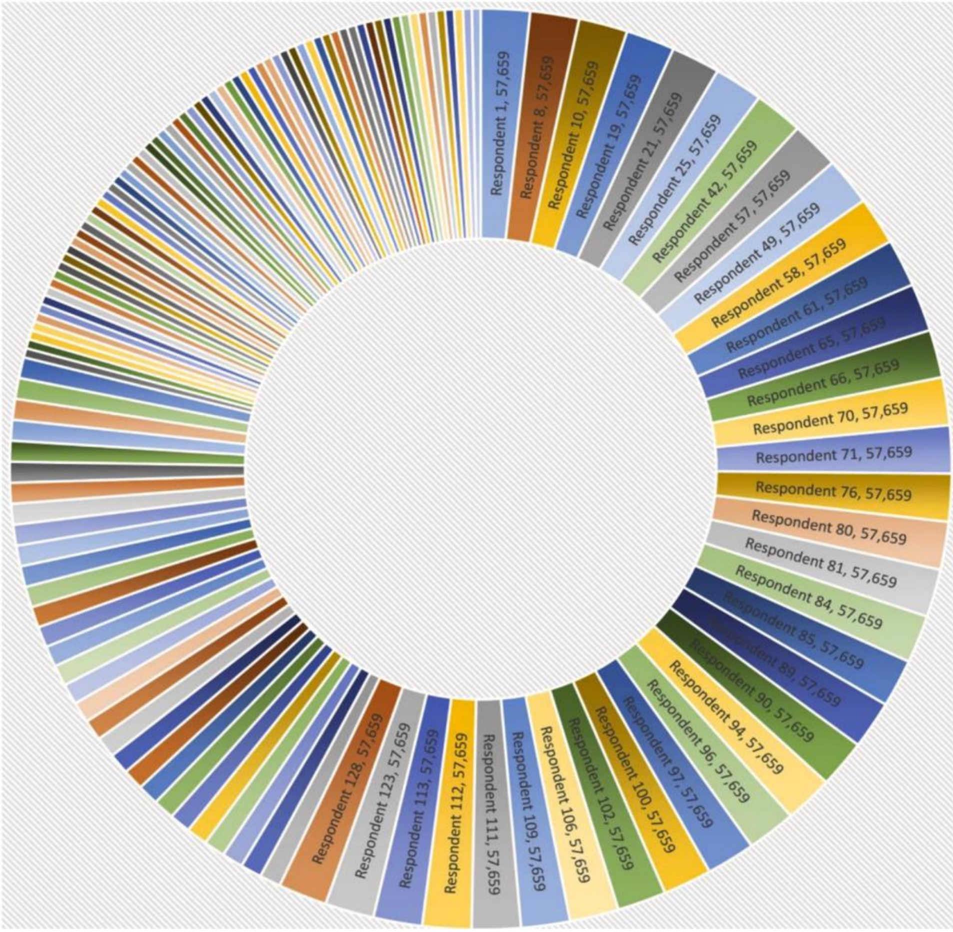


Figure 3. Residuals per participant/respondent (configuration).

variance reveals the relationship between the individual sample map and the consensus sample map (produced by the data obtained from all the respondents). The residual variance of respondents provides a measurement of goodness of fit of the consensus space of each respondent. It is expected that this can be as small as possible in order to facilitate a greater adjustment. Homogeneity of the scaling values observed in the present study indicated a reasonable efficacy in the training of the panel used in the evaluation of camels as touristic elements.

Generalized Procrustes analysis permits to minimize the differences among assessors, as it corrects for the different use of the scale by assessors to determine if semitrained assessors can still be used as suggested by Lorenzo, Purriños and Carballo (2016). A great degree of coincidence was found between the 131 testers with regard to the configuration of the 8 camels. After optimization, the first two main axes of the consensus explained 100% of the total variation among camels.

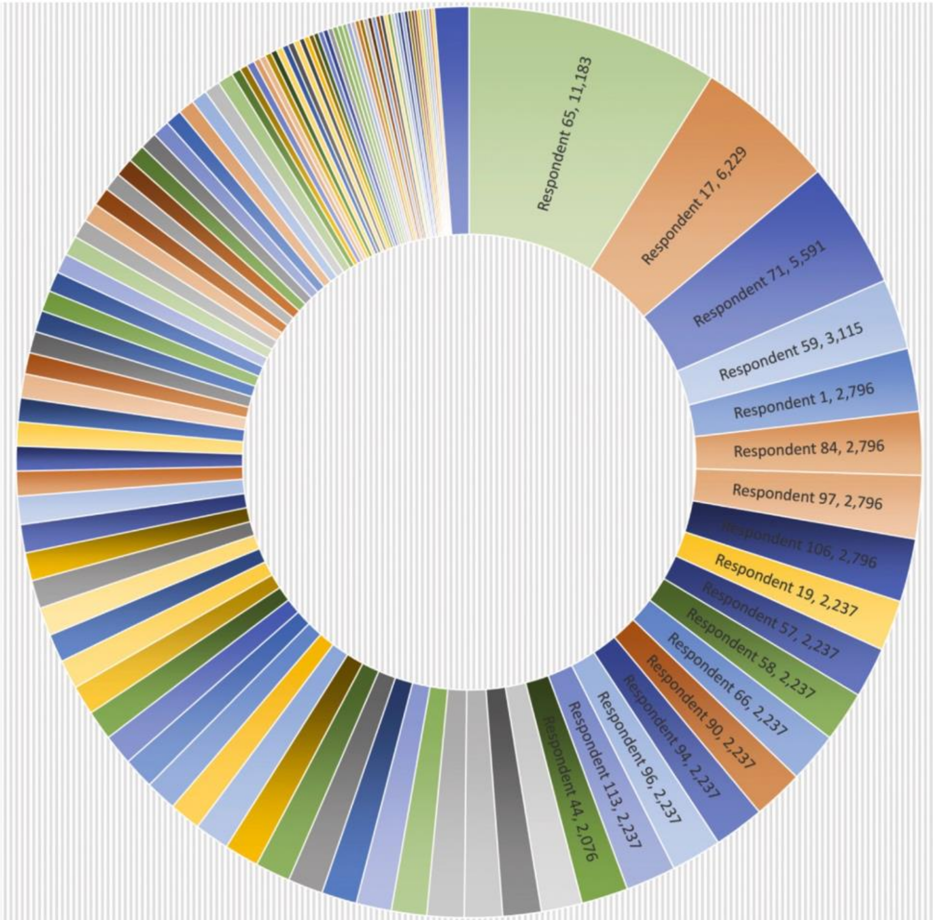


Figure 4. Scaling factors for each participant/respondent (configuration).

On the one hand, correlation circle for behavioural dimensions reported that all behavioural features were positively loaded, which reflected the existence of consensus when scoring for behavioural features. Correlations were in the range of obtained considering F1 captures a 99.99% of the variability of the data. Table 4 reports the values for the combined index (ICO) for the consensus on the perception of each particular behavioural feature by participants/respondents. Table 4 reports behavioural traits such as nervousness, caution and indifference and rejection, were highly differentiable among assessors. Oppositely, the lowest consensus was reached for calm and distracted statuses, that is these behavioural traits were less constantly identified among assessors.

On the other hand, Figure 7 shows the correlation circle for dromedary camels (objects). The points are close to the first axis because 99% of the variability is concentrated on the first axis, and because XLSTAT displays orthonormal maps to avoid

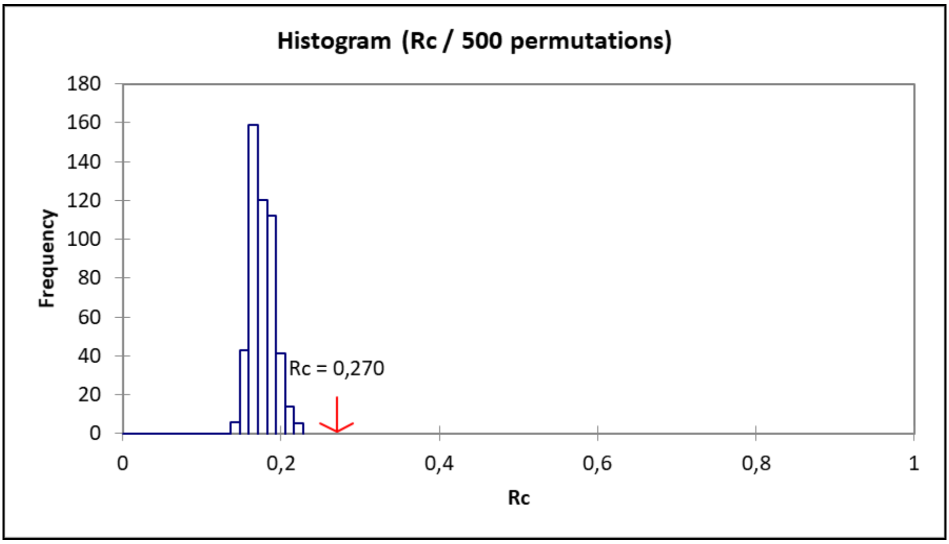


Figure 5. Histogram of the ratio between proportion of the original variance explained by the consensus configuration per 500 permutations.

Table 3. Results of the dimensions test.

Statistics	F1	F2
Permutations	500	500
F	58.9697	45.0793
Quantile	100.0000	100.0000
dF1	7	7
dF2	1040	1040
F (Critical value)	2.0184	2.0184
p-value	<0.0001	<0.0001
Alpha	0.05	0.05

misleading interpretations. However, Camel ID6/Male and Camel ID5/Male were highly positively loaded, which translated into these animals displaying extreme higher levels of the behavioural features considered in the analysis. Three clusters are formed. First, Camel ID4/Female, Camel ID3/Female, Camel ID7/Male and Camel ID8/Male. Second, Camel ID1/Male and Camel ID2/Male slightly separate while Camel ID6/Male and Camel ID5/Male are clearly separated on the map. These results suggest that the participants/respondents have a consensus on Camel ID4/Female, Camel ID3/Female, Camel ID7/Male and Camel ID8/Male, that they do not reach consensus in the cases of Camel ID1/Male and Camel ID2/Male, but also that this disagreement becomes extreme in the cases of Camel ID6/Male and Camel ID5/Male.

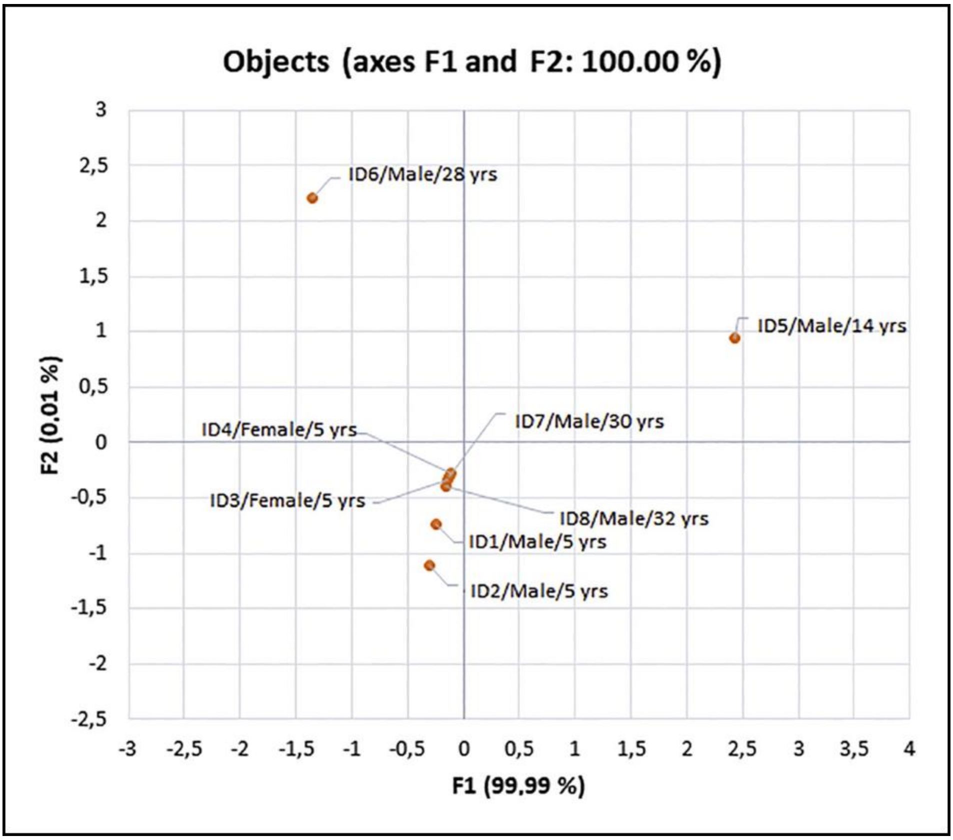


Figure 6. Biplot representing the dromedary camels involved in the touristic ride experiences (object).

Table 4. Combined Index (ICO) for correlations between dimensions in the initial consensus among respondents and the behavioural features.

	Correlation in F1	F1 Consensus Rank	Correlation in F2	F2 Consensus Rank	ICO
Nervous	0.466	11	0.605	3	5.50
Cautious	0.441	10	0.606	4	5.00
Indifferent	0.426	9	0.666	7	4.50
Rejectful	0.361	8	0.600	2	4.00
Surprised	0.317	7	0.693	10	3.50
Curious	0.314	6	0.583	1	3.00
Depressed	0.294	5	0.638	5	2.50
Scared	0.239	4	0.654	6	2.00
Mistrustful	0.194	3	0.676	8	1.50
Calm	0.159	2	0.712	11	1.00
Distracted	0.140	1	0.693	9	0.50

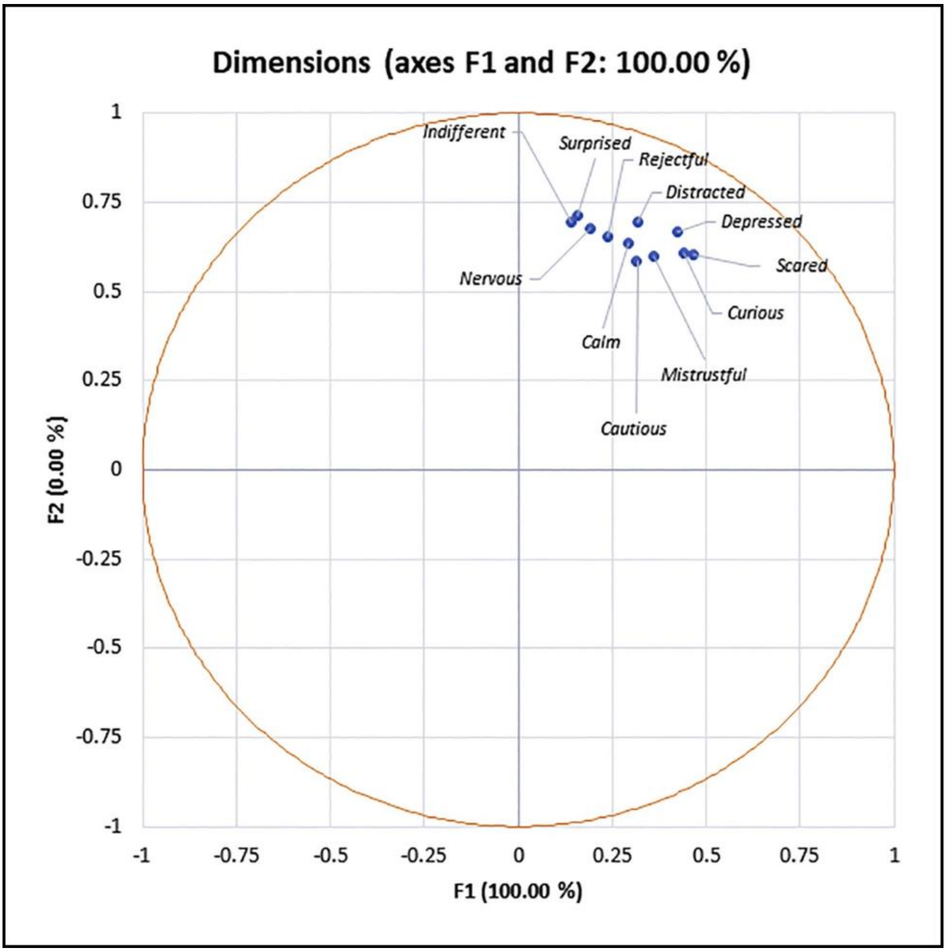


Figure 7. Biplot representing the behavioural traits dimensions considered.

Bayesian inference for ANOVA suggested coat colour does not influence behavioural feature perception while sex reported evidences differences in the mean for cautious, surprised and curious animals with males presenting significantly/evidently higher means than females. Participant satisfaction was evidently/significantly conditioned by the degree of expression of the behavioural features of curiousness and indifference evaluated in dromedary camels.

Concretely, as animal's environmental curiosity increases, the level of satisfaction progressively decreases, with highly curious animals being linked to mostly dissatisfied statuses. In line with these results, mild to high satisfaction statuses were associated to animals whose curiosity was directed towards the surrounding environment. Contrastingly, highly indifferent animals were linked to mostly dissatisfied statuses. Additionally, participants preferred that camels presented a neutral attitude, as an increased interest of the animals in the participants was associated to slight insatisfaction.

Bayesian Pearson's correlation analysis suggested the fact that as animal age increases the perception of the behavioural features of distraction, scare, rejection, indifference and nervousness reduces. However, calmness, mistrustfulness, curiousness, surprise and cautioness increase as age progresses.

Discussion

Generalized Procrustes Analysis has been used to date in research for the evaluation of behavioural patterns in the context of human-animal interaction in domestic species such as horses and ponies (Minero et al., 2009; Napolitano et al., 2008), dogs (Walker et al., 2010), pigs (Rutherford et al., 2012), sheep (Wickham et al., 2015) and zoo-housed giraffes (Patel, Wemelsfelder, & Ward, 2019). Except for the combined qualitative and quantitative appraisal conducted by Minero et al. (2009), behaviour assessment in domestic animals in human-influenced scenarios has been performed only for qualitative analysis. Notwithstanding, all these attempts reached observer consensus when assessing behavioural expression in the study subjects.

The present investigation was developed basing on the relative novelty of the knowledge on camel behaviour (Padalino & Menchetti, 2021) and considering no defined protocols for behavioural evaluation in reared-for-leisure camels are available. Consequently, this study presents and approach to fill the gap through a contrasted proposal which combines qualitative and quantitative behaviour assessment.

The efficiency of the statistical tools described was validated as suggested by our results, as general consensus among respondents when evaluating behavioural expressions in camels was soundly reached (see Figure 5). Furthermore, the outputs derived are supported on the scaling transformation effectiveness to handle heterogeneous data sets (see Table 1). According to Choo et al. (2012), nonmetric multidimensional scaling (MDS) is of valuable application when analysing relationships between different data sets despite being semantically related, as it might occurs in psychological constructs' research.

Although attempts to provide new insights on the dimensionality of dromedary camel behaviour have been made, experiences have not been translatable. For instance, a pioneer previous study evaluating the genetic regulation of the expression of personality in dromedary camels reared for purposes other than for leisure riding (Ramadan et al., 2018), mostly investigated some body language signals and time of reaction to novel stimuli. However, the premises proposed by these authors could not be specifically considered in the present research, provided behavioural responses displayed by camels along a dynamic interactive experience must be considered in the framework of the context that they take place. Consequently, differences in personalities may arise from different uses and the type of work performed by the subjects as suggested by Hausberger et al. (2004). Instead, descriptors of qualitative behaviour were adapted from other species such as the donkey (González et al., 2020) with whom camels may share similar historical background (being displaced from working activities due to agricultural mechanization) (Colli et al., 2013; Iglesias Pastrana et al., 2020) and contemporary utilitarian purposes (social activities) (Camillo et al., 2018; Schulz, 2008).

Not only participants/respondents rated every requested feature without exception but also a general consensus/agreement was reached. These findings suggested the behavioural traits considered in the present research were sufficiently recognizable and a certain affinity trend in the respondents participating in camel ride experiences could be foreseen (see Figure 5). The definition and prior clarification of descriptors to participants may also have helped to prevent subjective judgements arising from animal anthropomorphising or popular moral overtones (Minero et al., 2009).

In these regards, Kline (2008) recommendations were followed to ensure the proper definition of rating scales for behaviour quantitative assessment. This author advises that when evaluating psychological constructs, rating scales are preferred to be odd-numbered so that they include a mid, neutral option for respondents to be able to express a neutral opinion, thus diminishing ambiguity between adjacent categories. In this case, a significant proportion of the respondents' answers widely distributed along the scale hence the quantitative evaluation of camel behaviour was feasible (see Figure 3).

This finding adds consistency to the above-mentioned usefulness of an on-site guided instruction on animal behaviour to build up an objective unbiased criticism within the participants so that these latter have the chance to express right discrimination of camel behaviour responses' intensity on the Likert-type proposed scale.

Those cases in which a certain participant/respondent used a reduced number of the scale points, may be related to a lack of engagement of participants in the response to questionnaire and/or potential observer misunderstanding of the descriptors used. To prevent potential distorting effects, participants/respondents were asked about their overall impression on the behavioural patterns displayed by the individual with whom they had interacted, even if multiple behavioural patterns may have been detected during the course of the interactive experience (Clark et al., 2020).

Overall impressions can be conditioned by multiple animal intrinsic factors (Iglesias Pastrana et al., 2020). Despite the traditional testimonies ascribing a potential conditioning effect of coat colour phenotype on behaviour in dromedary camels (Volpato, Dioli, & Di Nardo, 2017) has been suggested, our results did not reported evidence of coat colour affecting behavioural patterns, as opposed to sex and age (see Tables 5 and 6). The relationship between coat colour phenotype and behaviour has been reported for other species such as equines (Finn et al., 2016), cattle (Finch, Bennett, & Holmes, 1984) and dogs (Kim et al., 2010).

The lack of evidences may be ascribed to the scarce intraherd variability for coat colour in our sample (light, medium and dark brown hair) hence, a limited power to detect potential associations in the framework of the possible interaction existing between phaneroptical traits and camel behaviour.

In regards sex-based differences, dromedary camel males were largely perceived as cautious, surprised and curious animals in com- parison to females (see Table 5), which can be justified on the basis that these behavioural features are predominantly linked to inherited traits in males of resource-defence polygynous mammals (Danell et al., 2006).

Table 5. Summary of Bayesian ANOVA outputs to determine differences in the mean for behavioural feature perception depending on the sex of the dromedary camel.

	Cautious	**Surprised**	**Curious**
Between Group Sum of Squares	2.288	0.663	2.891
Between Group df	1	1	1
Between Group Mean Square	2.288	0.663	2.891
Within Group Sum of Squares	1.590	0.618	2.452
Within Group df	6	6	6
Within Group Mean Square	0.265	0.103	0.409
F	8.636	6.441	7.074
Sig.	0.026	0.044	0.038
Bayes Factor	3.187	2.036	2.336
Female Posterior Mean	2.1	1	1.75
Female Posterior Variance	0.199	0.077	0.307
Female 95% Credible Interval	1.209-2.991	0.445-1.555	0.644-2.856
Male Posterior Mean	3.335	1.665	3.138
Male Posterior Variance	0.066	0.026	0.102
Male 95% Credible Interval	2.821-3.849	1.344-1.986	2.500-3.777

Older animals were evidently less fearful towards human contact than younger ones (see Table 6), which could have been expected as such a condition is pursued through the implementation of a standardized desensitization protocol and time-accumulated guided contact with human beings.

More specifically, Camel ID6/Male and Camel ID5/Male, for which intraobserver disagreement becomes extreme (see Figure 6), were likely to display emotionally unstable reactions during interactive experiences and thus may result undesirable to be used, and to act as potential breeders for this functional orientation. Besides, the fact that these animals exhibit the higher levels of the behavioural traits considered in the

Table 6. Summary of Bayesian Pearson's correlation outputs to determine the relationship between behavioural feature perception and age of the dromedary camel.

	Pearson Correlation	Bayes Factor
Distracted	-0.302	2.960
Calm	0.433	2.141
Mistrustful	0.284	3.062
Scared	-0.073	3.855
Depressed	0.013	3.914
Curious	0.605	1.057
Surprised	0.518	1.587
Rejective	-0.321	2.850
Indifferent	-0.386	2.450
Cautious	0.718	0.498
Nervous	-0.467	1.917

analysis are in line with the trend of respondents to use the medium values of the rating scale when evaluating animals displaying different behaviour expressions at similar proportion in a defined time frame.

For the particular case of Camel ID1/Male and Camel ID2/Male, although observer consensus for their behavioural performance is not remarkable (see Figure 6), such disagreement is not as extreme as for Camel ID6/Male and Camel ID5/Male. This lack of interobserver agreement can be supported on the basis that Camel ID1/Male and Camel ID2/Male are still young animals (4 years old) at early stages of desensitization, hence so they are expected to manifest a relatively wide variety of behavioural responses during the tourist ride. However, if domestication continues and not evident alterations appear in the environment that the animals live in, a general consensus for these dromedaries could be reached short term, which may also occur with their conspecifics Camel ID4/Female and Camel ID3/Female (5 years old). This means sex may not be as determinant as age at early ages up to the moment when animals reach five years of age.

This may be supported on the fact that Camel ID4/Female and Camel ID3/Female (5 years old), Camel ID7/Male and Camel ID8/Male (30 and 32 years old, respectively), were those for which observer general consensus was higher (see Figure 6), hence females may rather display more appropriate behavioural patterns than males at an earlier age. However, a similar progression of animals may be followed by both males and females until 5 years of age when field observations suggest that puberty is reached (between 3 and 5 years old) (Khanna et al., 1987; Marai et al., 2009; Sharma & Vyas, 1981). Overall, these four camels' behavioural aptitudes made them be the most suitable and the best-ranked candidates to become potential breeders seeking this functional aptitude.

ICO rank reported in Table 4 suggests Nervous, Cautious, Indifferent and Rejectful patterns were those among which a higher consensus was found scoring 4. Slightly behind them, Surprised, Curious, Depressed and Scared scored from 2 to 3.5. Mistrustful, Calm and Distracted animals were those for which a lower consensus was reached (ICO 1.5). This has been also reported by Lee et al. (2007) who stated that behavioural traits of assertiveness, excitability, human directed-agreeableness, sociability, and curiosity generally could be identified with high reliability. According to Wemelsfelder, Nevison, and Lawrence (2009) and their studies in Qualitative Behavioural Assessment (QBA), human respondents have the ability to integrate details of their perception of the attitude of animals in their contexts, using 'whole animal' descriptors such as calm, playful, content, indifferent or frustrated, such as those in the present study.

These results were then compared with the outputs from Bayesian ANOVA reported in Table 7. Bayesian inference for ANOVA suggested Curious and Indifferent behavioural patterns to condition the level of satisfaction of participants in touristic rides.

Table 7. Summary of Bayesian ANOVA outputs to determine differences in the mean for dromedary camel behavioural feature perception depending on the level of satisfaction of participants in touristic rides responding the survey.

Behavioural features	Between Group df	Between Group Mean Square	Within Group Sum of Squares	Within Group df	Within Group Mean Square	F	Sig.	Bayes Factor
Curious	3	3.793	78.334	59	1.328	2.857	0.045	0.154
Indifferent	3	2.504	42.017	51	0.824	3.039	0.037	0.226
Posterior Parameters		**Completely dissatisfied**	**Mostly dissatisfied**	**Somewhat dissatisfied**	**Neither satisfied or dissatisfied**	**Somewhat satisfied**	**Mostly satisfied**	**Completely satisfied**
Curious	Mean	N/A	4.00	N/A	N/A	1.00	1.35	1.47
	Variance	N/A	0.86	N/A	N/A	0.21	0.04	0.03
	95% Credible Interval	N/A	2.178-5.822	N/A	N/A	0.089-1.911	0.943-1.757	1.134-1.799
Indifferent	Mean	N/A	4.00	N/A	N/A	2.60	2.30	3.15
	Variance	N/A	1.37	N/A	N/A	0.28	0.06	0.04
	95% Credible Interval	N/A	1.694-6.306	N/A	N/A	1.569-3.631	1.824-2.785	2.752-3.542

Animals displaying indifferent statuses were linked to higher levels of dissatisfaction from users, hence negative selection against such patterns may be encouraged, first at a phenotypical level through training and at a genetical level through directed breeding. Animal friendliness towards unfamiliar users has been reported to be linked to caretaker or owner training abilities, but also to the diversity of users taking care of animals on a daily basis (Hausberger & Muller, 2002). Furthermore, Kim et al. (2018) provided evidence and supported the aforementioned findings from a genetic perspective as suggested by the considerably low heritability and variance of environmental permanent effect of caretaker/owner in friendliness when compared to other behavioural patterns such as Gentleness, Patience, Aggressiveness and Sensitivity behavioural patterns displayed by animals. Furthermore, there was a high genetic correlation between friendliness and the rest of traits which was not concomitant with a high phenotypic correlation which has been suggested to be ascribed to behavioural plasticity promoted by environmental factors such as for instance, the trainer of educator of the animals (Navas González et al., 2019).

This suggests behaviour patterns such as curiosity or indifference may relevantly be considered potential candidates as objective selection criteria, provided the interobserver consensus reported by our results, but also given their expression may translate into a greater or lesser level of satisfaction of the people participating in camel touristic ride experiences. However, models may need to compromise environmental non- permanent and permanent effects, as such behavioural patterns may be severely conditioned by them.

The present discriminating tool may constitute the basis on which to support the selection of animals for breeding depending on their behavioural traits and lays the opportunity to configure breeding criteria. In turn, the selection of better behaving individuals may translate into improved satisfaction of the participants/respondents in leisure-based interactive experiences, but also may enhance efficiency of livestock handling practices and thus the animal wellbeing (Boissy et al., 2005). Aiming to early select for less fearfulness and easy-to-handle dromedary camels, phenotype registry basing on this empirical proposal for camel behaviour performance has to be promptly put into practice so that its heritability can be estimated without more delay and accurate selective breeding for this local livestock breed performed.

Emerging niche applications (i.e., emerging interest in milking) may also benefit from this first selection attempt, given desirable behavioural patterns may be linked to easier handling and application of routinely husbandry practices. In this ongoing scenario, molecular tools will be of valuable usefulness for marker-assisted selection by identifying molecular markers linked to the trait(s) of interest and quantify the genetic correlations between them (Besson et al., 2020). On that account, it is also recommended to discuss if multiple selection criteria could arise on conflicting objectives in regards to the maintenance of genetic diversity and uniqueness of this camel endangered breed.

Conclusions

The Procrustes analyses-based selection tool described in the present research was validated as general consensus in regards behavioural evaluation was reached among respondents. Overall behavioural impressions suggest participants effectively distinguish between desirable or undesirable features. Females appear to be ready to participate in camel ride experiences earlier than males, although a similar progression may be observed until 5 years of age, when puberty is reached. Camel's indifference towards human was linked to user dissatisfaction, hence, negative selection approaches against it may be encouraged. Although curiosity was not a totally desirable trait, it still promoted the satisfaction of customers in many cases. Behavioural traits were sufficiently recognizable and certain affinity trends in respondents can be detected towards attentive animals through features which may act as potential desirable behavioural breeding criteria to be considered in leisure camel breeding programmes.

Supplementary materials: Supplementary data to this article can be found online at https://doi.org/10.1016/j.rvsc.2021.08.007.

Funding: The present research was carried out in the financing framework of the international project CA.RA.VA.N - "Toward a Camel Transnational Value Chain" (Reference APCIN-2016-00011-00-00) and during the covering period of a predoctoral contract (FPU Fellowship) funded by the Spanish Ministry of Science and Innovation.

Acknowledgments: The authors would like to thank "Aires Africanos" Eco-tourism Company for its direct technical help and assistance.

Conflicts of interest: The authors declare no conflict of interest.

References

Addinsoft, S. (2018). *XLSTAT software, versión 2018.5*. Addinsoft, Paris, France: Addinsoft.

Anup, K. (2016). Ecotourism and its role in sustainable development of Nepal. *Tourism: From Empirical Research Towards Practical Application*, 31.

Arora, J. S. (2017). Chapter 14 - Practical Applications of Optimization. In *Introduction to Optimum Design (Fourth Edition)* (J. S. Arora, Ed.)) (pp. 601-680): Academic Press.

Bakdash, J. Z., & Marusich, L. R. (2017). Repeated Measures Correlation. *Frontiers in psychology*, 8(456).

Besson, M., Komen, H., Rose, G., & Vandeputte, M. (2020). The genetic correlation between feed conversion ratio and growth rate affects the design of a breeding program for more sustainable fish production. *Genetics Selection Evolution*, 52(1), 5.

Boissy, A., Fisher, A., Bouix, J., Hinch, G., & Le Neindre, P. (2005). Genetics of fear in ruminant livestock. *Livestock Production Science*, 93(1), 23-32.

Breulmann, M., Böer, B., Wernery, U., Wernery, R., El Shaer, H., Alhadrami, G., Gallacher, D., Peacock, J., Chaudary, S.A., Brown, G., & Norton, J. (2007). *The Camel from Tradition to Modern Times–A Proposal Towards Combating Desertification Via the Establishment of Camel Farms Based on Fodder Production from Indigenous Plants and Halophytes*: UNESCO Doha.

Bulbeck, C. (2012). *Facing the wild: Ecotourism, conservation and animal encounters*: Earthscan.

Camillo, F., Rota, A., Biagini, L., Tesi, M., Fanelli, D., & Panzani, D. (2018). The current situation and trend of donkey industry in Europe. *Journal of Equine Veterinary Science*, 65, 44-49.

Campos, A. C., Mendes, J., do Valle, P. O., & Scott, N. (2017). Co-creating animal-based tourist experiences: Attention, involvement and memorability. *Tourism Management*, 63, 100-114.

Chapman, R. E. (1990). Conventional procrustes approaches. Proceedings of the Michigan morphometrics workshop.

Choo, J., Bohn, S., Nakamura, G. C., White, A. M., & Park, H. (2012). Heterogeneous data fusion via space alignment using nonmetric multidimensional scaling. Proceedings of the 2012 SIAM International Conference on Data Mining.

Clark, L., Butler, K., Ritchie, K. L., & Maréchal, L. (2020). The importance of first impression judgements in interspecies interactions. *Scientific Reports*, 10(1), 1-10.

Colli, L., Perrotta, G., Negrini, R., Bomba, L., Bigi, D., Zambonelli, P., Verini Supplizi, A., Liotta, L., & Ajmone-Marsan, P. (2013). Detecting population structure and recent demographic history in endangered livestock breeds: the case of the Italian autochthonous donkeys. *Animal genetics*, 44(1), 69-78.

Coria, J., & Calfucura, E. (2012). Ecotourism and the development of indigenous communities: The good, the bad, and the ugly. *Ecological Economics*, 73, 47-55.

Corp., I. (2017a). *IBM SPSS Statistics for Windows (Version 25.0)*. Armonk, NY: IBM Corp.

Corp., I. (2017b). *IBM SPSS Statistics Algorithms*. In Version 25.0 ed., pp. 110. Armonk, NY: IBM Corp.

Daher, R. F. (2006). *Tourism in the Middle East: Continuity, change and transformation*: Multilingual Matters.

Danell, K., Bergström, R., Duncan, P., & Pastor, J. (2006). *Large herbivore ecology, ecosystem dynamics and conservation (Vol. 11)*: Cambridge University Press.

Dijksterhuis, G. B., & Gower, J. C. (1991). The interpretation of generalized procrustes analysis and allied methods. *Food quality and preference*, 3(2), 67-87.

Edwards, G. P., Zeng, B., Saalfeld, W. K., & Vaarzon-Morel, P. (2010). Evaluation of the impacts of feral camels. *The Rangeland Journal*, 32(1), 43-54.

Faye, B. (2014). The camel today: assets and potentials. *Anthropozoologica*, 49(2), 167-176.

Fennell, D. A. (2020). *Ecotourism*: Routledge.

Finch, V. A., Bennett, I., & Holmes, C. (1984). Coat colour in cattle: effect on thermal balance, behaviour and growth, and relationship with coat type. *The Journal of Agricultural Science*, 102(1), 141-147.

Finn, J. L., Haase, B., Willet, C. E., van Rooy, D., Chew, T., Wade, C. M., Hamilton, N.A., & Velie, B. D. (2016). The relationship between coat colour phenotype and equine behaviour: A pilot study. *Applied Animal Behaviour Science*, 174, 66-69.

González, F. J. N., Vidal, J. J., Jurado, J. M. L., McLean, A. K., & Bermejo, J. V. D. (2020). Nonparametric analysis of noncognitive determinants of response type, intensity, mood, and learning in donkeys (Equus asinus). *Journal of Veterinary Behavior*, 40, 21-35.

Goodall, C. (1991). Procrustes methods in the statistical analysis of shape. *Journal of the Royal Statistical Society: Series B (Methodological)*, 53(2), 285-321.

Hausberger, M., Bruderer, C., Le Scolan, N., & Pierre, J.-S. (2004). Interplay between environmental and genetic factors in temperament/personality traits in horses (*Equus caballus*). *Journal of Comparative Psychology*, 118(4), 434-446.

Hausberger, M., & Muller, C. (2002). A brief note on some possible factors involved in the reactions of horses to humans. *Applied Animal Behaviour Science*, 76(4), 339-344.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S., & Bermejo, J. V. (2020a). Zoometric characterization and body condition score in Canarian camel breed. *Archivos de zootecnia*, 69(265), 14-21.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S., & Bermejo, J. V. (2020b). Ethological characterization of the Canarian camel breed. *Archivos de zootecnia*, 69(265), 108-115.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Nogales Baena, S., & Delgado Bermejo, J. V. (2020). Camel Genetic Resources Conservation through Tourism: A Key Sociocultural Approach of Camelback Leisure Riding. *Animals*, 10(9), 1703.

Jones, L. L. (2012). Prospective and retrospective processing in associative mediated priming. *Journal of Memory and Language*, 66(1), 52-67.

Kass, R. E., & Raftery, A. E. (1995). Bayes factors. *Journal of the American Statistical Association*, 90(430), 773-795.

Khanna, N., Rai, A., Tandon, S., & Jindal, H. (1987). Camel reproduction: A review. *Annals of arid zone*.

Kim, N. Y., Son, J. K., Cho, I. C., Shin, S. M., Park, S. H., Seong, P. N., Woo, J.H., Park, N.G., & Park, H. B. (2018). Estimation of genetic parameters for temperament in Jeju crossbred horses. *Asian-Australasian Journal of Animal Sciences*, 31(8), 1098-1102.

Kim, Y. K., Lee, S. S., Oh, S. I., Kim, J. S., Suh, E. H., Houpt, K. A., Lee, H.C., Lee, H.J, & Yeon, S. C. (2010). Behavioural reactivity of the Korean native Jindo dog varies with coat colour. *Behavioural Processes*, 84(2), 568-572.

Kline, R. B. (2008). *Becoming a behavioral science researcher: A guide to producing research that matters*: Guilford Press.

Lee, C. M., Ryan, J. J., & Kreiner, D. S. (2007). Personality in Domestic Cats. *Psychological reports*, 100(1), 27-29.

Liang, F., Paulo, R., Molina, G., Clyde, M. A., & Berger, J. O. (2008). Mixtures of g priors for Bayesian variable selection. *Journal of the American Statistical Association*, 103(481), 410-423.

Lorenzo, J. M., Purriños, L., & Carballo, J. (2016). A Survey on the Effect of Livestock Production System and Finishing Diet on Sensory Characteristics of Foal Meat Using Generalized Procrustes Analysis. *The Scientific World Journal*, 2016, 8729053.

Marai, I. F., Zeidan, A., Abdel-Samee, A., Abizaid, A., & Fadiel, A. (2009). Camels' reproductive and physiological performance traits as affected by environmental conditions. *Tropical and Subtropical Agroecosystems*, 10(2), 129-149.

Meleddu, M., & Pulina, M. (2016). Evaluation of individuals' intention to pay a premium price for ecotourism: An exploratory study. *Journal of Behavioral and Experimental Economics*, 65, 67-78.

Minero, M., Tosi, M. V., Canali, E., & Wemelsfelder, F. (2009). Quantitative and qualitative assessment of the response of foals to the presence of an unfamiliar human. *Applied Animal Behaviour Science*, 116(1), 74-81.

Morey, R., & Rouder, J. (2015). *BayesFactor 0.9. 12-2*. Comprehensive R Archive Network.

Napolitano, F., De Rosa, G., Braghieri, A., Grasso, F., Bordi, A., & Wemelsfelder, F. (2008). The qualitative assessment of responsiveness to environmental challenge in horses and ponies. *Applied Animal Behaviour Science*, 109(2-4), 342-354.

Navas, F. J., Jordana, J., León, J. M., Arando, A., Pizarro, G., McLean, A. K., & Delgado, J. V. (2017). Measuring and modeling for the assessment of the genetic background behind cognitive processes in donkeys. *Research in veterinary science*, 113, 105-114.

Navas González, F. J., Jordana Vidal, J., León Jurado, J. M., Arando Arbulu, A., McLean, A. K., & Delgado Bermejo, J. V. (2018). Genetic parameter and breeding value estimation of donkeys' problem-focused coping styles. *Behavioural Processes*, 153, 66-76.

Navas González, F. J., Jordana Vidal, J., León Jurado, J. M., McLean, A. K., & Delgado Bermejo, J. V. (2019). Dumb or smart asses? Donkey's (*Equus asinus*) cognitive capabilities share the heritability and variation patterns of human's (*Homo sapiens*) cognitive capabilities. *Journal of Veterinary Behavior*, 33, 63-74.

Padalino, B., & Menchetti, L. (2021). The First Protocol for Assessing Welfare of Camels. *Frontiers in veterinary science*, 7, 1230.

Patel, F., Wemelsfelder, F., & Ward, S. J. (2019). Using qualitative behaviour assessment to investigate human-animal relationships in zoo-housed Giraffes (*Giraffa camelopardalis*). *Animals*, 9(6), 381.

Pizarro Inostroza, M. G., Navas González, F. J., Landi, V., León Jurado, J. M., Delgado Bermejo, J. V., Fernández Álvarez, J., & Martínez Martínez, M. d. A. (2020). Bayesian Analysis of the Association between Casein Complex Haplotype Variants and Milk Yield, Composition, and Curve Shape Parameters in Murciano-Granadina Goats. *Animals*, 10(10), 1845.

Profillidis, V. A., & Botzoris, G. N. (2019). Chapter 5 - Statistical Methods for Transport Demand Modeling. In, *Modeling of Transport Demand* (pp. 163-224) (V. A. Profillidis & G. N. Botzoris, Eds.): Elsevier.

Ramadan, S., Nowier, A. M., Hori, Y., & Inoue-Murayama, M. (2018). The association between glutamine repeats in the androgen receptor gene and personality traits in dromedary camel (*Camelus dromedarius*). *PloS one*, 13(2), e0191119.

Rouder, J. N., & Morey, R. D. (2012). Default Bayes factors for model selection in regression. *Multivariate Behavioral Research*, 47(6), 877-903.

Rouder, J. N., Morey, R. D., Speckman, P. L., & Province, J. M. (2012). Default Bayes factors for ANOVA designs. *Journal of Mathematical Psychology*, 56(5), 356-374.

Rutherford, K. M., Donald, R. D., Lawrence, A. B., & Wemelsfelder, F. (2012). Qualitative Behavioural Assessment of emotionality in pigs. *Applied Animal Behaviour Science*, 139(3-4), 218-224.

Schulz, U. (2008). *El camello en Lanzarote*: Aderlan.

Schulz, U., Tupac-Yupanqui, I., Martínez, A., Méndez, S., Delgado, J. V., Gómez, M., Dunner, S., & Cañón, J. (2010). The Canarian camel: a traditional dromedary population. *Diversity*, 2(4), 561-571.

Seifu, E., Angassa, A., & Boitumelo, W. (2018). Community-based camel ecotourism in Botswana: Current status and future perspectives. *Journal of Camelid Science*, 11, 33-48.

Sharma, S., & Vyas, K. (1981). Studies on sexual physiology of stud camel (*Camelus dromedarius*). *Indian Veterinary Journal*.

Sindhu, D., & Singh, D. (2014). Ecotourism and Local Perception about its Impacts a Study of Village Sam, Jaisalmer, Rajasthan. *International Journal of Environment, Ecology, Family and Urban Studies (IJEEFUS)*, 4(6), 1-6.

Tefera, M. (2004). Observations on the clinical examination of the camel (*Camelus dromedarius*) in the field. *Tropical animal health and production*, 36(5), 435-449.

Van Vleck, L. D. (1993). *Selection index and introduction to mixed model methods for genetic improvement of animals*: The Green Book.

Volpato, G., Dioli, M., & Di Nardo, A. (2017). Piebald camels. *Pastoralism*, 7(1), 1-17.

Walker, J., Dale, A., Waran, N., Clarke, N., Farnworth, M., & Wemelsfelder, F. (2010). The assessment of emotional expression in dogs using a Free Choice Profiling methodology. *Animal Welfare*, 19(1), 75-84.

Wemelsfelder, F., Nevison, I., & Lawrence, A. B. (2009). The effect of perceived environmental background on qualitative assessments of pig behaviour. *Animal Behaviour*, 78(2), 477-484.

Wickham, S. L., Collins, T., Barnes, A. L., Miller, D. W., Beatty, D. T., Stockman, C. A., Blache, D., Wemelsfelder, F., & Fleming, P. A. (2015). Validating the use of qualitative behavioral assessment as a measure of the welfare of sheep during transport. *Journal of Applied Animal Welfare Science*, 18(3), 269-286.

Wilson, R., & Gutierrez, C. (2015). The one-humped camel in the Canary Islands: History and present status. *Tropicultura*, 33(4).

Wilson, T. (2013). The one-humped camel in Southern Africa: use in Police, Postal Service and Tourism in Botswana, c. 1900-2011. *Botswana Notes and Records*, 45, 180-188.

Xu, J. B., & Chan, S. (2016). A new nature-based tourism motivation model: Testing the moderating effects of the push motivation. *Tourism Management Perspectives*, 18, 107-110.

CHAPTER 7

EXPLORATION OF NEW POTENTIAL FUNCTIONAL NICHES FOR 'CANARIAN CAMEL' BREED

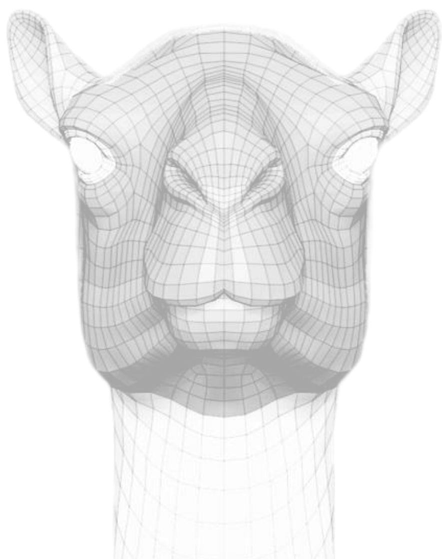
7.1 A comparison of physical properties between Merino wool and camel hair through discriminant analysis

Carlos Iglesias Pastrana[1], Francisco Javier Navas González[1], Elena Ciani[2], Beatriz López de los Santos[3] and Juan Vicente Delgado Bermejo[1]

[1]Department of Genetics, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain

[2]Department of Biosciences, Biotechnologies and Biopharmaceutics, Faculty of Veterinary Sciences, University of Bari 'Aldo Moro', 70121 Bari, Italy

[3]Ovino del Suroeste Sdad Coop Ltda (Oviso SCL), 06700 Villanueva de la Serena, Badajoz, Spain



Quality indicator information provided on the publication
Latest information available (2022)

Status of the manuscript: Under review

Journal (year, volume, page(s)): *Journal of Natural Fibers*

International database in which it is indexed: Journal of Citation Reports (JCR)

Thematic area in the reference database: Materials Science & Textiles

Impact index of the journal in the year of the article's publication: 3.5

Rank/number of thematic area journals: 4/25 (Q1)

Abstract

The applicability of camel hair is still conditioned by a gap in the knowledge about this raw material, which in turn hinders its supply chain, commercial possibilities, and the market value that the product reaches. The present research compares the physical-mechanical properties of Canarian camel hair versus Merino sheep wool, the world's most popular proteinic fabric material, using a discriminant canonical analysis. The attributes that maximized differences between both types of animal-origin fibers were related to the average fiber diameter, fineness, length staple, and residual dirt. Although slightly shorter than sheep wool, camel hair can reach a prominent fabric quality and spinning performance given its greater average diameter and its lower variation within small fragments along the snippet, as well as the higher distance from the tip to the finest point in the staple, which is an indicator for the breaking point. Such characteristics are known to increase bending rigidity during the manufacturing process. Residual dirt may be associated with the low-input, extensive exploitation of camels. The present paper provides a reference for maturing pre-process and manufacture techniques for the further valorization of camel hair in the present-day textile industry and, thus, engages income opportunities for this livestock production.

Keywords

Camel hair, sheep wool, optical fiber measurement, comparative analysis, niche market, OFDA

Introduction

Despite the fact that natural vegetable fibers (cotton, linen) and plastic-derived synthetic fibers (polyurethane, polyamide, and acrylic) have emerged within the textile and apparel manufacturing scene (Purvis & Franklin, 2005), sheep wool and other mammal hairs (i.e., goat, camel, or yak hair) remain among the most demanded natural fibers in the textile industry (Harizi et al., 2007). Particularly, Merino sheep wool is highly demanded and acknowledged as the finest and softest crimped fiber (Wang et al., 2014). However, other coarser but still smoother animal fibers, such as mohair, cashmere, camelid fleece, large bovid fiber, and Angora rabbit hair, are generally less appreciated for clothing fashion design but for the home textiles market (Yam & Khomeiri, 2015), despite the product diversification that the broad public often demands (Yondonsambuu & Altantsetseg, 2003).

In this context, Old-World camels' hair fibers may constitute a huge, valuable textile resource due to their diverse nature (Burger, Ciani, & Faye, 2019). Bactrian or two-humped camels (*Camelus bactrianus*) have been addressed as a source for quality thin fiber production in Asian local communities. The main niche that this specific fiber covers is the satisfaction of self-consumption and emerging European and North American exportation demands (Babu, 2015; Zarrin et al., 2020). By contrast, dromedary or one-humped camel (*Camelus dromedarius*) fiber has been reported to attract consumers due to the comfortability this fiber confers to fabrics (Sharma & Pant, 2013), which makes it especially suitable for the clothing industry. Still, this wide range of applications has not translated into increased attention paid by researchers in terms of production systems, selective breeding, best processing practices, and market opportunity fulfillment (McGregor, 2018).

Furthermore, the exploration of hair production could lead to the consolidation of camel hair as a high-value functional niche for these species, which in turn may ensure the sustainability of endangered camel populations. Among these endangered populations, the Canarian camel is an autochthonous breed originally from Spain and unique in Europe (Iglesias Pastrana et al., 2020a), which may find in this market niche a viable opportunity for its long-term viability.

Considering all the aforementioned, the present research aims to perform a comprehensive comparison of the physical-mechanical properties of Canarian camel hair versus the widely acknowledged Merino sheep wool. Empirical evidence about the possibilities of the further use of camel hair in the present-day textile industry is also explored. The comparative analysis of camel hair opportunities as a source of income linked to the textile industry and camel production systems may in turn benefit entrepreneurs and camel breeders who may be presented with an alternative niche that camel hair could competitively cover.

Material and methods

Animal sample

Clumps of camel outer hair were gathered by shearing from 139 Canarian dromedaries (77 males and 62 females; aged between 3 months and 35 years old; Table 1) during the moulting season (Babu, 2015). The samples were collected from six different body regions (shoulder, hump, belly, rump, tail dock, and tail skirt) per dromedary camel (Figure 1). These areas were chosen because the density of the hair coat is higher (Bhakat, 2019) hence, larger samples can be obtained.

Merino sheep wool from 395 animals (214 males and 181 females; aged between 3 months and 5 years old; Table 1) was clipped with curved scissors from an area of 6 cm2. The anatomical regions from which the wool samples were collected are the shoulder, belly, and rump (Figure 1). For 55 adult animals, the fibers from each region were analyzed independently as well as a blended sample of them. The rest of the animals' wool samples were analyzed once blended.

Table 1. Age group classification of dromedary camels and sheep.

Animal species	Group 1 *Prepuber*	Group 2 *Sexually mature*	Group 3 *Reproductively senescent*	Source of information
Dromedary camel	<3 years	3-15 years	>15 years	Al-Qarawi et al. 2000, 2001
Sheep	<6 months	6 months – 6 years	>6 years	Nieto et al. 2013; Mysterud et al. 2002

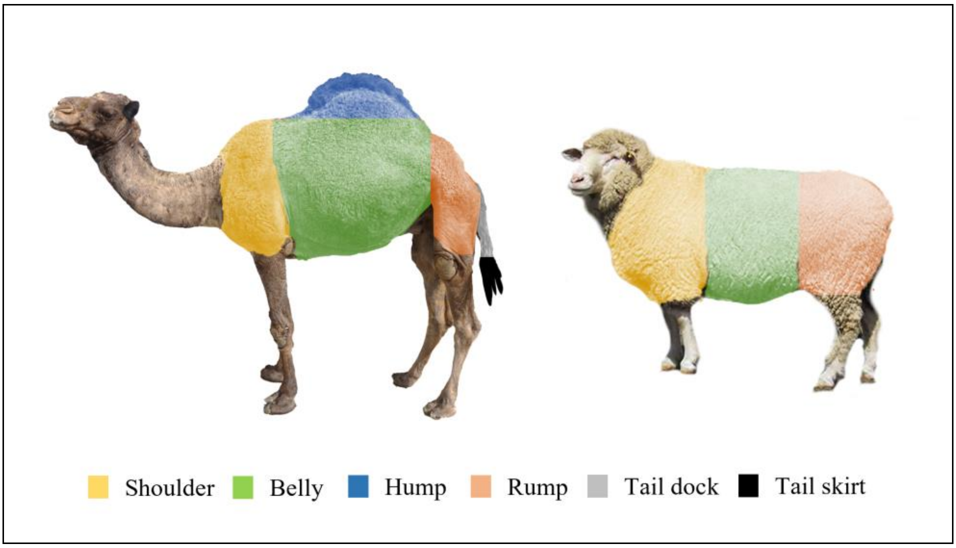


Figure 1. Graphical representation of Canarian camel hair and Merino sheep wool sampling regions.

Sample preparation and physical-mechanical analysis

Once obtained and before physical-mechanical analysis, camel hair and sheep wool samples were scoured with a mix of solid surfactant (hexane) and hot water (Allafi et al., 2021) to discard the animal grease and the dirty materials associated with the secretion of sweat glands and environmental pollution.

After scouring, fibers were dried at ambient temperature and analyzed using an optical fiber diameter measurement analysis (OFDA 2000, McLaughlin (2000)). A minimum of 1,500 fibers were measured and averaged for each sample. The average values for the temperature and relative humidity at the time of fiber measurement were 25°C and 45.7%, respectively.

Parameter description

Fiber parameters measured by the optical fiber diameter analyzer are listed in Table 2.

Table 2. Set of fiber parameters quantified by using an optical fibre diameter analysis and mean values per each parameter and species (Canarian camel and Merino sheep).

Parameter	Abbreviation	Unit of measurement	Mean value	
			Canarian camel	Merino sheep
Average fiber diameter	meanD	μm	40.76	21.42
Standard deviation of fiber diameter	SDD	μm	13.43	3.97
Standard deviation expressed as a % of the sample's average diameter	CVD	%	35.37	18.79
Difference between the top 5% of fibers in the histogram and the average fiber diameter	CEM	μm	24.36	7.06
Percentage of fibers less than or equal to 30 microns	CF	%	41.23	96.86
Millimeters from the tip to the finest point in the staple. It is an indicator for the 'point of break'	fiFromTip	mm	25.43	24.45
Percentage of fibres in a sample less than 15 microns	%<15μm	%	2.05	5.93
Maximum diameter along the staple	maxD	μm	41.96	16.62
Minimum diameter along the staple	minD	μm	34.56	14.77
Mean diameter at the base of the fiber	baseD	μm	37.76	15.39
Standard deviation of fibre diameter along the staple	SD Along Profile	μm	2.25	0.64
Standard deviation of fibre diameter across the staple	SD Across	μm	11.64	2.6
Spin fineness	spinF	μm	40.37	20.47
Average fiber curvature	meanC	Degrees per millimeter	23.24	114.71
Standard deviation of fiber curvature	SDC	Degrees per millimeter	24.98	74.94

Table 2. *Cont.*

Parameter	Abbreviation	Unit of measurement	Mean value	
			Canarian camel	Merino sheep
Length of the relaxed staple	length staple	mm	40.71	58.23
Fat cover correction factor	GCF	μm	0	0
Total percentage area of blobs. It is an objective measure of fibre cleanliness	All blob%	%	1.87	0.78
Total percentage area of large blobs	large blob%	%	1.02	0.27
Total percentage area of small blobs	small blob%	%	0.85	0.51
Fibre diameter variation along about 200μm of the snippet	sdD along 200μm	μm	0.88	1
Minimum diameter along about 200μm of the snippet	minD along 200μm	μm	40.33	20.2
Number of fibers measured for diameter	numD	Number of fibers	2689.9	3137.3
Density of fibers on the slide	density	%	32.37	33.59
Standard deviation of density	denseSD	%	24.71	25.11
Current temperature during fiber analysis	temp C	°C	26.12	23.51
Current air humidity during fiber analysis	RH%	%	43.85	48.16
Number of video images analyzed in the run	numFields	Number of video images	1684.47	1486.52
Time taken by the measurement	tmTaken	Seconds	10	10
Sharpness of fiber images	Focus	μm	10.19	11.14
Standard deviation of focus	focusSD	mm	3.38	3.35
Number of fibres out of focus	outFocus	Number of fibres	7.16	51.9
Number of fibres outside accepted light range	outLight	Number of fibers	0	0
Horizontal image width	horWidth	μm	0	0
Camera dark level at start	darkSt	Lumens %	11.88	11.94
Camera dark level in measure	dark	Lumens %	10	10

Table 2. *Cont.*

Parameter	Abbreviation	Unit of measurement	Mean value	
			Canarian camel	Merino sheep
Standard deviation of camera dark level	darkSD	Lumens %	0	0
Minimum grey level inside fibre	min	ISO	15.81	20.69
Standard deviation of minimum grey level inside fibre	minSD	ISO	3.69	4.92
Light level next to fibre	light	nm wavelength	103.59	101.35
Standard deviation of light level next to fibre	lightSD	nm wavelength	1.14	1.52
Maximum light level next to fibre	max	nm wavelength	108.04	110.75
Standard deviation of maximum light level next to fibre	maxSD	nm wavelength	2.71	2.85
Camera noise standard deviation	noiseSD	EMVA Standard 1288	0	0
Microsecond flash length	Flash	microsecond	19.47	20.61
Home error in across stepper motor	hmErAc	degree	-0.42	-0.46
Home error in in out stepper motor	hmErIO	degree	-0.24	-0.27
Fibre density in OFDA4000 beard	Dense0 beard	mg/mm	0	0
Uniformity of fibre density in beard	Dense0 uniformity beard	mg/mm	0	0
Percentage of fibres hanging out in OFDA4000 beard	Pcnt hang 5mm	%	0	0
Total number of runs since the instrument was built	totalRunCtr (12128.58)	Number of runs	14032.91	9592.11
Counter of the number of runs since the 'Zero job counter' menu item was selected	jobRunCtr (4722.66)	Number of runs	5157.21	3595.13
Level of focus motor	focusMM	mm	1.42	1.24

Statistical analysis

A discriminant canonical analysis was performed in the present study to develop a tool that evaluates linear combinations of physical-mechanical hair/wool quality-related traits able to determine within and between population clustering patterns across species (Canarian camel and Merino sheep) and age groups (prepuber, sexually mature and reproductively senescent), following the methodology on González Ariza et al. (2021).

Results

Statistical analysis

Discriminant canonical analysis model reliability

After multicollinearity analyses, only the variables of light, maxSD, sdD along 200um, %<15um, fiFromTip, spinF, SD Along Profile, numD, densSD, minSD, CEM, lightSD, baseD, large blob%, and length staple were retained in the discriminant canonical analyses (VIF values < 5; Table 3).

Table 3. Multicollinearity analysis of physical-mechanical hair/wool quality related traits in Canarian camel and Merino sheep to discard for redundant variables.

Statistic	Tolerance (1-R^2)	VIF (1/Tolerance)
light	0.6342	1.5768
maxSD	0.5874	1.7024
sdD along 200um	0.5258	1.9019
%<15um	0.4901	2.0406
fiFromTip	0.4783	2.0906
spinF	0.4107	2.4349
SD Along Profile	0.3700	2.7024
numD	0.3675	2.7213
densSD	0.3571	2.8006
minSD	0.3241	3.0850
CEM	0.2830	3.5336
lightSD	0.2732	3.6606
baseD	0.2529	3.9542
large blob%	0.2524	3.9617
length staple	0.2225	4.4935

Interpretation thumb rule: VIF ≥ 5 (highly correlated); 1 < VIF < 5 (moderately correlated); VIF = 1 (not correlated).

A significant Pillai's trace criterion (Pillai's trace criterion: 2.5160; df1: 120; df2: 11720; P<0.0001) determined the validity of the discriminant canonical analysis. Significant discriminant abilities were reported for six out of the eight functions revealed after the discriminant analysis, as reported in Table 4. The discriminatory power of the F1 function was high (eigenvalue of 11.21; Figure 2) with 99.91% of the variance significantly explained by F1, F2, F3, F4, F5, and F6.

Table 4. Canonical discriminant analysis efficiency parameters to determine the significance of each canonical discriminant function.

Function	Canonical Correlation	Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
F1	0.9582	1 through 8	0.004	7034.445	120	<0.0001
F2	0.9123	2 through 8	0.054	3793.908	98	<0.0001
F3	0.6458	3 through 8	0.33	1439.932	78	<0.0001
F4	0.4626	4 through 8	0.623	613.23	60	<0.0001
F5	0.2893	5 through 8	0.834	236.36	44	<0.0001
F6	0.1860	6 through 8	0.931	92.605	30	<0.0001
F7	0.1016	7 through 8	0.979	28.187	18	0.059
F8	0.0769	8	0.993	9.496	8	0.302

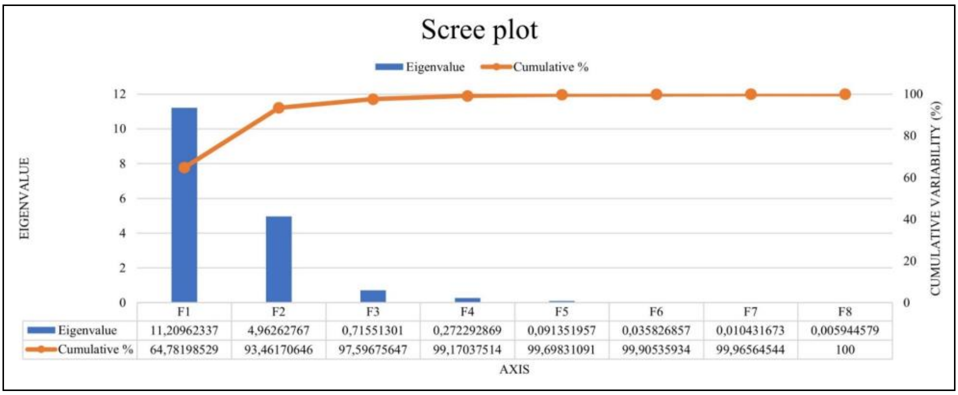


Figure 2. Canonical variable functions and their percentages of self-explained and cumulative variance.

Canonical coefficients, loading interpretation, and spatial representation

The different variables studied in this research were ranked according to their discriminating ability. A test of equality of group means of physical-mechanical hair/wool quality related traits was used, as shown in Table 5. A better discriminating power is indicated by greater values of F and, consequently, lower values of Wilks' Lambda. The present analysis revealed that all physical-mechanical hair/wool quality related traits significantly contributed (P < 0.0001) to the discriminant functions.

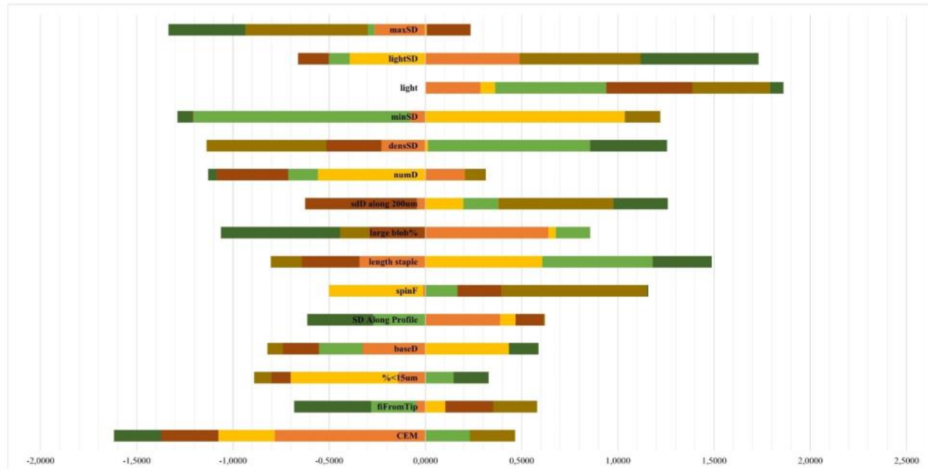
Table 5. Results for the tests of equality of group means to test for difference in the means across sample groups once redundant variables have been removed.

Variable	Wilks' Lambda	F	df1	df2	P-value	Rank
CEM	0.2122	683.0005	8	1472	< 0.0001	1
large blob%	0.2266	628.1749	8	1472	< 0.0001	2
lightSD	0.4544	220.9554	8	1472	< 0.0001	3
baseD	0.4662	210.6743	8	1472	< 0.0001	4
%<15um	0.5076	178.4672	8	1472	< 0.0001	5
light	0.5416	155.7634	8	1472	< 0.0001	6
minSD	0.5715	137.9877	8	1472	< 0.0001	7
numD	0.7243	70.0222	8	1472	< 0.0001	8
length staple	0.7311	67.6842	8	1472	< 0.0001	9
sdD along 200um	0.7876	49.6291	8	1472	< 0.0001	10
densSD	0.7917	48.4095	8	1472	< 0.0001	11
SD Along Profile	0.8107	42.9770	8	1472	< 0.0001	12
maxSD	0.8117	42.6957	8	1472	< 0.0001	13
fiFromTip	0.8318	37.1998	8	1472	< 0.0001	14
spinF	0.8644	28.8751	8	1472	< 0.0001	15

Standardized discriminant coefficients measure the relative weight of each trait across the established discriminant functions (Figures 3 and 4). The two most relevant functions were used to depict a standardized discriminant coefficients biplot, which captures the highest fraction of data variability (Figure 4). Variables whose vector extends further beyond the origin more relevantly contribute to the F1 and F2 discriminant functions.

In Figure 5, centroids from different species and age groups considered in this study are represented. The relative position of each centroid was determined by substituting the mean value for the observations depicted in the two first discriminant functions (F1 and F2).

Mahalanobis distances across species and age groups were represented in a cladogram (Figure 6). Male prepuber sheep was the most distant age group when compared to the rest. A close connection between Sexually Mature Male and Female Sheep and Sexually Mature and Reproductively Senescent Male Camels was evidenced. Male Prepuber Camels are closer to Female Camels (even if they are reproductively senescent or sexually mature) than Camel Males, with Female Prepuber Camels being the most distant from the rest of the age groups within the Canarian camel cluster.



	CEM	fiFromTip	%<15um	baseD	SD Along Profile	spinF	length staple	large blob%	sdD along 200um	numD	densSD	minSD	light	lightSD	maxSD
F1	-0,7828	-0,0451	-0,1408	-0,3256	0,3879	-0,0108	-0,3422	0,6392	-0,0442	0,2059	-0,2288	-0,0799	0,2851	0,4893	-0,2629
F2	-0,2929	0,1033	-0,5597	0,4340	0,0807	-0,4904	0,6071	0,0389	0,1974	-0,5588	0,0130	1,0359	0,0779	-0,3943	0,0076
F3	0,2314	-0,2370	0,1473	-0,2262	-0,2711	0,1668	0,5730	0,1776	0,1816	-0,1530	0,8421	-1,1261	0,5770	-0,1069	-0,0357
F4	-0,2954	0,2486	-0,0988	-0,1885	0,1443	0,2294	-0,2994	-0,2932	-0,5811	-0,3732	-0,2856	-0,0032	0,4463	-0,1602	0,2267
F5	0,2351	0,2289	-0,0905	-0,0807	0,0083	0,7566	-0,1614	-0,1495	0,5991	0,1081	-0,6228	0,1846	0,4045	0,6293	-0,6364
F6	-0,2473	-0,3993	0,1813	0,1544	-0,3419	0,0057	0,3077	-0,6194	0,2812	-0,0436	0,4008	-0,0785	0,0690	0,6116	-0,4003

Figure 3. Discriminant coefficients for physical-mechanical hair/wool quality related traits in Canarian camel and Merino sheep in each canonical discriminant function. Each bar represents the relative weights (loadings) of each particular trait across the six significant discriminant functions evidenced by the discriminant canonical analysis.

Data mining CHAID decision tree

The underlying basis for these classification patterns was represented in Supplementary Table S1, after the evaluation of the data mining CHAID decision tree obtained from the chi-square dissimilarity matrix. In these regards, Supplementary Table S2 describes data mining CHAID differential criteria across species, sex, and age groups (significant differences were found at $\chi2<0.05$). The only significant differences reported across sexes and age groups were found for the variables numD, minSD, denseSD, based, large blob %, CEM, light, lightSD, maxSD, fiFromtip, length staple, sdD along 200um, %<15um, spinF and SD Along Profile.

Discriminant function cross-validation

Cross-validation reported that 71.9% of original grouped cases correctly were classified, while 69.9% of cross-validated grouped cases were correctly classified. These results supported the robustness of the results obtained and the validity of the conclusions drawn from them. A Press' Q value of 4271.52 (n = 1481; n' = 955; K = 9) was computed. Thus, predictions can be considered better than chance at 95% (Chan, 2005).

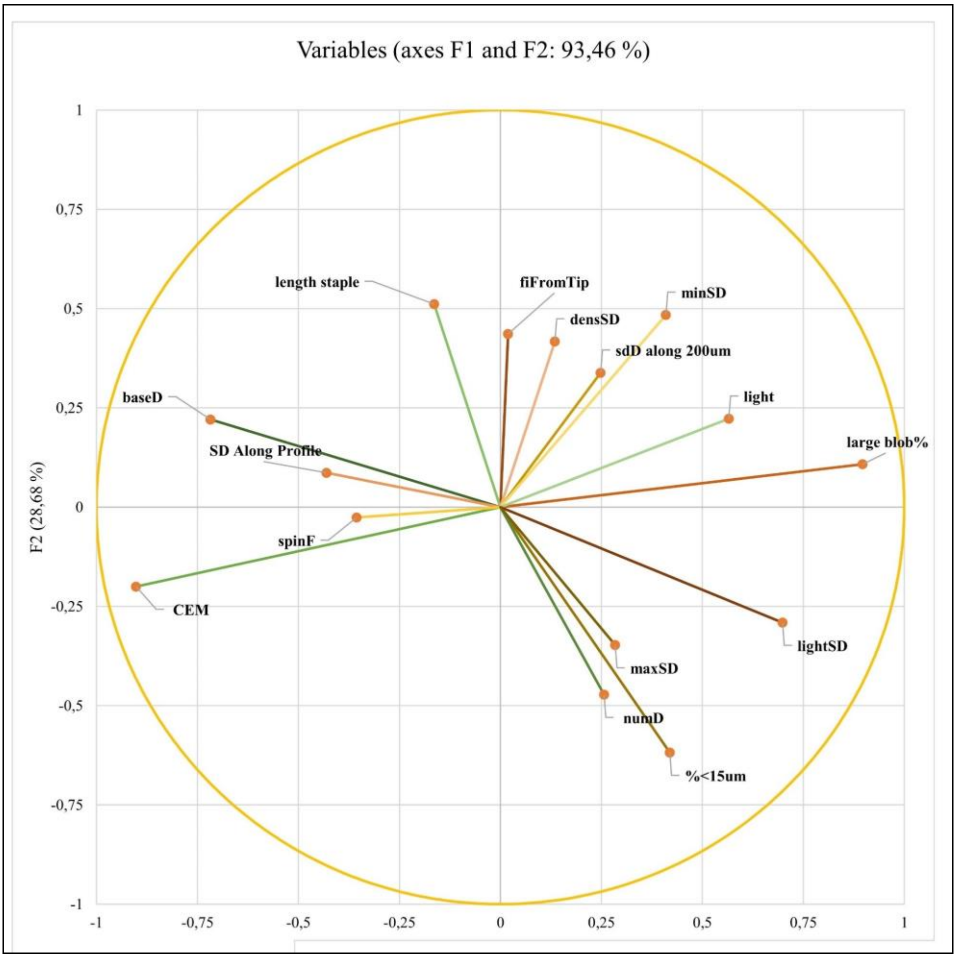


Figure 4. Vector plot for discriminant loadings for the traits considered in discriminant analysis.

Discussion

In general, the variables that best discriminate between the fibers belonging to both species, through the particular examples of the Canarian camel breed and Merino Sheep, are those related to the diameter, density, length, their ability to reflect light, and residual dirt that is present. Among these attributes, we found characteristics of marked importance for fibers to present enough strength for industrial processing, that is, for fiber breakage to be minimized given the resultant degradation percentage, which is known to affect both the quality of the final fabrics and the opportunities for their commercialization (Peña, Gutiérrez, & Unanua, 2013).

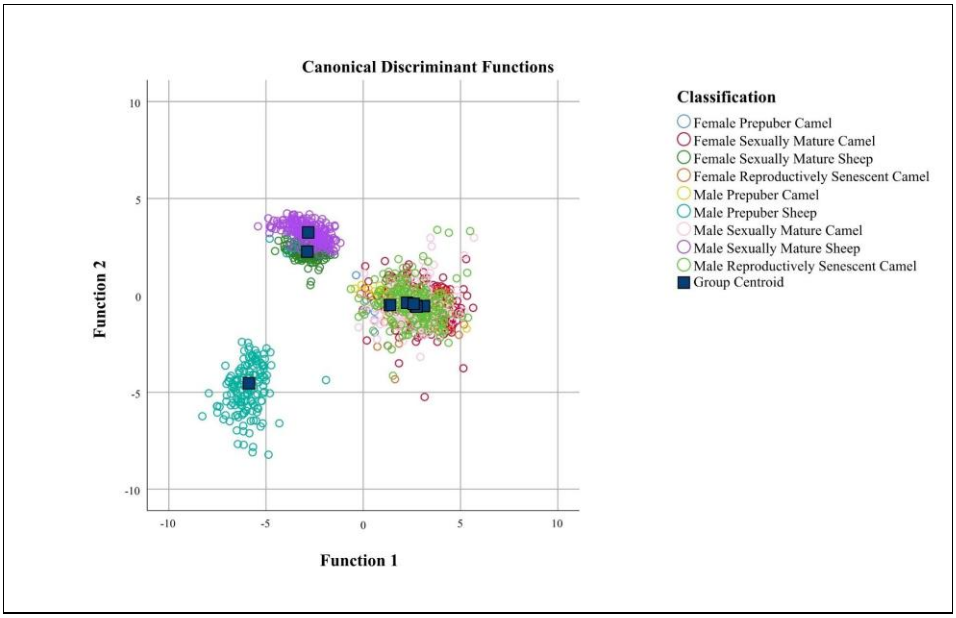


Figure 5. Territorial map depicting the centroids of the different observations considered in the discriminant canonical analysis sorted across species/breeds and age groups.

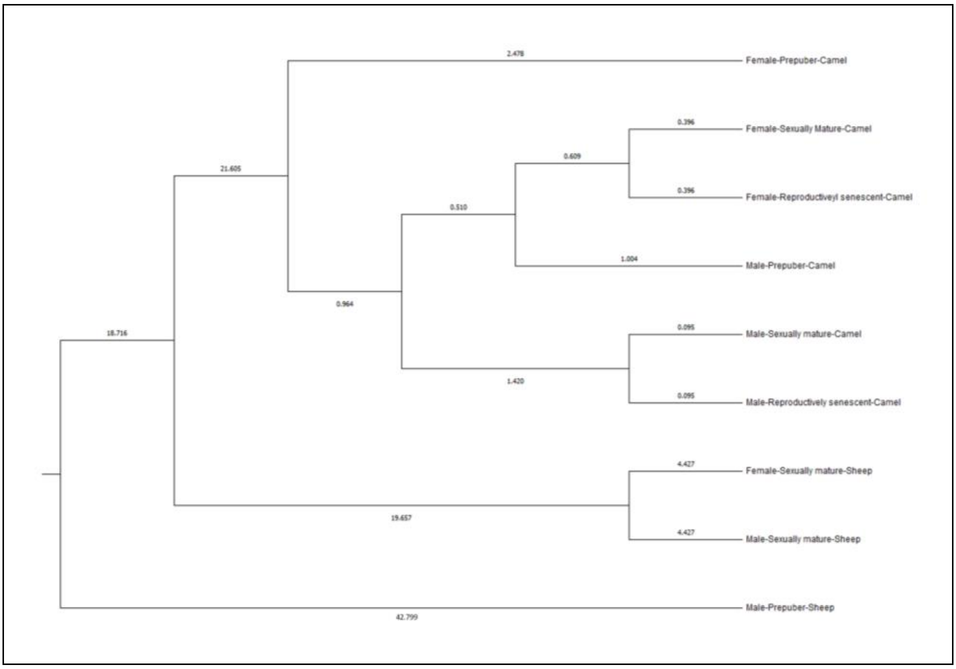


Figure 6. Cladogram constructed from Mahalanobis distances across species/breeds and age groups.

The diameter at the base of the fiber is greater for camel hair, with higher mean values being observed for adult males (> 55.0 microns) when compared to females (25.06-55.00 microns) of the same age class. This variable is closely related to the volume of the primary follicles, from which the raw guard coat grows (Ansari-Renani et al., 2010), and to the volume of the follicular papilla found within this type of follicle (Burns & Clarkson, 1949).

The higher the density of follicles, the greater the cellular volume and the secretory activity of the follicular papilla. Such physiological mechanisms are found to be linearly and positively related to both the size of the hair shaft produced (van Scott and Ekel 1958) and the hair's general growth (Matsuzaki and Yoshizato 1998; Robinson et al., 2001).

In this context, Hekal (2014) reported the mean internal diameter of the primary follicle and the mean diameter of the guard hair fiber in Maghrabi and Sudani African camel breeds to be 75.01 μ and 45.5 μ, respectively, values in the range of what was found for the Canary camel, although these may be located at the lower end of the aforementioned range, which makes them approach the values found for Merino sheep in our study.

In these regards, for sheep wool, values reported in the literature are lower, with an average value of 23 μ (McCloghry, Brown, & Uphill, 1997), which is set at the minimum values found for Canary she-camels. These may derive from the fact that hair from Canary camels was already used for the fabrication of cloths such as those used in tents, as carpets, or cloaks, hence a certain interest in the mass selection for better coats could be presumed.

Our study reported mean fiber diameters of 31.8 μ for camels and 21.47 μ for sheep wool, respectively. These results are confirmed by the CEM (Coarse Edge Micron) variable. This suggests that the percentage of fibers less than 15 microns in diameter, is lower in camels when compared to sheep, as was also confirmed in the present study.

In parallel, higher mean fiber length values were reported when sheep wool (55.77 mm) was compared to camel hair (53.92 mm). Such a finding would contrast with that reported by Banamali et al. (2000), who obtained fiber lengths greater than 60 mm when comparing Bikaneri, Jaisalmeri and Kachchhi camel breeds in India. However, our results are in line with the general conclusions stated by Bhakat (2019) for camels and Valera et al. (2002) for Merino sheep. These authors point out that the diameter and length of these fibers increase with age, and thus the skin coarseness goes up, a correlation that can be corroborated within our dataset.

When sexes are compared, in both species, males present slightly lower fiber diameter and length, as stated by previous studies (Baba et al., 2020; Banamali et al., 2000). In any case, the significance of the effects of age and sex on the physical attributes of the fibers varies between investigations, which would indicate that the fiber attributes are not only influenced by genetic factors but also by other environmental factors (diet, health status, and/or climatology). This quantitative variability between breeds and genetic lines for these traits indicates scope for further improvement through selective breeding.

The diameter of the fiber is susceptible to variation along its length (Hutchinson & Thompson, 1997). This variability, as shown in our data (sdD along 200 μm, SD Along profile, and denSD) and as would be expected according to the aforementioned influence of the size and secretion of the follicular papilla on general hair growth, is critical to sheep wool performance. Although the standard deviation of fiber diameter along the staple is higher for camel hair, as would be expected considering its superior mean diameter, sheep wool is a fiber with greater irregularity in its diameter along short segments (200 um) of the fiber. This characteristic could be directly correlated to the smaller relative distance from the tip of the fiber to the thinnest point and thus to a potential break point in sheep wool.

Although both fibers are keratin fibers, the spatial overlapping of the scales along the cuticle sheath and the cystine content in the protein chairs differ between camel hair and sheep wool. In the first case, Tridico (2009) identified, by low-power microscopy, that camel hair is quite regular in outline, exhibits a uniform diameter along its length, and the cuticular scale edges project so very slightly from the hair shaft that its profile appears almost straight. Concerning the cystine content, evidence shows that camel hair, both the inner and outer coat, hardly contains non-cystine, sulfur-containing compounds (Rimington, 1931).

In this connection, several implications for textile production derived from these exotic fiber particularities will be discussed. As both fiber diameter and its variation play an important role in fiber processing (Helal, 2015), the homogeneity of camel fibers should be a value-added characteristic for textile manufacturing since it would provide major resistance to different processing techniques in the textile industry (Wang, 2000). In those areas where there is a smaller fiber diameter (quantitatively, the number of areas with a low average diameter is higher in sheep's wool), the tensile resistance is lower (Bolormaa, Drean, & Enkhtuya, 2008) and, consequently, the probability of fiber breakage is higher (Li et al., 2011). Closely linked, the low coefficient of friction of camel hair due to its particular homogeneous, straight scale overlapping along its surface (Shakyawar, Patni, & Gupta, 2007) confers special slippery and smooth properties and thus comfortable tactile perception to textile fabrics (Ramalho, Szekeres, & Fernandes, 2013).

In the matter of cysteine content, Campbell, Whiteley, and Gillespie (1972) found a positive relationship between this characteristic and curvature in wool. That is, the greater the content of cystine, the greater the crimping rate of wool. On the one hand, such a trait could be the main reason that explains the greater mean number of wool fibers measured (numD) in the present study, since natural crimping makes fibers coil and thus confers extra resilience to fibers when they are intended to be separated for optical analysis (Miao & Gordon, 2018).

Given that the concentration of cysteine in camel hair remains low in comparison with sheep wool, the respective crimping rate is therefore expected to be low as well. This lower rate can be additionally explained based on their high and uniform hair fiber diameter (Nissimov & Das Chaudhuri, 2014) and thus higher elastic modulus (Tang et al., 2016). All in all, this set of reasons is further supported by the notably higher spin fineness of camel hair. This characteristic provides an estimate of the performance of the sample when it is converted into yarn. Its estimate comes from the combination of the mean fiber diameter and its coefficient of variation (Quispe-Ccasa et al., 2020).

For ecology-based evolutionary reasons, the distinguished attributes of camel hair may further brighten the multiple adaptations of these animals to live in arid land areas where they are constantly exposed to abrasion by sand at the same time they have to deal with extreme temperatures. The hair coats of desert-living mammals might have evolved to be as strong and straight as possible to provide a non-bendable, smooth surface for light reflection since this physical property is negatively affected as long as fiber curvature increases (Wortmann, Schulze zur Wiesche, & Bourceau, 2004). Through NIR (Near Infrared Spectroscopy) analysis, Chen, Lin, and Tan (2019) confirmed a higher light scattering for camel hair fibers and correlated this property with fiber diameter and homogeneous surface in this species' hair.

Our results support this hypothesis, as the ability to reflect light is higher for camel hair, as well as the variability found for this property is greater in sheep, the latter in turn related to its also greater variability for the diameter along the fiber. According to Young, Hale, and Mechels (1993), the absorption and scattering of light energy within an optical fiber (gray-scale analysis) are dependent both on the homogeneity of the circularity of the outer or cladding diameter of the fiber and the natural impurities along the fiber length.

This greater ability to reflect light, but what's more important, the presence of a medulla inside the fiber, may provide important benefits for thermal insulation not only to camels in their natural habitat but also to textile products made with their fibers. Indeed, the mere presence of inner medullation in the camel fibers reduces their heat transmittance (Øritsland & Ronald, 1978), being this correlation is superior as the diameter of the fiber increases its value (Moore, Blache, & Maloney, 2011). Within a practical framework in which camel breeding programs may become patent for functional selection on fiber fineness, we propose to first establish a minimum value of fiber diameter to be respected in all cases to avoid negative effects on the camel's thermal balance and thus their general health status and production performance. For example, Lakshmanan, Jose, and Chakraborty (2016) established camel-origin luxury fibers for the fashion industry about 18-26 in diameter and 30-120 mm in length, but no evaluation of the heat transmittance effect for these values was done. Thus, extended research to determine the critical value of this camel hair fiber attribute is urgently needed for animal welfare procurement.

In line with the aforementioned and considering the scene of an increasing technification of camel-rearing systems due to the emerging interests in this species' production potentialities (Iglesias Pastrana et al., 2020b), it is expected camels to be reared under controlled environments. The improved technical assistance and supervision may enhance not only their welfare but also the preventive care that the animals receive. Hence, among others, the percentage of fiber impurities (% large blob) that are known to affect the efficiency of technological operations at textile manufacturing, should be minimized as much as possible to make camel's hair cleaner. According to our results, this percentage is higher in Canary camels than in Merino ewes, which could be explained based on the extensive or semi-extensive regime and a lower degree of technification of most camel farms (McGregor, 2018), but this conditioning factor could be dealt with relative ease in the short-to-medium term. Regarding the influence of sex, the value of this variable is higher in males, which could be directly and proportionally related to the greater amount (kg) of fiber produced by this sex (Babu, 2015).

Eventually, by the increasing technological development of the textile industry and the ongoing reinforcing of camel breeding programs for the improved production of textile fibers, a preliminary screening of the fibers at their reception in the industry could help with their differential classification for different applicative purposes. That is the case, for example, those fibers that do not meet the preferred requirements for a certain product or textile market, but that would have applicability both in engineering and bioengineering due to their insulating properties, with special attention to sustainability issues (Parlato & Porto, 2020).

Conclusions

Despite the slightly shorter length of Canarian camel hair when compared to Merino sheep wool, the general performance of camel fibers in terms of fiber diameter and light reflection capacity can be a source of benefit in the textile industry. The greater diameter at the base and the spin fineness of camel hair gives it greater resistance to industrial processing in addition to providing a softer sensation to the touch. The ability to reflect light and the internal medullation make camel-origin fiber a valuable textile material for the lightness and heat-insulating properties of final textile products when compared to other widespread fiber such as Merino wool. Residual dirt must be exhaustively controlled to ensure a high percentage of fiber suitable for profitable processing. That being so, it is decisive that farmers become conscious of the potential of camel hair as an income source and that textile stakeholders become aware of the characteristic attributes of this exotic animal fiber.

Supplementary materials: The supplementary materials derived from the present study are available on request from the first author.

Funding: The present research was carried out in the financing framework of the international project CA.RA.VA.N—'Toward a Camel Transnational Value Chain' (Reference APCIN-2016-00011-00-00) and during the covering period of a predoctoral contract (FPU Fellowship) funded by the Spanish Ministry of Science and Innovation and was developed under the context a Ramón y Cajal Post-Doctoral fellowship financially supported by MCIN/AEI/10.13039/501100011033 and European Union "NextGenerationEU"/PRTR" (Recovery, Transformation and Resilience Plan—Funded by the European Union—NextGenerationEU).

Data availability statement: The data presented in this study are available on request from the first author.

Acknowledgments: The authors would like to thank 'Aires Africanos' Aires Africanos" Eco-tourism Company, Oasis Park Fuerteventura and 'Camelus' Camellos de Almería, for their direct technical help and assistance.

Declaration of interest statement: No potential conflict of interest was reported by the authors.

References

Allafi, F. A., Hossain, M. S., Shaah, M., Lalung, J., Ab Kadir, M. O., & Ahmad, M. I. (2021). A review on characterization of sheep wool impurities and existing techniques of cleaning: industrial and environmental challenges. *Journal of Natural Fibers*, 1-19.

Al-Qarawi, A. A., Abdel-Rahman, H. A., El-Belely, M. S., & El-Mougy, S. A. (2000). Age-related changes in plasma testosterone concentrations and genital organs content of bulk and trace elements in the male dromedary camel. *Animal Reproduction Science*, 62(4), 297-307.

Al-Qarawi, A. A., Abdel-Rahman, H. A., El-Belely, M. S., & El-Mougy, S. A. (2001). Intratesticular morphometric, cellular and endocrine changes around the pubertal period in dromedary camels. *The Veterinary Journal*, 162(3), 241-249.

Ansari-Renani, H., Salehi, M., Ebadi, Z., & Moradi, S. (2010). Identification of hair follicle characteristics and activity of one and two humped camels. *Small Ruminant Research*, 90(1-3), 64-70.

Baba, M. A., Ahanger, S., Hamadani, A., Rather, M., & Shah, M. M. (2020). Factors affecting wool characteristics of sheep reared in Kashmir. *Tropical animal health and production*, 1-5.

Babu, K. (2015). Natural textile fibres: Animal and silk fibres. In *Textiles and Fashion* (pp. 57-78): Elsevier.

Banamali, Y., Mishra, B., Bhakat, C., & Sahani, M. (2000). Hair quality attributes of *Camelus dromedarius*. *Indian Journal of Animal Sciences*, 70(2), 211-212.

Bhakat, C. (2019). Camel hair-production, quality and prospects. In *The Indian amel: a research profile* (pp. 104-111): National Research Centre on Camel, Bikaner, India.

Bolormaa, B., Drean, J. Y., & Enkhtuya, D. (2008). A study of the diameter distribution and tensile property of horse tail hair. *Journal of Natural Fibers*, 4(4), 1-11.

Burger, P. A., Ciani, E., & Faye, B. (2019). Old World camels in a modern world–a balancing act between conservation and genetic improvement. *Animal Genetics*, 50(6), 598-612.

Burns, M., & Clarkson, H. (1949). Some observations on the dimensions of follicles and of other structures in the skin of sheep. *The Journal of Agricultural Science*, 39(4), 315-334.

Campbell, M., Whiteley, K., & Gillespie, J. (1972). Compositional studies of high-and low-crimp wools. *Australian Journal of Biological Sciences*, 25(5), 977-988.

Chan, Y. (2005). Biostatistics 303. Discriminant analysis. *Singapore medical journal*, 46(2), 54.

Chen, H., Lin, Z., & Tan, C. (2019). Classification of different animal fibers by near infrared spectroscopy and chemometric models. *Microchemical Journal*, 144, 489-494.

González Ariza, A., Arando Arbulu, A., Navas González, F. J., Delgado Bermejo, J. V., & Camacho Vallejo, M. E. (2021). Discriminant canonical analysis as a validation tool for multivariety native breed egg commercial quality classification. *Foods*, 10(3), 632.

Harizi, T., Msahli, S., Sakli, F., & Khorchani, T. (2007). Evaluation of physical and mechanical properties of Tunisian camel hair. *Journal of the Textile Institute*, 98(1), 15-21.

Hekal, S. A. (2014). Histological study of the skin and leather characteristics in two types of Arabian Camels (*Camelus dromedarius*). *The Journal of American Science*, 10(9), 41-47.

Helal, A. (2015). Relationships among physical, chemical and industrial characteristics of different dromedary camel's hair types. *The Journal of American Science*, 11, 67-75.

Hutchinson, P., & Thompson, J. (1997). The cross–sectional size and shape of human terminal scalp hair. *British Journal of Dermatology*, 136(2), 159-165.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Nogales Baena, S., & Delgado Bermejo, J. V. (2020a). Camel Genetic Resources Conservation through Tourism: A Key Sociocultural Approach of Camelback Leisure Riding. *Animals*, 10(9), 1703.

Iglesias Pastrana, C., Navas González, F. J., Ciani, E., Barba Capote, C. J., & Delgado Bermejo, J. V. (2020b). Effect of Research Impact on Emerging Camel Husbandry, Welfare and Social-Related Awareness. *Animals*, 10(5), 780.

Lakshmanan, A., Jose, S., & Chakraborty, S. (2016). Luxury hair fibers for fashion industry. In *Sustainable fibres for fashion industry* (pp. 1-38): Springer.

Li, Q., Hurren, C. J., Ding, C., Wang, L., Lin, T., & Wang, X. (2011). Ultrasonic scouring of wool and its effects on fibre breakage during carding. *Journal of the Textile Institute*, 102(12), 1059-1064.

McCloghry, C., Brown, G., & Uphill, G. (1997). Computer-assisted image analysis for the measurement of wool follicle density and fibre diameter in skin sections. New *Zealand journal of agricultural research*, 40(2), 239-244.

McGregor, B. A. (2018). Physical, chemical, and tensile properties of cashmere, mohair, alpaca, and other rare animal fibers. In *Handbook of Properties of Textile and Technical Fibres* (pp. 105-136): Elsevier.

McLaughlin, I. (2000). Innovative wool testing – OFDA: Australian Wool Taskforce 2000.

Miao, M., & Gordon, S. (2018). Fiber selection and substitution. In *Engineering of High-Performance Textiles* (pp. 3-26): Elsevier.

Moore, K., Blache, D., & Maloney, S. (2011). Fibre diameter and insulation in alpacas: The biophysical implications. *Small Ruminant Research*, 96(2-3), 165-172.

Mysterud, A., Steinheim, G., Yoccoz, N. G., Holand, Ø., & Stenseth, N. C. (2002). Early onset of reproductive senescence in domestic sheep *Ovis aries*. *Oikos*, 97(2), 177-183.

Nieto, C. R., Ferguson, M. B., Macleay, C. A., Briegel, J. R., Martin, G. B., & Thompson, A. N. (2013). Selection for superior growth advances the onset of puberty and increases reproductive performance in ewe lambs. *animal*, 7(6), 990-997.

Nissimov, J. N., & Das Chaudhuri, A. B. (2014). Hair curvature: a natural dialectic and review. *Biological Reviews*, 89(3), 723-766.

Øritsland, N., & Ronald, K. (1978). Solar heating of mammals: observations of hair transmittance. *International journal of biometeorology*, 22(3), 197-201.

Parlato, M., & Porto, S. (2020). Organized Framework of Main Possible Applications of Sheep Wool Fibers in Building Components. *Sustainability*, 12(3), 761.

Peña, E. Q., Gutiérrez, A. P., & Unanua, A. P. (2013). Caracteristicas productivas y textiles de la fibra de alpacas de raza huacaya/a review of huacaya alpacas fiber traits. *Revista Complutense de Ciencias Veterinarias*, 7(1), 1.

Purvis, I. W., & Franklin, I. R. (2005). Major genes and QTL influencing wool production and quality: a review. *Genetics Selection Evolution*, 37, S97-S107.

Quispe-Ccasa, H., Lloccallasi, N., Choquepuma, W., Huanca, N., Cayo-Colca, I., Saucedo, J., Ampuero, E., & Cucho, H. (2020). Evaluación objetiva de características de finura y resistencia en vellones de llama (*Lama glama*) Ch'aku. *Revista de Investigaciones Veterinarias del Perú*, 31(2).

Ramalho, A., Szekeres, P., & Fernandes, E. (2013). Friction and tactile perception of textile fabrics. *Tribology International*, 63, 29-33.

Rimington, C. (1931). The relation between cystine yield and total sulphur in kemp and outer-coat animal fibres. *Biochemical Journal*, 25(1), 71.

Shakyawar, D., Patni, P., & Gupta, N. (2007). Studies on animal fibre blended handmade felts: Part II—Frictional, compressional and thermal properties. *International Journal of Fibre & Textile Research*, 32, 301-305.

Sharma, A., & Pant, S. (2013). Studies on camel hair-merino wool blended knitted fabrics. *International Journal of Fibre & Textile Research*, 38, 317-319.

Tang, W., Zhang, S., Zhang, J., Chen, S., Zhu, H., & Ge, S. (2016). Ageing effects on the diameter, nanomechanical properties and tactile perception of human hair. *International journal of cosmetic science*, 38(2), 155-163.

Tridico, S. (2009). Natural animal textile fibres: Structure, characteristics and identification. In *Identification of Textile Fibers* (pp. 27-67): Elsevier.

Valera, M., Molina, F. A. A., Molina, A., López, F. B., & Ambrona, F. (2002). La producción lanar del merino autóctono español después de 20 años de selección hacia la aptitud cárnica. *Feagas*, 22, 89-94.

Wang, X. (2000). Predicting the strength variation of wool from its diameter variation. *Textile research journal*, 70(3), 191-194.

Wang, Z., Zhang, H., Yang, H., Wang, S., Rong, E., Pei, W., Li, H., & Wang, N. (2014). Genome-wide association study for wool production traits in a Chinese Merino sheep population. *PloS one*, 9(9), e107101.

Wortmann, F. J., Schulze zur Wiesche, E., & Bourceau, B. (2004). Analyzing the laser-light reflection from human hair fibers. II. Deriving a measure of hair luster. *International journal of cosmetic science*, 26(4), 219-219.

Yam, B. A. Z., & Khomeiri, M. (2015). Introduction to Camel origin, history, raising, characteristics, and wool, hair and skin: A Review. *Research Journal of Agriculture and Environmental Management*, 4(11), 496-508.

Yondonsambuu, G., & Altantsetseg, D. (2003). *Survey on production and manufacturing of the wool, cashmere, and camel hair*: Mongolian Wool and Cashmere Association.

Young, M., Hale, P. D., & Mechels, S. E. (1993). Optical fiber geometry: Accurate measurement of cladding diameter. *Journal of research of the National Institute of Standards and Technology*, 98(2), 203.

Zarrin, M., Riveros, J. L., Ahmadpour, A., de Almeida, A. M., Konuspayeva, G., Vargas-Bello-Pérez, E., Faye, B., & Hernández-Castellano, L. E. (2020). Camelids: new players in the international animal production context. *Tropical animal health and production*, 1-11.

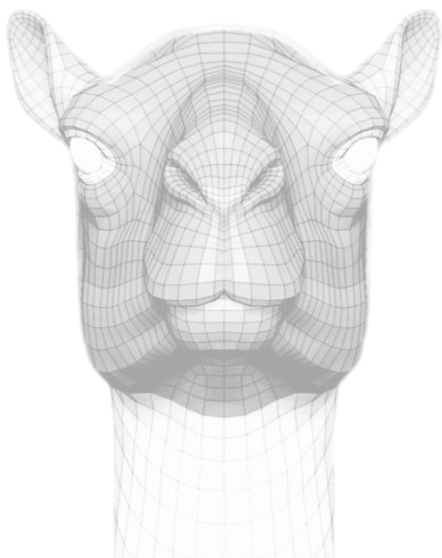
7.2 Body region sampling areas- and phaneroptics-associated hair fiber phenotypes in Canarian camel versus Merino sheep

Carlos Iglesias Pastrana[1], Francisco Javier Navas González[1], Elena Ciani[2], Beatriz López de los Santos[3] and Juan Vicente Delgado Bermejo[1]

[1]Department of Genetics, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain

[2]Department of Biosciences, Biotechnologies and Biopharmaceutics, Faculty of Veterinary Sciences, University of Bari 'Aldo Moro', 70121 Bari, Italy

[3]Ovino del Suroeste Sdad Coop Ltda (Oviso SCL), 06700 Villanueva de la Serena, Badajoz, Spain



Quality indicator information provided on the publication
Latest information available (2022)

Status of the manuscript: Under review

Journal (year, volume, page(s)): *Journal of Natural Fibers*

International database in which it is indexed: Journal of Citation Reports (JCR)

Thematic area in the reference database: Materials Science & Textiles

Impact index of the journal in the year of the article's publication: 3.5

Rank/number of thematic area journals: 4/25 (Q1)

Abstract

The variability of camel hair fibers physical-mechanical properties across sampling body areas and phaneroptics continue to be relatively unexplored topics in scientific literature. With the aim to valorize camel hair fibers, the present investigation has examined, through discriminant canonical analysis, fiber properties of Canarian camel hair in regards to the body region sampled by comparing them with Merino sheep wool, world's most demanded textile fiber. Additionally, camel hair attributes differences depending on phaneroptics such as coat or eye colour and particularities have been determined. Diameter at the base of the fiber is higher for adult camels and increases from the mid-region to the back of the animal. Besides, the highest variability in both staple length and mean diameter was found for camel shoulder and hump fibers. Camel tail dock was the region with the finest fibers but also the one accounting for the highest percentage of residual dirt. Coat color and particularities were unlikely to significantly ($P<0.05$) affect fiber diameter and strength but did affect the brightness of final textile products. These results may help to tailor strategies within camel farming systems seeking the maximization of their productive outcomes, which is of utter relevance in endangered animal genetic resources.

Keywords

Camel hair, Merino sheep wool, optical fiber measurement, eye colour, coat colour, product valorization, OFDA

Introduction

Camel hair fiber remained a minor income source for breeders for decades which made them relatively disregarded from textile manufacturers (Kerven, Russel, & Laker, 2002). Their recent specialized research recognition as a long, strong, soft and light-coloured fiber (Sharma & Pant, 2013) has considerably increased the commercial significance and interest on this exotic animal fiber (Zarrin et al., 2020).

The industrial performance and end-uses of camel hair fiber, as in other fiber-producing species, extendedly depend on physical structure-related properties such as mean diameter and staple length. Despite these are the main determinants of the fineness and sensory tactile perception of fiber fabrics (Allain & Renieri, 2010), other phenotypic traits of commercial interest include colour, fleece type and body region (Gerken et al., 2019).

This has been made patent in other fiber-producing camelids. In these regards, Bathrachalam et al. (2019) widely illustrated the genetic basis of coat colour in alpacas, which indeed was supported by Solano and Raggi (2019) who provided some evidence for differences in fleece weight and physical properties among coat colours and body regions in the aforementioned species, the most important fiber-producing member of the New World *Camelidae* group (Wuliji et al., 2000). Similar conclusions are reported for vicuña fleece (Quispe et al., 2014), sheep wool (Fish, Mahar, & Crook, 2002; Tabbaa, Al-Azzawi, & Campbell, 2001) and goat cashmere (McGregor & Butler, 2008; McGregor, Kerven, & Toigonbaev, 2009; Taddeo et al., 2000).

Particularly focusing on the dromedary species, Harizi, Msahli, Sakli, and Khorchani (2007) and Bhakat (2019) discussed the effect of the factor sampling body area on some physical and mechanical properties of Tunisian and Indian dromedary camel hair, respectively. For double-humped camels, Sahani et al. (2003) found significant variations in hair properties at different body sites, with the mid-side region fibers having the lowest mean diameter and the highest strength. Other topics, such as the role of coat colour as a source of variation contributing to differential quality attributes in camel hair, continue to be unexplored topics in the literature (Almathen et al., 2018).

In light of the aforementioned context, the description of the qualitative phenotypic characteristics affecting fiber yield and product value contributes both to an advanced understanding of underlying pleiotropic effects and to the adapted design of genetic improvement programs seeking economically valuable production traits (Galbraith, 2010; Purvis & Franklin, 2005b) as a driving agent for market opportunities for camel hair fibers.

For these reasons, the present study aims to further test and compare the physical-mechanical properties of Canarian camel hair (an endangered camel breed) and Merino sheep wool (the world's most demanded textile fiber) concerning the body region sampled. Additionally, we performed a comparative analysis to unravel the differences in camel hair attributes in relation to coat colour, given the huge variability reported for this phaneroptic trait in the studied camel breed.

Material and methods

Animal sample

A total of 139 Canarian dromedaries (77 males and 62 females; aged between 3 months and 35 years old; Table 1) were sampled for outer hair fibers (Hasi, Amu, & Zhang, 2020) during the moulting season, a six-to-eight-week period starting in late spring (Babu 2015). Six different samples were collected from each animal (shoulder, hump, belly, rump, tail dock and tail skirt) and classified in regards of the coat colour phenotypes according to the breed standard (Figure 1) (Fernández de Sierra & Fabelo Marrero, 2017).

Merino sheep wool from 395 animals (214 males and 181 females; aged between 3 months and 5 years old; Table 1) was clipped with curved scissors for the regions of shoulder, belly and rump. For 55 out of 395 adult Merino sheep, wool samples from each

Table 1. Criteria for the classification of dromedary camel and sheep by age group.

Animal species	Group 1 *Prepuber*	Group 2 *Sexually mature*	Group 3 *Reproductively senescent*	Source of information
Dromedary camel	<3 years	3-15 years	>15 years	Al-Qarawi et al. 2000, 2001
Sheep	<6 months	6 months – 6 years	>6 years	Nieto et al. 2013; Mysterud et al. 2002

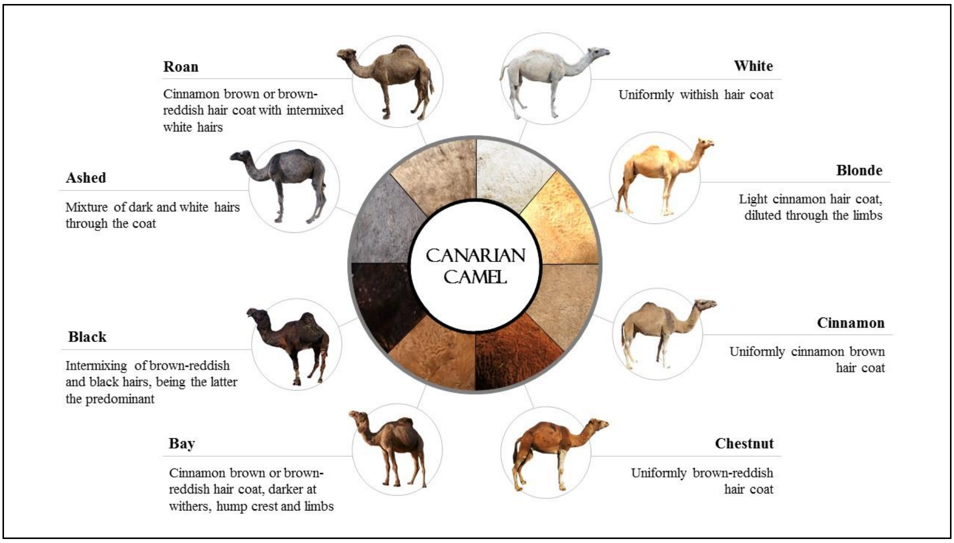


Figure 1. Coat colour phenotypes accepted within the Canarian camel breed standard (Fernández de Sierra & Fabelo Marrero, 2017).

body region were analysed independently as well as a unique blended sample of them. The samples from the rest of the animals were analysed once blended.

Sample pre-processing and physical-mechanical analysis

Prior to physical-mechanical analysis, raw hair samples were cleaned with a mix of solid surfactant (hexane) and hot water was used to remove impurities (vegetable matter, suint, and hair grease) (Allafi et al. 2021), and then dried at ambient temperature.

The analysis of the physico-mechanical properties of hair fibers were performed using an optical fiber diameter measurement tool (OFDA 2000, McLaughlin (2000)). Hair attributes were measured and averaged for a minimum number of 1,500 fibers per sample, at a mean temperature and relative humidity of 25°C and 45.7%, respectively.

Parameter description

A list of the fiber parameters measured by the optical fiber diameter analyser across sampling site, depending on the phaneroptics for coat and eye colour and sorted by species and their descriptors is presented in Supplementary Table S1.

Statistical analysis

Following the methodology on González Ariza et al. (2021), a discriminant canonical analysis was first used to develop a tool that evaluates the best possible linear combinations of physical-mechanical quality-related traits of hair fibers that shape within and between population clustering patterns across species/body region (Canarian camel and Merino sheep; shoulder, hump, belly, rump, tail dock and tail skirt).

A second discriminant canonical analysis was run to evaluate the linear combinations of physical-mechanical quality-related traits of hair fibers that are able to determine within population clustering patterns across coat colour phenotypes in Canarian camels, excluding Merino sheep given that no variability is respectively officially registered.

Results

Statistical analysis

Discriminant canonical analysis model reliability

Following the multicollinearity analyses, only specific variables were retained in the discriminant canonical analyses, namely: light, maxSD, sdD along 200um, %<15um, fiFromTip, spinF, SD Along Profile, numD, densSD, minSD, CEM, lightSD, baseD, large blob%, and length staple (with VIF values < 5; refer to Table 2 and Figure 2).

Pillai's trace criterion was highly statistically significant when either phaneroptics (Pillai's trace criterion: 1.0938; df1: 465; df2: 11940; P<0.0001) or sampling site (Pillai's trace criterion: 3.0593; df1: 330; df2: 21870; P<0.0001) were considered clustering criteria. Hence, the validity of the discriminant canonical analysis is ensured.

When phaneroptics (coat and eye colour and particularities), four out of the fifteen functions revealed after the discriminant analysis were reported to be significant for their discriminant ability. However, ten out of the fifteen functions were revealed to be significant when the clustering pattern considered was the sampling site (Table 3). The discriminatory power of the F1 function was moderate for phaneroptics and high for sampling site (eigenvalue of 0.3288 and 11.9580, respectively; Figure 3) with 66.85% and 99.72% of the variance significantly explained by F1 to F4 and F1 to F10, respectively.

Table 2. Summary of the value of tolerance and VIF after multicollinearity analysis of physical-mechanical fiber quality-related traits in Canarian camel and Merino sheep.

Statistic	Tolerance (1-R^2)	VIF (1/Tolerance)
light	0.6342	1.5768
maxSD	0.5874	1.7024
sdD along 200um	0.5258	1.9019
%<15um	0.4901	2.0406
fiFromTip	0.4783	2.0906
spinF	0.4107	2.4349
SD Along Profile	0.3700	2.7024
numD	0.3675	2.7213
densSD	0.3571	2.8006
minSD	0.3241	3.0850
CEM	0.2830	3.5336
lightSD	0.2732	3.6606
baseD	0.2529	3.9542
large blob%	0.2524	3.9617
length staple	0.2225	4.4935

Interpretation thumb rule: VIF ≥ 5 (highly correlated); 1 < VIF < 5 (moderately correlated); VIF = 1 (not correlated).

Canonical coefficients and loading interpretation

The different variables studied in this research were ranked according to their discriminating ability. A test of equality of group means of physical-mechanical hair/wool quality related traits was used as shown in Table 4. A better discriminating power is indicated by greater values of F and consequently, lower values of Wilks' Lambda. The present analysis revealed that all physical-mechanical hair/wool quality related traits highly significantly contributed ($P < 0.0001$) to the discriminant functions when Sampling site was considered the clustering criterion while, SD Along Profile (um), maxSD, spinF (um) and fiFromTip (mm) did not significantly contribute to the discriminant functions when Phaneroptics were considered the clustering criterion.

Standardized discriminant coefficients measure the relative weight of each trait across the established discriminant functions (Figures 4 and 5). The two most relevant functions were used to depict a standardized discriminant coefficients biplot which captures the highest fraction of data variability (Figure 5). Variables whose vector extends further beyond the origin more relevantly contributed to F1 and F2 discriminant functions.

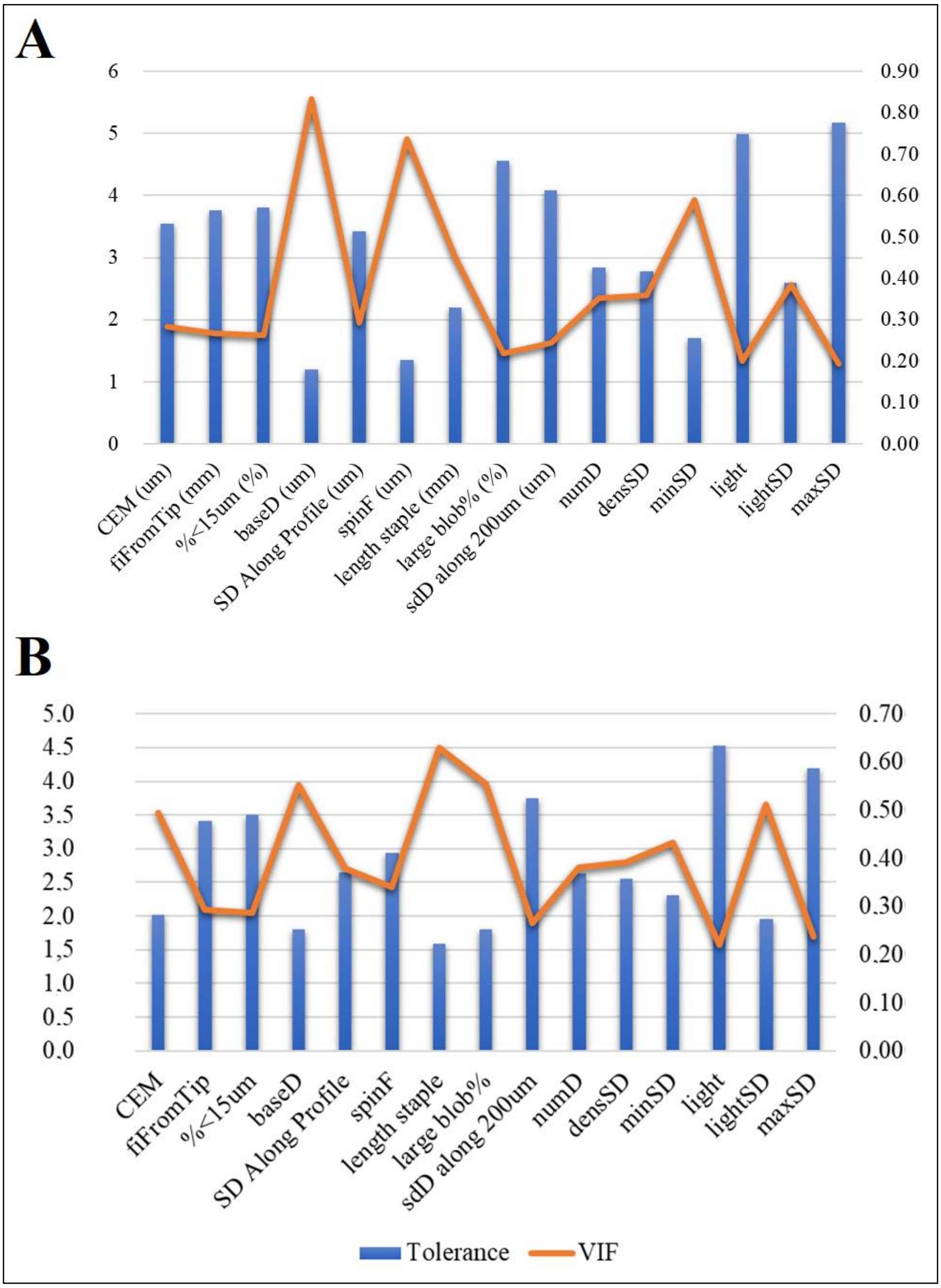


Figure 2. Summary of the value of tolerance and VIF after multicollinearity analysis of physical-mechanical of Canarian camel hair and Merino sheep quality-related traits when clustering patterns are phaneroptics (A) and sampling site (B), respectively. Interpretation thumb rule: VIF ≥ 5 (highly correlated); 1 < VIF < 5 (moderately correlated); VIF = 1 (not correlated).

Table 3. Canonical discriminant analysis efficiency parameters to determine the significance of each canonical discriminant function.

Phaneroptics				Sampling Site			
Test functions	Canonical Correlations	Bartlett's Statistic	P-value	Test functions	Canonical Correlations	Bartlett's Statistic	P-value
1 through 15	0.4975	949.0281	<0.0001	1 through 15	0.9606	8778.8594	<0.0001
2 through 15	0.4412	720.5938	<0.0001	2 through 15	0.9106	5036.1988	<0.0001
3 through 15	0.3865	546.6064	<0.0001	3 through 15	0.7763	2454.5680	<0.0001
4 through 15	0.3157	416.6371	0.0018	4 through 15	0.4802	1105.9331	<0.0001
5 through 15	0.2859	332.2742	0.0777	5 through 15	0.3725	722.8758	<0.0001
6 through 15	0.2590	263.7639	0.4233	6 through 15	0.3053	504.6912	<0.0001
7 through 15	0.2496	207.9908	0.7856	7 through 15	0.2579	361.7887	<0.0001
8 through 15	0.2203	156.3157	0.9721	8 through 15	0.2410	261.2242	<0.0001
9 through 15	0.1947	116.3267	0.9968	9 through 15	0.1895	173.7717	<0.0001
10 through 15	0.1654	85.2779	0.9995	10 through 15	0.1690	120.3599	0.0015
11 through 15	0.1458	62.9845	0.9996	11 through 15	0.1426	78.0297	0.0588
12 through 15	0.1360	45.7177	0.9993	12 through 15	0.1267	48.0219	0.3131
13 through 15	0.1260	30.7250	0.9983	13 through 15	0.0804	24.3638	0.7553
14 through 15	0.1137	17.8753	0.9950	14 through 15	0.0759	14.8839	0.6699
15	0.0959	7.4209	0.9774	15	0.0664	6.4501	0.5969

A Press' Q value of 345.972 (n = 828; n' = 119; K = 32) and of 4553.949 (n = 1481; n' = 594; K = 23) were computed for Phaneroptics combinations (Coat colour and particularities and Eye colour) and Sampling sites (across species and age group), respectively. Thus, predictions can be considered to be better than chance at 95% (Chan 2005).

Centroids from different phaneroptic possibilities and sampling sites considered in this study are calculated. The relative position of each centroid was determined by substituting the mean value for the observations depicted in the two first discriminant functions (F1 and F2).

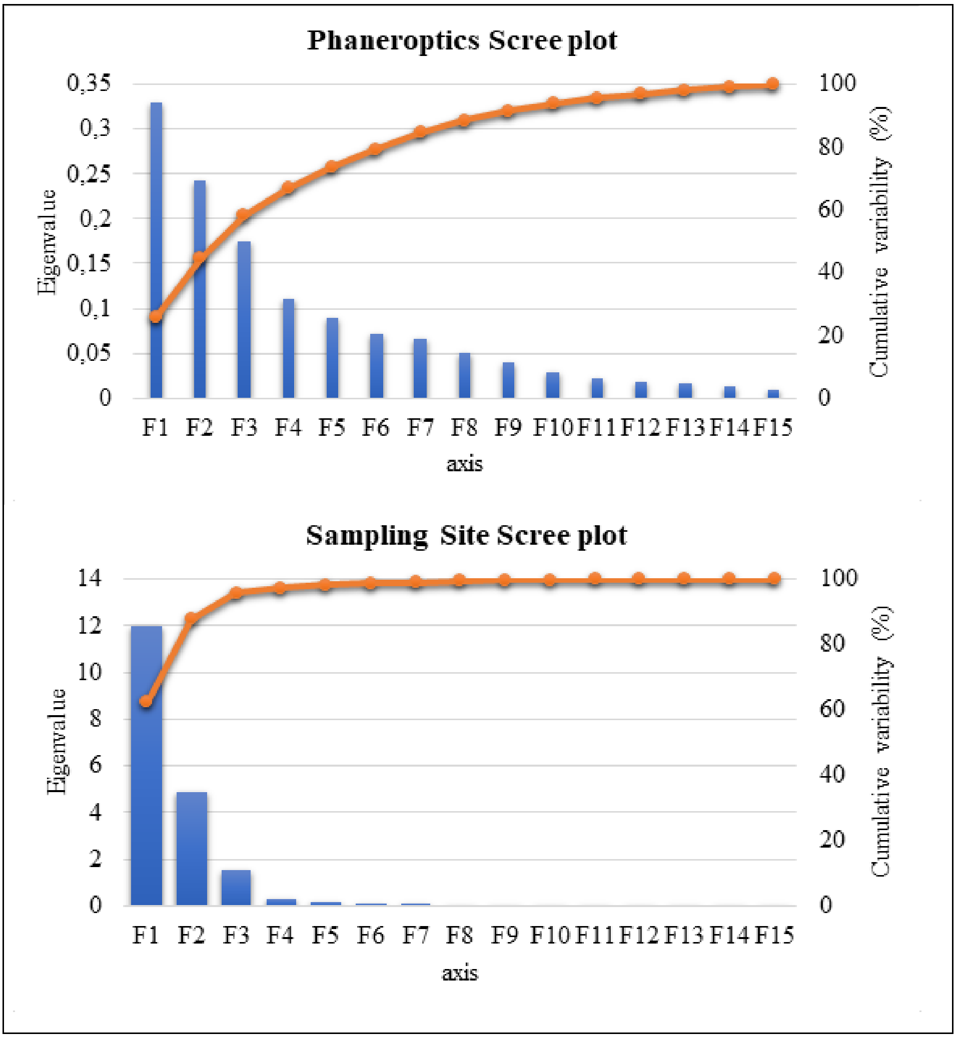


Figure 3. Canonical variable functions and their percentages of self-explained and cumulative variance.

Mahalanobis spatial representation and data mining CHAID decision trees

Mahalanobis distances across phaneroptic possibilities (Figure 6) and sampling sites and species/age groups (Figure 7) were represented in two cladograms.

Figure 6 represents a dendrogram depicting the proximity across phaneroptics (coat and eye colour and particularities), in regards fiber parameters quantified by using an optical fibre diameter analysis. A clear distinction can be appreciated between darker and lighter coats and between depigmented areas and white coats. This also concerns eye colour and particularities as the clustering patterns that are revealed focus on the

Table 4. Results for the tests of equality of group means to test for difference in the means across sample groups once redundant variables have been removed.

Phaneroptics					Sampling site				
Variable	**Wilk's Lambda**	**F**	**P-value**	**Rank**	**Variable**	**Wilk's Lambda**	**F**	**P-value**	**Rank**
large blob%	0.810	6.029	< 0.0001	1	CEM	0.211	248.150	< 0.0001	1
light	0.869	3.886	< 0.0001	2	large blob%	0.233	217.680	< 0.0001	2
%<15um	0.886	3.296	< 0.0001	3	lightSD	0.416	93.201	< 0.0001	3
minSD	0.888	3.233	< 0.0001	4	baseD	0.418	92.174	< 0.0001	4
CEM	0.909	2.558	< 0.0001	5	minSD	0.469	75.110	< 0.0001	5
lightSD	0.911	2.518	< 0.0001	6	%<15um	0.493	68.064	< 0.0001	6
length staple	0.929	1.952	0.0016	7	length staple	0.518	61.679	< 0.0001	7
sdD along 200um	0.930	1.934	0.0018	8	spinF	0.541	56.128	< 0.0001	8
baseD	0.939	1.677	0.0125	9	numD	0.568	50.354	< 0.0001	9
numD	0.941	1.610	0.0198	10	densSD	0.572	49.551	< 0.0001	10
densSD	0.941	1.608	0.0201	11	light	0.594	45.315	< 0.0001	11
SD Along Profile	0.947	1.444	0.0572		SD Along Profile	0.629	39.053	< 0.0001	12
maxSD	0.954	1.249	0.1671		sdD along 200um	0.662	33.815	< 0.0001	13
spinF	0.960	1.074	0.3604		fiFromTip	0.698	28.635	< 0.0001	14
fiFromTip	0.963	0.979	0.5006		maxSD	0.810	15.530	< 0.0001	15
Df1=22; Df2=1458 (Clustering criterion: Sampling site); Df1=31; Df2=796 (Clustering criterion: Phaneroptics)									

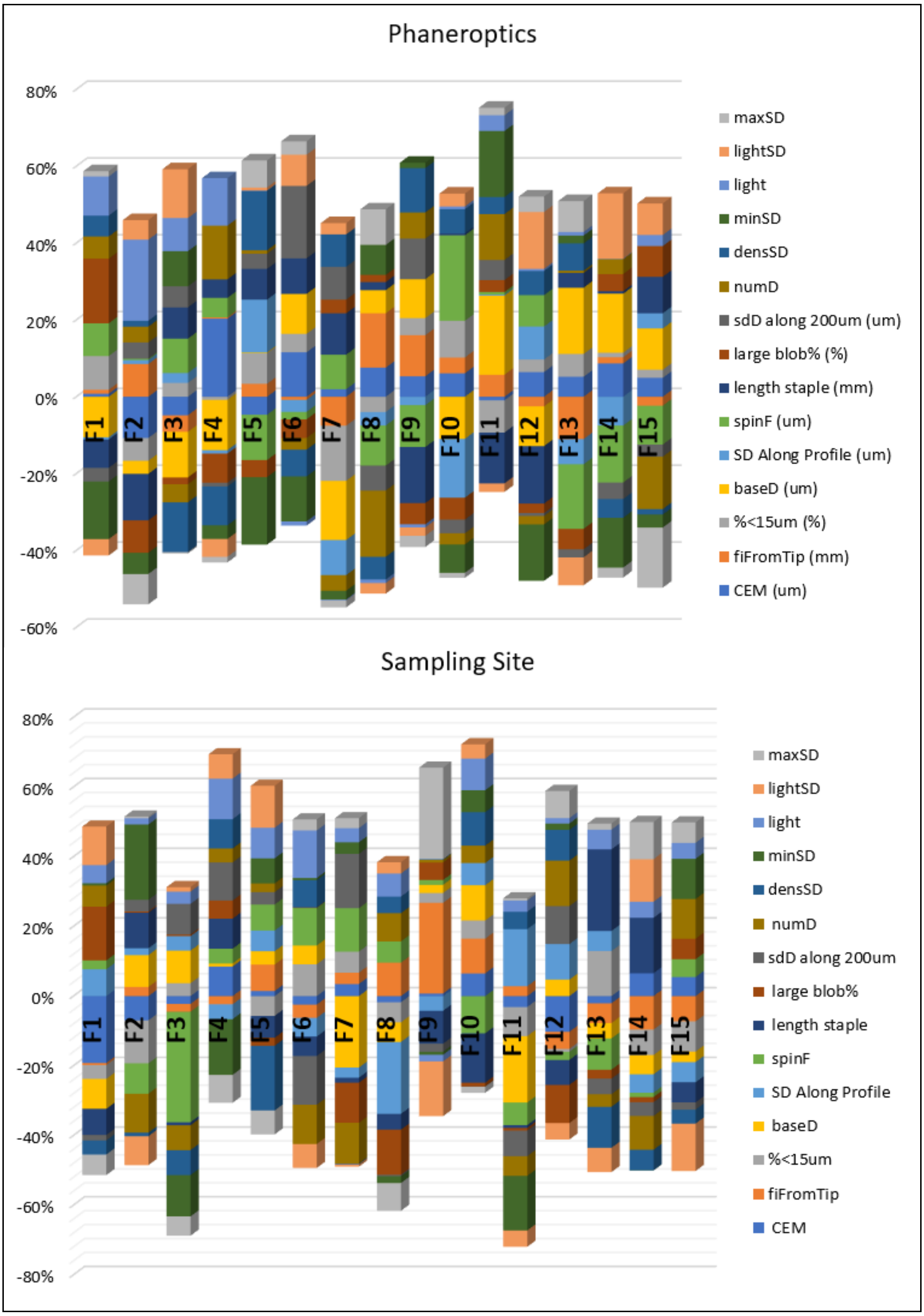


Figure 4. Vector plot for discriminant loadings for the traits considered in discriminant analysis.

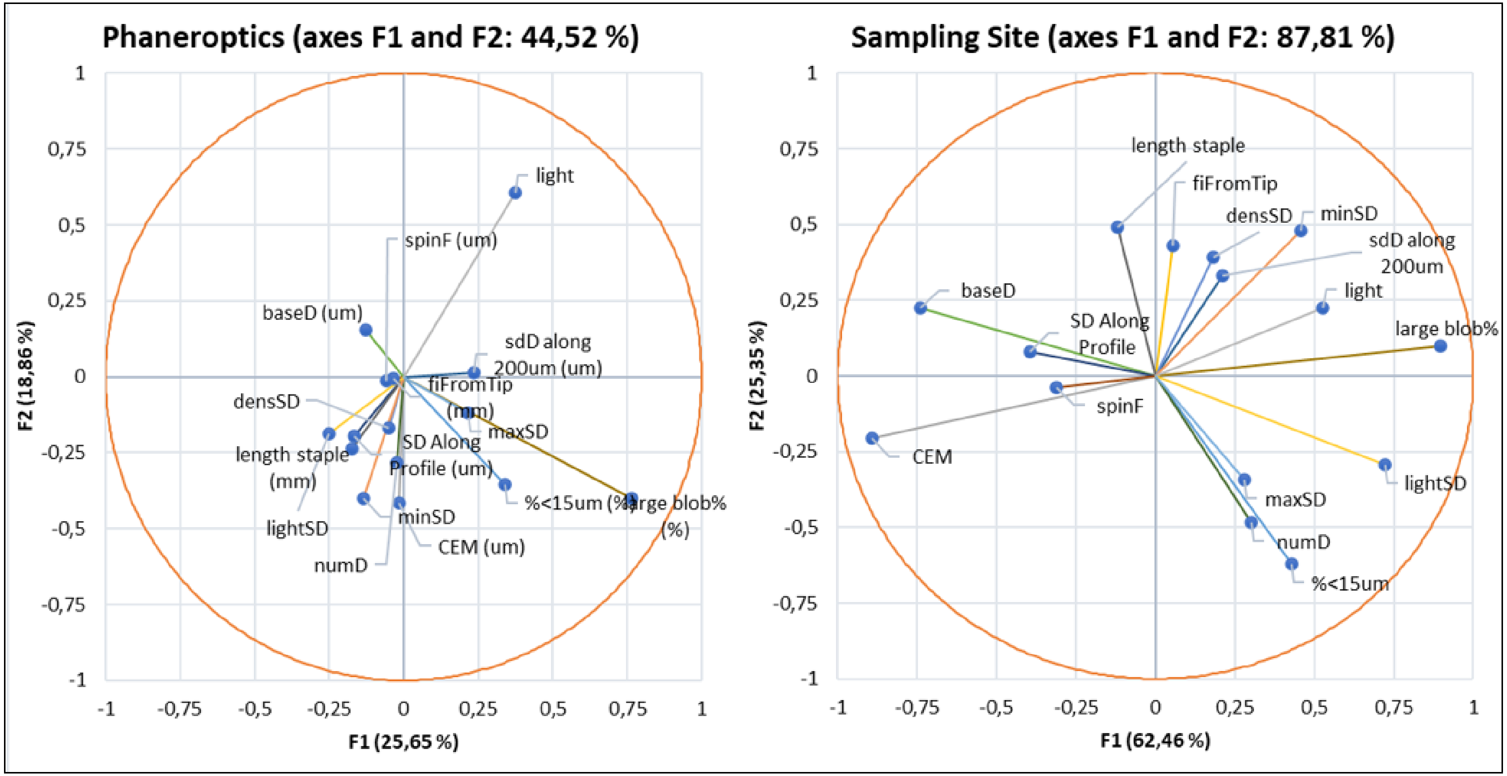


Figure 5. Territorial map depicting the centroids of the different observations considered in the discriminant canonical analysis sorted across species/breeds and age groups.

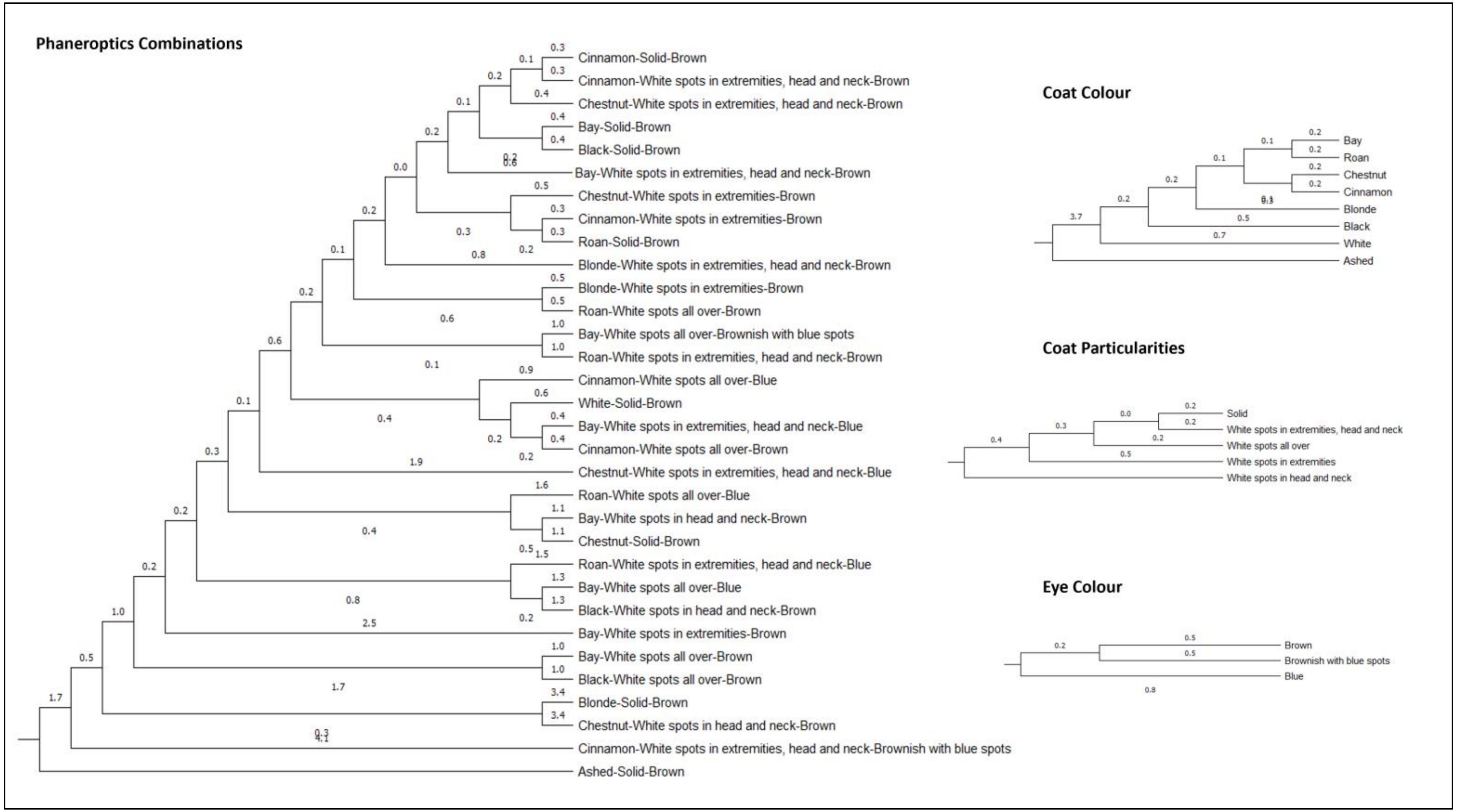


Figure 6. Cladogram constructed from Mahalanobis distances across phaneroptics combinations of coat colour, coat particularities and eye colour in Canarian camel.

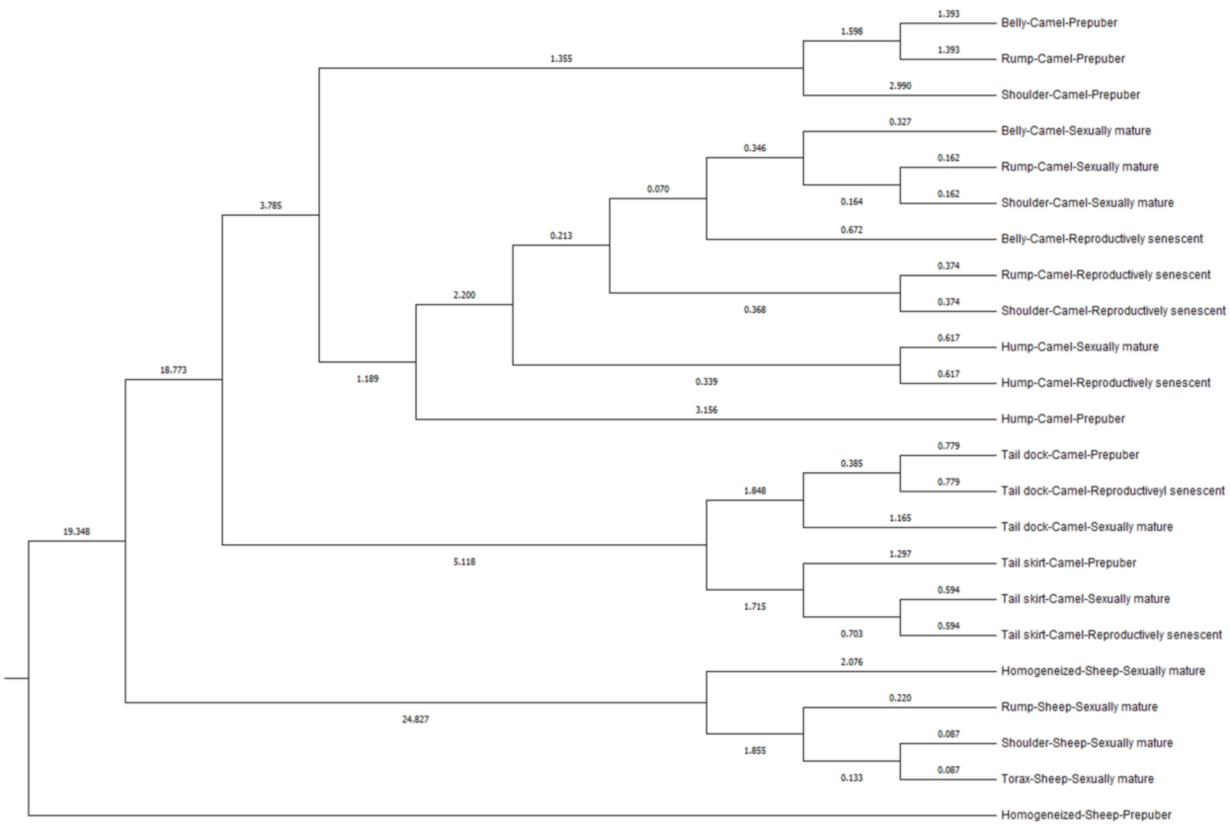


Figure 7. Cladogram constructed from Mahalanobis distances across sampling sites and age groups in Canarian camel and Merino sheep.

similarities between solid coats with those in which clear and extense areas (covering head, body and extremities) of depigmentation are shown, in opposition to those lighter coloured coats and for which depigmentation circumscribes to rather limited areas as represented in the dendrograms for coat colours, coat particularities and eye colours. Additionally, respective CHAID decision trees suggest that light and minSD parameters, which are a measure of the light level next to fibre and indirectly a measure of the absorbance properties of the fiber, and the standard deviation of minimum grey level inside fibre, are the main discriminant parameters (Supplementary Table 2).

The main ramification in the dendrogram in Figure 7 splits data into two clusters; the first at 46.3 and the second at 19.3. This ramification bases upon the differences in baseD. First cluster comprises homogenized samples from prepuber sheep, which is the group accounting for the lowest baseD while presenting the highest lightSD (>1.3) in comparison to the rest (<1.3) (CHAID decision tree; Supplementary Table 2).

Afterwards, two additional subclusters form from the second cluster. First, a subcluster comprising sexually mature sheep which ramifies into two, the first separates samples per areas (with thorax and shoulder being closer than rum) while the second constitutes the homogenized sample from sexually mature sheep basing upon the fibers from these groups presenting baseD< 25.06, CEM<8.6, with independence from length staple.

Two subclusters ramify from the second cluster, one comprising the fibers from the tail dock from sexually mature camels and a second one comprising the tail dock from prepuber and reproductively senescent camels. the second subcluster comprises the fibers from the tail skirt of camels, with sexually mature and reproductively senescent camels being clustered together while the fibers from the tail skirt of prepuber camels separate apart basing upon baseD>42.5 and large blob% >0.10.

From the second cluster, two subclusters ramify, one with the prepuber camel fibers from rump and belly and a second cluster comprising the fibers from the hump from camel from either age subgroup (prepuber, sexually mature or reproductively senescent) basing upon this presenting a >0.8 sdD along 200μm. The second subcluster comprises the fibers from rump (which also characterized by 25.06 to 28.9 baseD and <0.95 sdD along 200μm), belly, and shoulder (sdD along 200μm <0.87) from sexually mature and reproductively senescent camels.

Discriminant function cross-validation

Resubstitution and cross-validation parameters for the phaneroptics evaluation were 0.801 (80.1%) with error being 0.015. Parallelly, resubstitution and cross-validation parameters for sampling areas across species and age groups evaluation were 0.597

(59.7%) and 0.649 (64.9%) with errors of 0.014 and 0.013, respectively. These results support the validity and reliability of the CHAID decisions tree in this study.

Discussion

Animal fiber value hugely depends on mean fiber diameter and length, quantitative attributes in which the phenotypic expression is known to be relatively regulated by qualitative traits that segregates according to Mendel's laws (Bolormaa et al., 2021; Purvis & Franklin, 2005a). Contrastingly to other domestic fiber-producing species, the empirical knowledge on the influence of qualitative traits such as body region and coat colour on camel fiber quality are of short supply for the definition of selection criteria with genetic improvement purposes (Alshanbari et al., 2019). Attempting to further address this research gap, a theoretical grounding on the hair fiber quantitative attributes differentially affected by the location of the fiber by corporal region and fiber colour is presented for a distinctive camel breed (Canarian camel), that presents a particular morphometry due to their functionality (Iglesias et al., 2020; Schulz, 2008) and a notably phaneroptic intraherd variability (Fernández de Sierra & Fabelo Marrero, 2017).

Body region-associated hair fiber phenotypes

From the mid-region to the back of the animal, the diameter at the base of the fiber is higher for adult camels' hair. As previously stated by Petrie (1995), the coarseness of animal coats is greater for animals inhabiting hot climates. More specifically, this characteristic is known to be strongly linked to the thickness of skin (Taha, 2010), which increase as age does (Nomura, Okuma, & Kitamura, 2000); to the volume and internal diameter of the primary follicle (Abdou, Hekal, & Khamis, 2006; Ansari-Renani et al., 2010); and to the diameter and secretory activity of the follicular papilla (Burns & Clarkson, 1949) in camels.

According to our results, the value the diameter at the fiber base in adult camels increases, in ascendent order, for rump, hump, tail dock and belly region, that may be ascribed to the local coarser skin due to the more exposition of these areas to abrasion by sand (i.e. belly), their location around pronounced articular joints (i.e. tail dock) and the combination of pressure and friction induced by saddles (i.e. hump and rump). However, the hair fibers sampled at the shoulder region were encountered not to have high diameter at their base but the greatest value for the variable CEM (Coarse Edge Micron). Such finding is probably determined by the particular homogeneous higher length and larger thickness of fibers along this body area in this camel breed (Fernández de Sierra & Fabelo Marrero, 2017). From a genomics perspective, this special character could be further confirmed following the premises of the research performed by

Alhaddad and Alhajeri (2019), who identified that variations at FGF5gene sequence are associated with hair length variability in dromedary camels.

Linked to this late statement, huge variability is also appreciated for fibers around hump region in Canarian camels both at their mean diameter and length values as well as for their colour or shade (Fernández de Sierra & Fabelo Marrero, 2017). In fact, our results confirm that the variability for the mean diameter along the fiber is greatest for those fibers sampled from the hump of adult camels in contrast to the shoulder', whereas the highest values for this trait in sheep pertain to fibers sampled from the rump. In this scenario, Tridico (2009) postulated, by means of low power microscopy evaluation, that camel hair is effectively more regular in outline than sheep wool, that provides benefits such as higher resistance to processing at textile industry (Wang, 2000) and smoother tactile perception for customers wearing clothes made with this type of fiber (Ramalho, Szekeres, & Fernandes, 2013). What's more, the homogeneous surface along their length for camel hair may explain the comparatively higher capacity of light reflection for camel hair fibers (Chen, Lin, & Tan, 2019; Wortmann, Schulze zur Wiesche, & Bourceau, 2004), which provide benefits for the manufacturing of textile products with higher lightness.

Therefore, not only the mean diameter along the fiber is more variable for sheep wool but also the variability for this fiber related to its ability to reflect light does, as could be expected on the basis of the upper referred literature. Besides, regarding the mentioned local variation in fiber length at some body areas in Canarian camels, this condition is also more prevalent at studied blended sheep wool samples, which are composed by fibers from different parts of the body of the animal and used routinely in this way for textile manufacturing. Hence, we put in evidence that although sheep wool is slightly larger than camel hair, the potential industrial yield and end uses of the late basing on its particularities for diameter homogeneity and light reflection capacity compels the innovative development of preparation technologies and the recognition of the industrial scope of this animal fiber.

In strict terms of fineness, the body region with the highest percentage of fibers with mean diameter less than 15 μ is the tail dock in adult camels. That is, however, the body area with the greatest amount of residual dirt that might affect the industrial performance of fibers. A possible explanation could be the fact that it exists a special sensitivity in this body region (Karolewicz & Paul, 2001) so the thickness of the hair is lesser in comparison with the rest of the body so as to favour the proper perception of surrounding stimuli. In addition, the local cleanliness is relatively low and may be more exacerbated in aged animals that hardly dedicates time for self-grooming. So, despite being the finest fibers and thus its market price superior, it is important to note that the preliminary processing of these fibers for physical removal of impurities could diminish the final yields and further increase their monetary value. Aiming to decrease the impact of this inconvenient, intraherd management practices should include the procuration of regular general hygiene of the animals and take care of the materials used as litters.

By comparing the results from the present research with other related with the same species and genus, quite different observations can be identified. For Indian camels, the lowest diameter was reported for belly and scapula regions, whereas the highest values for this parameter were present at hump fibers (Bhakat, 2019). Similar trends are defined for mid-side region fibers in double-humped camels (Sahani et al., 2003). Conversely, Harizi et al. (2007) found that the diameter of hair fibers sampled from scapula, hump and rump is greater than that of fibers from the belly region in Tunisian dromedaries. These differences between researches may be probably ascribed to animal morphotype (Frank et al., 2006a), that is specific for each breed depending on both environmental factors and functional destinations and that might influence, by pleiotropic effects, the phenotypic expression of hair attributes.

For other camelid and ruminant species in which the selection for functional traits related to fiber production is well practiced, the existing literature is also great in number. In New Zealand and Ecuador alpacas, the fleece tends to coarse and enlarge from the mid-side body region to both the scapula and rump points as well as toward distal points such as extremities and neck, having a such negative correlation with comfort factor as long as these quality attributes increase in value (Solano & Raggi, 2019; Wuliji et al., 2000). For vicuñas, the average diameter of the fibers is known to increase from the dorsal area to the flanks and extremities, and from the anterior area towards the hump region (Quispe et al., 2014). This finding agrees with those reported for Angora mohair (McGregor & Butler, 2008; Taddeo et al., 2000), Bolivian and Peruvian alpacas (Aylan-Parker & McGregor, 2002; McGregor, Ramos, & Peña, 2012), Merino sheep wool (Fish et al., 2002) and American bison wool (McGregor, 2012). In terms of variability, the vicuña fleece has comparatively greater variance in fiber attributes among sampling sites but smaller among fibers of the same sampling area and along the length of the fiber. Thus, the vicuña fleece is more homogeneous than sheep wool, Angora mohair and alpaca fleece (Quispe et al., 2014), which is in turn comparable to our conclusions for camel hair.

Coat colour-associated hair fiber phenotypes

The phaneroptic variability documented for the studied camel breed (Fernández de Sierra & Fabelo Marrero, 2017) is expected to affect the phenotype of hair fibers. Indeed, the quantitative trait that best discriminate between coat colours is the differential ability to reflect light, which can be translated in preferable appearances in terms of brightness at textile manufacturing. In point of fact, the hair fibers from chestnut and bay camels with discoloured areas at extremities, head and neck, have lower capacity to reflect light. By contrast, fibers sampled from bay, cinnamon, blonde and chestnut camels both with solid colour around the whole body or with defined white spots at extremities, showed a higher light reflection potential. As suggested by Khattab and Tributsch (2015), two kind of apparently white hair can be found, but these hair can be either transparent or solid white. Transparent hairs are present scattered along the fur of some other species like polar bears or grow in depigmented areas of skin like white spotting due to local failure in melanocyte's migration. Although these two types of white hair may appear white, light absorbance studies have revealed a greater ability to reflect light on white hair growing on pigmented skin, while transparent hair may absorb most of the incident radiation, behaving as solid darker coloured patterns.

Contrastingly, in other fiber producing species, the variability in fiber characteristics that is attributed to coat colour-related influences, has been reported for fiber coarseness, medullation, length, compressive strength, comfort factor and yield in alpacas (Solano & Raggi, 2019; Wuliji et al., 2000); fiber diameter in llamas (Frank et al., 2006b) and cashmere goats (McGregor et al., 2009); and density, length, diameter and thermal insulation in sheep wool (Leite et al., 2020). Hence, the fact that coat colour in camels does not significantly affect other quality-related traits of hair fibers apart from lightness could be the reason why it does effectively exist huge variability for coat colour, from dark to bright colours, in desert-living animals such as camels. What's the same, the inner medullation of the hair fibers of camels might be the major influencing factor of thermal insulation in these animal species.

The genomic research in this field, using the existing knowledge on other livestock and companion animals (Chandramohan et al., 2013; Eizirik et al., 2003; Fontanesi et al., 2011; Kerje et al., 2003; Rieder et al., 2001), points out that the polymorphisms in the KIT (Holl et al., 2017), MC1R and ASIP genes (Almathen et al., 2018; Bitaraf Sani et al., 2022), may be associated with coat colour variation in dromedaries. More specifically, the TYRP1 gene was proposed as a candidate gene responsible for shade variability at brown coats in Arabian camels (Alshanbari et al., 2019).

Conclusions

From the mid-region to the back of the animal, the diameter at the base of the fiber increases for adult camels, which can be correlated to the higher thickness of skin at these areas due to their major risk of abrasion by sand and the saddles used for riding activities. In addition, a notable variability does exist for both staple length and mean diameter of hair fibres from the regions of shoulder and hump of this animal species. By contrast, such variability for Merino sheep wool is present at hair fibers obtained from the rump area as well as for the blended samples, which are composed of fibers mixed from different body regions. In regards of fineness, camel hair fibers from tail dock are generally lower than 15 µ of diameter, with the inconvenient that this area is also the one with the highest percentage of residual dirt that can affect the final industrial performance of fibers. Besides, our results show that selection for coat colour and particularities is unlikely to significantly affect fiber diameter and strength but light reflection capacity of camel hair fibers, which in turn has a potential basis for the manufacturing of textile products depending on the preferred brightness. These results are intended to serve as a fundamental basis for the recognition of the industrial scope of camel hair fibers and the definition of camel selection schemes and fiber pre-processing techniques depending on the targeted physical-mechanical attributes at the final textile products.

Supplementary materials: The supplementary materials derived from the present study are available on request from the first author.

Funding: The present research was carried out in the financing framework of the international project CA.RA.VA.N—'Toward a Camel Transnational Value Chain' (Reference APCIN-2016-00011-00-00) and during the covering period of a predoctoral contract (FPU Fellowship) funded by the Spanish Ministry of Science and Innovation and was developed under the context a Ramón y Cajal Post-Doctoral fellowship financially supported by MCIN/AEI/10.13039/501100011033 and European Union "NextGenerationEU"/PRTR" (Recovery, Transformation and Resilience Plan—Funded by the European Union—NextGenerationEU).

Data availability statement: The data presented in this study are available on request from the first author.

Acknowledgments: The authors would like to thank 'Aires Africanos' Aires Africanos" Eco-tourism Company, Oasis Park Fuerteventura and 'Camelus' Camellos de Almería, for their direct technical help and assistance.

Declaration of interest statement: No potential conflict of interest was reported by the authors.

References

Abdou, A., Hekal, S., & Khamis, H. (2006). Effect of supplementary feeding under different grazing conditions on the skin follicles and hair coat in camels raised at Halaieb Shalateen and Abo-Ramad triangle, Egypt. Egyptian *Egyptian Journal of Animal Production*, 43(2), 139-151.

Alhaddad, H., & Alhajeri, B. H. (2019). Cdrom archive: a gateway to study camel phenotypes. *Frontiers in genetics*, 10, 48.

Allain, D., & Renieri, C. (2010). Genetics of fibre production and fleece characteristics in small ruminants, Angora rabbit and South American camelids. *Animal*, 4(9), 1472-1481.

Almathen, F., Elbir, H., Bahbahani, H., Mwacharo, J., & Hanotte, O. (2018). Polymorphisms in MC1R and ASIP genes are associated with coat color variation in the Arabian camel. *Journal of Heredity*, 109(6), 700-706.

Alshanbari, F., Castaneda, C., Juras, R., Hillhouse, A., Mendoza, M. N., Gutiérrez, G. A., Ponce de León, F.A., & Raudsepp, T. (2019). Comparative FISH-Mapping of MC1R, ASIP, and TYRP1 in new and old world camelids and association analysis with coat color phenotypes in the dromedary (*Camelus dromedarius*). *Frontiers in genetics*, 10, 340.

Ansari-Renani, H., Salehi, M., Ebadi, Z., & Moradi, S. (2010). Identification of hair follicle characteristics and activity of one and two humped camels. *Small Ruminant Research*, 90(1-3), 64-70.

Aylan-Parker, J., & McGregor, B. (2002). Optimising sampling techniques and estimating sampling variance of fleece quality attributes in alpacas. *Small Ruminant Research*, 44(1), 53-64.

Al-Qarawi, A. A., Abdel-Rahman, H. A., El-Belely, M. S., & El-Mougy, S. A. (2000). Age-related changes in plasma testosterone concentrations and genital organs content of bulk and trace elements in the male dromedary camel. *Animal Reproduction Science*, 62(4), 297-307.

Al-Qarawi, A. A., Abdel-Rahman, H. A., El-Belely, M. S., & El-Mougy, S. A. (2001). Intratesticular morphometric, cellular and endocrine changes around the pubertal period in dromedary camels. *The Veterinary Journal*, 162(3), 241-249.

Babu, K. (2015). Natural textile fibres: Animal and silk fibres. In *Textiles and Fashion* (pp. 57-78): Elsevier.

Bathrachalam, C., Nocelli, C., Pazzaglia, I., Pallotti, S., Pediconi, D., La Terza, A., & Renieri, C. (2019). Interaction between ASIP and MC1R in Black and Brown Alpaca. In *Advances in Fibre Production Science in South American Camelids and other Fibre Animals* (p. 163): Deutsche Nationalbibliothek.

Bhakat, C. (2019). Effect of certain factors on hair quality attributes in Indian Dromedary camel management in an organized farm. *Indian Journal of Animal Sciences*, 71(10), 992-994.

Bitaraf Sani, M., Zare Harofte, J., Banabazi, M. H., Faraz, A., Esmaeilkhanian, S., Naderi, A. S., Salim, N., Teimoori, A., Bitaraf, A., Zadehrahmani, M., Burger, P.A., Asadzadeh, N., Silawi, M., Taghipour Sheshdeh, A., Nazari, B.M., Faghihi, M.A., & Roudbari, Z. (2022). Identification of Candidate Genes for Pigmentation in Camels Using Genotyping-by-Sequencing. *Animals*, 12(9), 1095.

Bolormaa, S., Swan, A. A., Stothard, P., Khansefid, M., Moghaddar, N., Duijvesteijn, N., van der Werf, J.H.J., Daetwyler, H.D., & MacLeod, I. M. (2021). A conditional multi-trait sequence GWAS discovers pleiotropic candidate genes and variants for sheep wool, skin wrinkle and breech cover traits. *Genetics Selection Evolution*, 53(1), 1-14.

Burns, M., & Clarkson, H. (1949). Some observations on the dimensions of follicles and of other structures in the skin of sheep. *The Journal of Agricultural Science*, 39(4), 315-334.

Chandramohan, B., Renieri, C., La Manna, V., & La Terza, A. (2013). The alpaca agouti gene: genomic locus, transcripts and causative mutations of eumelanic and pheomelanic coat color. *Gene*, 521(2), 303-310.

Chen, H., Lin, Z., & Tan, C. (2019). Classification of different animal fibers by near infrared spectroscopy and chemometric models. *Microchemical Journal*, 144, 489-494.

Eizirik, E., Yuhki, N., Johnson, W. E., Menotti-Raymond, M., Hannah, S. S., & O'Brien, S. J. (2003). Molecular genetics and evolution of melanism in the cat family. *Current biology*, 13(5), 448-453.

Fernández de Sierra, G., & Fabelo Marrero, F. J. (2017). *El camello canario*: Asociación de Criadores del Camello Canario.

Fish, V., Mahar, T., & Crook, B. (2002). Sampling variation over a fleece for mean fibre diameter, standard deviation of fibre diameter and mean fibre curvature. *Wool Technology and Sheep Breeding*, 50(4).

Fontanesi, L., Dall'Olio, S., Beretti, F., Portolano, B., & Russo, V. (2011). Coat colours in the Massese sheep breed are associated with mutations in the agouti signalling protein (ASIP) and melanocortin 1 receptor (MC1R) genes. *Animal*, 5(1), 8-17.

Frank, E., Hick, M., Lamas, H., Gauna, C., & Molina, M. (2006a). Effects of age-class, shearing interval, fleece and color types on fiber quality and production in Argentine llamas. *Small Ruminant Research*, 61(2-3), 141-152.

Frank, E., Hick, M., Gauna, C., Lamas, H., Renieri, C., & Antonini, M. (2006b). Phenotypic and genetic description of fibre traits in South American domestic camelids (llamas and alpacas). *Small Ruminant Research*, 61(2-3), 113-129.

Galbraith, H. (2010). Animal fibre: connecting science and production. *animal*, 4(9), 1447-1450.

Gerken, M., Renieri, C., Allain, D., Galbraith, H., Gutiérrez, J. P., McKenna, L., Niznikowski, R., & Wurzinger, M. (2019). *Advances in Fibre Production Science in South American Camelids and other Fibre Animals*: Universitätsverlag Göttingen.

González Ariza, A., Arando Arbulu, A., Navas González, F. J., Delgado Bermejo, J. V., & Camacho Vallejo, M. E. (2021). Discriminant canonical analysis as a validation tool for multivariety native breed egg commercial quality classification. *Foods*, 10(3), 632.

Harizi, T., Msahli, S., Sakli, F., & Khorchani, T. (2007). Evaluation of physical and mechanical properties of Tunisian camel hair. *Journal of the Textile Institute*, 98(1), 15-21.

Hasi, S., Amu, G., & Zhang, W. (2020). Camel hair structure, properties, and commercial products. In *Handbook of research on health and environmental benefits of camel products* (pp. 328-347): IGI Global.

Holl, H., Isaza, R., Mohamoud, Y., Ahmed, A., Almathen, F., Youcef, C., Gaouar, S., Antczak, D.F., & Brooks, S. (2017). A frameshift mutation in KIT is associated with white spotting in the Arabian camel. *Genes*, 8(3), 102.

Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S., & Bermejo, J. V. (2020). Zoometric characterization and body condition score in Canarian camel breed. *Archivos de zootecnia*, 69(265), 14-21.

Karolewicz, B., & Paul, I. A. (2001). Group housing of mice increases immobility and antidepressant sensitivity in the forced swim and tail suspension tests. *European journal of pharmacology*, 415(2-3), 197-201.

Kerje, S., Lind, J., Schütz, K., Jensen, P., & Andersson, L. (2003). Melanocortin 1-receptor (MC1R) mutations are associated with plumage colour in chicken. *Animal genetics*, 34(4), 241-248.

Kerven, C., Russel, A. J., & Laker, J. P. (2002). *Potential for increasing producers' income from wool, fibre and pelts in Central Asia* (Vol. 45): ILRI (aka ILCA and ILRAD).

Leite, J. H. G. M., Da Silva, R. G., Asensio, L. A. B., de Sousa, J. E. R., da Silva, W. S. T., da Silva, W. E., & Façanha, D. A. E. (2020). Coat color and morphological hair traits influence on the mechanisms related to the heat tolerance in hair sheep. *International Journal of Biometeorology*, 64(12), 2185-2194.

McGregor, B. (2012). Production, properties and processing of American bison (Bison bison) wool grown in southern Australia. *Animal Production Science*, 52(7), 431-435.

McGregor, B., & Butler, K. (2008). Variation of mean fibre diameter across mohair fleeces: implications for within flock animal selection, genetic selection, fleece classing and objective sale lot building. *Small Ruminant Research*, 75(1), 54-64.

McGregor, B., Kerven, C., & Toigonbaev, S. (2009). Sources of variation contributing to production and quality attributes of Kyrgyz cashmere in Osh and Naryn provinces: Implications for industry development. *Small Ruminant Research*, 84(1-3), 89-99.

McGregor, B., Ramos, H., & Peña, E. Q. (2012). Variation of fibre characteristics among sampling sites for Huacaya alpaca fleeces from the High Andes. *Small Ruminant Research*, 102(2-3), 191-196.

McLaughlin, I. (2000). Innovative wool testing – OFDA: Australian Wool Taskforce 2000.

Mysterud, A., Steinheim, G., Yoccoz, N. G., Holand, Ø., & Stenseth, N. C. (2002). Early onset of reproductive senescence in domestic sheep *Ovis aries*. *Oikos*, 97(2), 177-183.

Nieto, C. R., Ferguson, M. B., Macleay, C. A., Briegel, J. R., Martin, G. B., & Thompson, A. N. (2013). Selection for superior growth advances the onset of puberty and increases reproductive performance in ewe lambs. *animal*, 7(6), 990-997.

Nomura, Y., Okuma, Y., & Kitamura, Y. (2000). The Senescence-Accelerated Mouse as a Possible Animal Model of Senile Dementia. In *Central Nervous System Diseases* (pp. 113-122): Springer.

Petrie, O. (1995). *Harvesting of textile animal fibres*: Food and Agriculture Organization of the United Nations (FAO) editions.

Purvis, I. W., & Franklin, I. R. (2005a). Major genes and QTL influencing wool production and quality: a review. *Genetics Selection Evolution*, 37(Suppl. 1), S97-S107.

Purvis, I. W., & Franklin, I. R. (2005b). Major genes and QTL influencing wool production and quality: a review. *Genetics Selection Evolution*, 37(1), 1-11.

Quispe, E. C., Sánchez, F., Filella, J. B., & Alfonso, L. (2014). Variation of commercially important characteristics among sampling sites for vicuña (*Vicugna vicugna mensalis*) fleeces. *Journal of Camelid Science*, 7, 1-14.

Ramalho, A., Szekeres, P., & Fernandes, E. (2013). Friction and tactile perception of textile fabrics. *Tribology International*, 63, 29-33.

Rieder, S., Taourit, S., Mariat, D., Langlois, B., & Guérin, G. (2001). Mutations in the agouti (ASIP), the extension (MC1R), and the brown (TYRP1) loci and their association to coat color phenotypes in horses (*Equus caballus*). *Mammalian genome*, 12(6), 450-455.

Sahani, M., Yadav, B., Mal, G., & Dhillon, R. (2003). Quality attributes of double-humped camel hair fibres. *Indian Journal of Fibre & Textile Research*, 28, 227-229.

Schulz, U. (2008). *El camello en Lanzarote*: Aderlan.

Sharma, A., & Pant, S. (2013). Studies on camel hair-merino wool blended knitted fabrics. *Indian Journal of Fibre & Textile Research*, 38, 317-319.

Solano, S., & Raggi, L. (2019). Lanametric Determination of the Alpaca Fiber (*Vicugna Pacos*) in Tucayta, Province of Cañar. *Journal of Veterinary Science & Medicine*, 7(1), 4.

Tabbaa, M., Al-Azzawi, W., & Campbell, D. (2001). Variation in fleece characteristics of Awassi sheep at different ages. *Small Ruminant Research*, 41(2), 95-100.

Taddeo, H., Duga, L., Almeida, D., Willems, P., & Somlo, R. (2000). Variation of mohair quality over the body in Angora goats. *Small Ruminant Research*, 36(3), 285-291.

Taha, E. (2010). Seasonal changes in some coat traits of growing dromedary camels under egyptian semi-arid conditions. *Egyptian Journal of Animal Production*, 47(1), 65-74.

Tridico, S. (2009). Natural animal textile fibres: Structure, characteristics and identification. In *Identification of Textile Fibers* (pp. 27-67): Elsevier.

Wang, X. (2000). Predicting the strength variation of wool from its diameter variation. *Textile research journal*, 70(3), 191-194.

Wortmann, F. J., Schulze zur Wiesche, E., & Bourceau, B. (2004). Analyzing the laser-light reflection from human hair fibers. II. Deriving a measure of hair luster. *International journal of cosmetic science*, 26(4), 219-219.

Wuliji, T., Davis, G., Dodds, K., Turner, P., Andrews, R., & Bruce, G. (2000). Production performance, repeatability and heritability estimates for live weight, fleece weight and fiber characteristics of alpacas in New Zealand. *Small Ruminant Research*, 37(3), 189-201.

Zarrin, M., Riveros, J. L., Ahmadpour, A., de Almeida, A. M., Konuspayeva, G., Vargas-Bello-Pérez, E., Faye, B., & Hernández-Castellano, L. E. (2020). Camelids: new players in the international animal production context. *Tropical animal health and production*, 1-11.

7.3 Camel (*Camelus* spp.) urine bioactivity and metabolome: a systematic review of knowledge gaps, advances, and directions for future research

Carlos Iglesias Pastrana[1], Juan Vicente Delgado Bermejo[1], Maria Noemi Sgobba[2], Francisco Javier Navas González[1,3], Lorenzo Guerra[2], Diana C.G.A. Pinto[4], Ana M. Gil[5], Iola F. Duarte[5], Giovanni Lentini[6] and Elena Ciani[2]

[1]Department of Genetics, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain

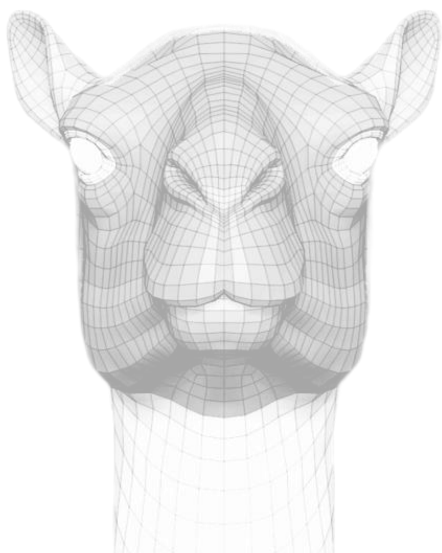
[2]Department of Biosciences, Biotechnologies and Biopharmaceutics, Faculty of Veterinary Sciences, University of Bari 'Aldo Moro', 70121 Bari, Italy

[3]Andalusian Institute of Agricultural and Fisheries Research and Training (IFAPA), Alameda del Obispo, 14004 Cordoba, Spain

[4]LAQV-REQUIMTE, Department of Chemistry, University of Aveiro, 3810-193 Aveiro, Portugal

[5]Department of Chemistry, CICECO Aveiro Institute of Materials, University of Aveiro, 3810-193 Aveiro, Portugal

[6]Department of Pharmacy-Drug Sciences, University of Bari 'Aldo Moro', 70125 Bari, Italy



Quality indicator information provided on the publication

Status of the manuscript: Published

Journal (year, volume, page(s)): *International Journal of Molecular Sciences* 2022, *23*, 15024

International database in which it is indexed: Journal of Citation Reports (JCR)

Thematic area in the reference database: Biochemistry & Molecular Biology

Impact index of the journal in the year of the article's publication: 5.6

Rank/number of thematic area journals: 66/285 (Q1)

Abstract

Up to the present day, studies on the therapeutic properties of camel (*Camelus* spp.) urine and the detailed characterization of its metabolomic profile are scarce and often unrelated. Information on inter individual variability is noticeably limited, and there is a wide divergence across studies regarding the methods for sample storage, pre-processing, and extract derivatization for metabolomic analysis. Additionally, medium osmolarity is not experimentally adjusted prior to bioactivity assays. In this scenario, the methodological standardization and interdisciplinary approach of such processes will strengthen the interpretation, repeatability, and replicability of the empirical results on the compounds with bioactive properties present in camel urine. Furthermore, sample enlargement would also permit the evaluation of camel urine's intra- and interindividual variability in terms of chemical composition, bioactive effects, and efficacy, while it may also permit researchers to discriminate potential animal-intrinsic and extrinsic conditioning factors. Altogether, the results would help to evaluate the role of camel urine as a natural source for the identification and extraction of specific novel bioactive substances that may deserve isolated chemical and pharmacognostic investigations through preclinical tests to determine their biological activity and the suitability of their safety profile for their potential inclusion in therapeutic formulas for improving human and animal health.

Keywords

Dromedary, active principles, metabolomics, metabolomic profile, standard operating procedures

Introduction

Urine utilization (either consumed or locally applied) has attracted the interest of health academicians and intellectuals since ancient times due to the widespread belief of the many preventive and curative potentialities of this biofluid as a treatment against several ailments (Savica et al., 2011). Despite the controversial nature of the topic, the availability of worldwide references from current and ancient civilizations (Cuenca-Estrella & Martín, 2004; Silva, 2010) across cultures and societies is remarkable. However, a systematic review of its bioactivity, metabolomic profiling, key biochemical parameters for pharmacological research and drug design, and repercussions on public health has not been performed to date as it has for the controversial utilization of other biological substrates by humans (Beacock, 2012; Campbell et al., 2021; Khoruts & Brandt, 2019; Stanhope, 2016; Vartanian, Schwartz, & Brownell, 2007). Similar to other bioactive substances of animal origin, further standardized research is needed for the optimization of the process of their isolation as well as high-quality clinical trials to evaluate their efficacy and the safety of their use for the treatment of certain diseases (Zhang, Chen, & Wang, 2015).

The 5000-year-old document 'Damar Tantra' is the oldest known medical treatise to first mention the therapeutical use of human urine ('Shivambu Kalpa Vidhi') in the Indian ayurvedic tradition. Among other prescriptions, this miscellanea recommended that one should drink one's own urine in the morning for general revitalization, prophylaxis, and as an adjunct to conventional treatments (Mills & Faunce, 1991). Similarly, historical records on the use of camel urine for medical purposes date back to a text from 1020 titled The Canon of Medicine by Avicenna, a Persian Muslim scientist who authored numerous globally acknowledged scientific papers and medical books (Alhaider et al., 2011). Urine consumption was not exclusively practiced by oriental cultures (Gader & Alhaider, 2016; Thakur, 2004); urine would also appear cited in Greco- Roman classical medical texts (13–20th centuries BC) in which it was referred both as a remedy and diagnostic tool (Casquero, 2005; Casquero, 2006; García, 2006; Plinio, 2007).

Multiple *in vivo* research undertaken since the early 1990s have evidenced the effects that urotherapy (both with autogenous or heterogeneous urinary extracts) has on different pathological processes, such as urinary infections, gonarthritis, desensitization, endocrinological problems, migraine, pruritus, asthma, urticaria, eczema, psoriasis, acute and subacute glomerulonephritis, experimental ulcers, lymphoid depletion in intestinal segments, the induction of thrombocytosis in peripheral blood and megakaryocytosis in the spleen, and the neutralization of the bone marrow colony-stimulating factor (Eldor, 1997). Some descriptive studies also referred to this alternative practice as a remedy for the treatment of many human diseases such as abdominal tumors, gastro-intestinal disorders, and other chronic conditions with the urine of different animal species, including small and large domestic ruminants, llamas, camels, buffaloes, elephants, and equids (Al-Abdalall, 2010; Christy, 1994; Thakur, 2004). In the contemporary scene, Armstrong (1944) would praise the value of urine as a polyvalent curative agent by comparing its bioactivity with the natural occurrence of organic composting. Subsequent research has made revolutionary findings in relation to the potentialities of urotherapy for patients with cancer, which is a leading global health issue (Vaidya et al., 2003; Wu et al., 2020). However, camel urine's alkalinity (high levels of potassium and magnesium, albuminous protein, and low concentrations of uric acid, sodium, and creatine), unlike other animal urine, may be the source for the comparatively higher historical prevalence of its use (Alkhamees & Alsanad, 2017). Concretely, high alkalinity is the property to which other human medicines' desirable properties such as antimicrobial potential activity has been ascribed (El-Reash et al., 2019).

In particular, drinking camel urine alone or mixed with milk is a widely renowned practice within the scope of folk medicine (Mok et al., 2021). This habit has frequently been described in Arabian countries, especially among Bedouin tribes with a strong heritage from the Muslim religion (Ali, Baby, & Vijayan, 2019; Al-Yousef et al., 2012), among which the urine of virgin female camels is the most appreciated (Abdelzaher et al., 2020). In line with the aforementioned uses, Gole and Hamido (2020) contextualize their review on the fact that despite its traditional use as medicine, there is no scientific dosage at which camel urine can be applied as a medicine for different diseases, and the methods for camel urine's formulation and utilization for the care of patients vary internationally. Furthermore, these authors suggest that there is a need for the biochemical composition of camel urine to be scientifically extracted and formulated as a therapy to prevent its raw consumption and, consequently, its negative effects on human health (Gole & Hamido, 2020).

Recently, several *in vitro* and *in vivo* studies have explored the biological effects of camel urine, namely, its bioactivity towards a range of tumoral and non-tumoral cells (Alebie, Yohannes, & Worku, 2017). However, information on the bioactivity of specific urine metabolites, their potential interactions, and safety profiles is very scarce. Thus, further investigation is needed to perform a detailed characterization of the chemical composition of this biofluid and to assess how its metabolic profile and properties are affected by different extrinsic and intrinsic factors. As stated by Kumar et al. (2021), urine is constituted by different secretions that aid the protection of the urogenital tract against environmental pathogens/threats and organic failures. Once the biological activity of whole urine is tested and confirmed under experimental conditions based on standardized principles established through international conventions, the proceeding steps involve the characterization of its chemical composition and the subsequent isolated prediction and testing of the bioactivity, through in-silico and *in vitro/in vivo* experiments, respectively, of each of the molecules encountered to classify them into functional groups (Joseph et al., 2012; Sharma et al., 2016). This would help to rationalize and expand the potential value of camel urine as a natural substrate for the discovery of novel bioactive substances with applications in biomedicine. Furthermore, the isolation and testing of new bioactive compounds may also enhance the opportunities for their application in a range of other industrial fields such as the synthesis of nanomaterials and the generation of hydrogen (Ajiboye et al., 2022).

In this context, the identification and quantification of the low-molecular-weight (<1 kDa) small molecules present in urine as a biological system, based on metabolomic technologies, may constitute a powerful tool for the detailed characterization of urine metabolomic profiles and in turn individual phenotypes (Suarez et al., 2017; Suhre & Gieger, 2012). By using complementary analytical methodologies such as gas chromatography–mass spectrometry (GC-MS), liquid chromatography–mass spectrometry (LC–MS), and nuclear magnetic resonance (NMR) spectroscopy, metabolomics enables a large number of metabolites to be detected simultaneously, enhancing the possibility of identifying new biologically active compounds (Nalbantoglu, 2019). However, given the expected complexity and variability of biological samples, it is of paramount importance to ensure that standardized protocols are in place for the samples' handling and processing so as to avoid undesirable sources of variation (Hernandes, Barbas, & Dudzik, 2017; Zhao & Li, 2020).

While previous review articles on camel urine's therapeutic benefits have mainly summarized the bioactivity test results conducted by separate studies (Alebie, Yohannes, & Worku, 2017; Ali, Baby, & Vijayan, 2019; Alkhamees & Alsanad, 2017; Gader & Alhaider, 2016; Salamt et al., 2021), this review aims to offer a comprehensive view of the current knowledge on the camel urine metabolome and its biological effects, as well as highlight the main knowledge gaps and research challenges around the topic that need to be addressed for a contrasted and safe use of this animal-derived substrate in drug discovery focused on public health (Vuorela et al., 2004). A detailed outline of the camel urine metabolome is provided herein based on the nature and uses of each molecule reported to be present in this biofluid, thereby enforcing the existing body of scientific literature aimed at describing the therapeutic role of any specific components in urine. Additionally, the implications of different pre-processing and analytical methods in the metabolomics research outcomes are discussed and recommendations on sampling methodologies that could improve ongoing industrial and biomedical applied research are issued. Afterwards, this review contributes to the pioneering creation of a repository for camel urine metabolomics and related metadata, and encourages the integration of documented clinical experiences and experiential observations through transdisciplinary, robust preclinical and clinical research that aids the definition of new drug candidates (reverse pharmacology) (Patwardhan & Khambholja, 2011) that are contained in camel urine. All in all, this function- ally multidisciplinary research will promote the sustainable conservation of traditional medicines derived from autochthonous animal populations in line with the 2003 UNESCO Convention on the Safeguarding of the Intangible Cultural Heritage.

Methods

The present review was carried out in four stages, namely, the definition of the most relevant topics to be included in the review, database generation and pruning, document content evaluation, and the performance of a complementary review on camel urine's chemical composition. PRISMA 2020 guidelines were followed to conduct the present systematic review (Page et al., 2021).

Literature search strategy and exclusion criteria

Search repositories

According to the criteria defined for the selection of peer-reviewed literature platforms to be used for the compilation of published research (Gusenbauer & Haddaway, 2020; Iglesias Pastrana et al., 202; McLean & Gonzalez, 2018), ScienceDirect (www.sciencedirect.com) was selected as the primary search system used in our study. However, since only one paper addressing the camel urine metabolome was indexed in this platform and considering that Booth et al. (2016) proposed to include an average of 8–12 studies to effectively address a review question, Google Scholar (www.scholar.google.es) was used as an additional source to search for articles on the metabolomic profile of camel urine.

Following the premises given by Piasecki, Waligora and Dranseika (2018), this freely accessible web search constitutes a great source of grey literature that is governmental alongside institutional reports that are sometimes not published in indexed journals, but which help to improve the conceptual comprehensiveness of qualitative systematic reviews. Lastly, seeking an in- depth review of the chemical information and experimental data identifying the biological activity of the small molecules present in camel urine, the freely accessible repository of PubChem (https://pubchem.ncbi.nlm.nih.gov) was used.

Search criteria

As search repositories are constantly updating their content, the evaluation of document databases was closed on October 1st, 2021. To filter among the vast number of documents that can be found in such repositories, the keywords 'camel', 'urine', 'metabolomics', 'bioactivity', '*in vivo*', '*in vitro*', and 'effects' were used in the ScienceDirect search engine without setting any limitations concerning time, date, language, and/or document type. The same search strategy was followed in Google Scholar to collect additional documents to be included in the database (Ridley, 2012).

Sample

A total number of 141 and 621 documents were collected from ScienceDirect and Google Scholar sites, respectively. From the first database, 140 references were related to camel urine's bioactivity and one referenced camel urine metabolome. On the other hand, 614 and 7 references were related to camel urine's bioactivity and the camel urine metabolome, respectively, in Google Scholar database. Only those documents in which either an *in vitro*, *in vivo*, or combined study of camel urine's bioactivity was performed or those specifically dealing with the analysis and/or evaluation of the cytotoxic effects of active compounds of camel urine were retained in the database. Hence, those documents in which an anecdotal reference to urine, its bioactivity, and/or that of its compounds was made were considered to fall outside of the scope of this review and were thus discarded. Additionally, the final dataset comprised information on two reviews based on the bioactive effects of camel urine, while the rest of the documents described experimentally based studies. The first review included a detailed analysis of six already-published documents describing research studies on the therapeutic potential of camel urine, which were also individually considered (Salamt et al., 2021). Three of these papers had already been considered during the data collection process carried out when using the ScienceDirect repository (Alhaider et al., 2011; Al-Harbi et al., 1996; Al-Yousef et al., 2012); hence, their duplicates were removed to ensure each document had been accounted for only once. The second review gathered a comprehensive theoretical presentation of the known traditional uses of some plants and animal-derived products and subproducts for cancer treatment in Algeria (Taïbi et al., 2020). As a result, 132 and 614 documents were discarded from the databases initially constructed from ScienceDirect and Google Scholar, respectively.

As a result, final data sample consisted of 18 research papers (11 documents from ScienceDirect and 7 from Google Scholar database, wherein 10 were focused on camel urine's bioactivity and 8 studied its metabolome).

Document review

Data collected were sorted into two datasets: the first related to journal identification and impact indicators, and the second to the content of the documents. The information included in the first data set for each article was as follows: the journal in which the article was published or the conference proceedings in which conference contributions were presented, the year of publication/presentation, the yearly Journal Citation Report (JCR) impact factor of the journal in which the article was published, the total number of citations of each paper, the number of contributing authors, the country of the corresponding author, the camel species studied, the breeding location of the camels from which the urine was collected, and the number of animals comprising the sample, their sex, their average age, (in years) and their reproductive status. Each publication's digital object identifier (doi) was also included in the database in order to be able to ensure document traceability and access each manuscript in case it was necessary a posteriori.

Each journals' JCR impact factor and total number of citations per paper was accessed from the Web of Science site. The computation of the impact factor for the journals publishing papers in 2021 (up to October) was executed by dividing the number of current year citations by the total number of items published during the 2 previous years, as suggested in the literature (Garfield, 2006).

Afterwards, the second data set comprised the following information extracted from each article. For papers investigating the biological activity of the urine, special attention was paid to the different research methods and materials employed, focusing on the type of substrate used (raw or pre-processed urine), cell line(s) and/or organic tissue(s) tested, and model type (*in vivo* and/or *in vitro*). In studies analyzing the camel urine metabolome, the information retrieved consisted of the list of metabolites found, and the methodologies or protocols used for sample preparation, storage, and analysis. Then, for each reported chemical substance, the following information was registered: IUPAC name, synonyms, source(s) of origin/formation, and therapeutic and industrial uses.

Results and discussion

Bibliometrics quantitative and qualitative analysis

Figure 1 depicts the outputs of the systematic document-screening stages. Afterwards, a description of the variables included in the present study, their type, and the levels that they correspond to is reported in Table 1. After testing the preliminary parametric assumptions (using the Shapiro–Francia test and Levene's test to evaluate normality and homoscedasticity, respectively) (Supplementary Table S1) with the Stata software, version 15.0, the descriptive statistic parameters for normally and non-normally distributed data were calculated (Table 2) using SPSS software, Version 25.0 (Corp, 2017).

The reviewed documents on camel urine's bioactivity (n = 12) and metabolome (n = 8) were published between 1996–2021 and 1925–2019, respectively. For these periods, the mean numbers of articles published per year for each topic were 0.48 and 0.08, respectively. Fourteen documents (six for urine's bioactivity and twelve for the urine metabolome) were published under an open-access policy. Figure 2 presents the total number of articles published per topic and year. As it can be observed, large time gaps between the publication of papers are present for both research aims.

According to Faye (2013), five levels of the economic importance of camel populations could be identified considering the percentage of Tropical Livestock Units (TLU) and density (number of camels/km^2). First, those countries in which camels have a marginal importance (population represents less than 2% of the total TLU), such as South Asia and the Near-East, mainly, or anecdotal uses in Europe (Spain, The Netherlands, and France) (<1 camel/km^2); countries in which they have a low economic importance (2–5% of the total TLU), such as Egypt, Libya, Central Asia, Iraq (<1 camel/km^2), Pakistan, and Afghanistan (more than 2 camels/km^2); countries in which camels have a medium

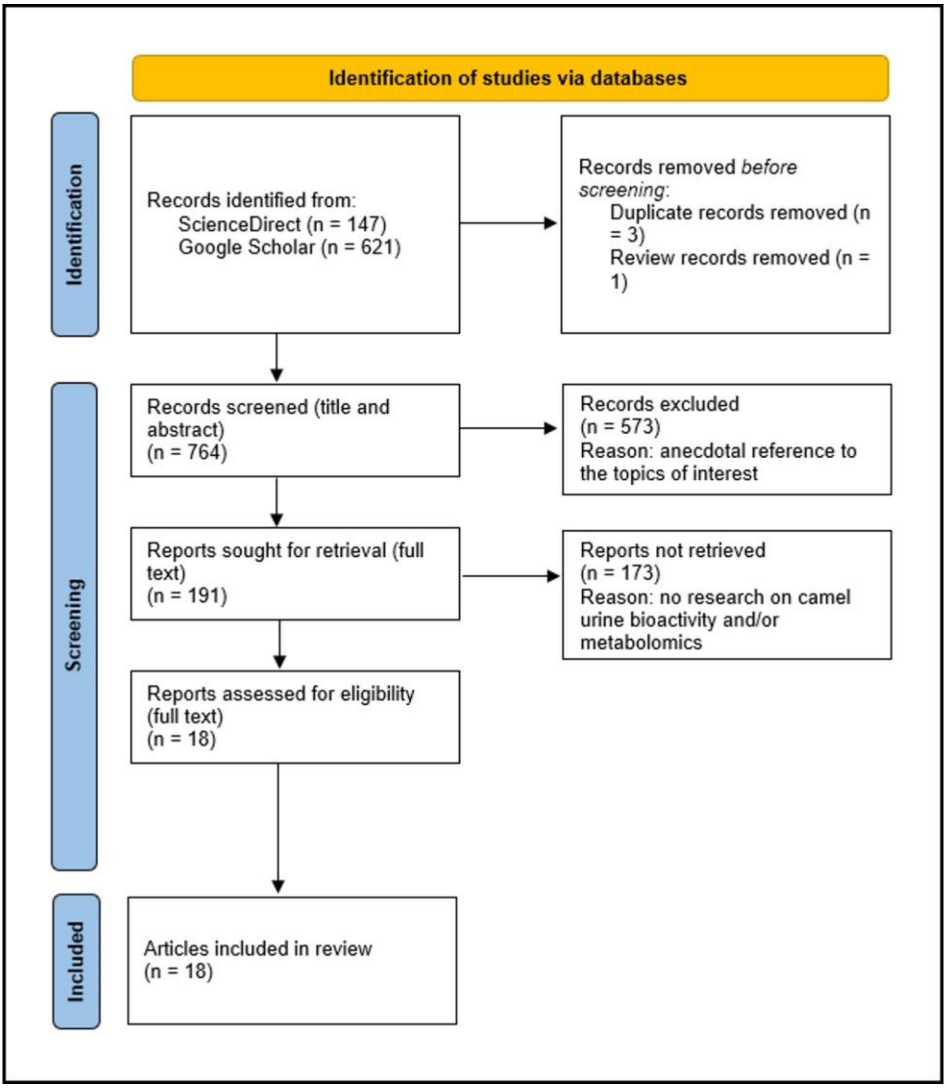


Figure 1. Process flow chart showing the sequential steps of literature search and review in the present study.

importance (5–10% of the total TLU) such as Algeria, Kenya, and Ethiopia (<1 camel/km^2); countries in which camels are quite important (10–25% of the total TLU), mainly Sahelian countries (1 camel/km^2) and those in the Arabian Peninsula (more than 2 camels/km^2); and those countries in which camels represented more than 25% of the whole TLU (Mauritania and Somalia) (more than 2 camels/km^2). These two indicators (percentage of TLU and density) show that the economic importance of camels is quite predominant in Sub-Saharan countries and in the Arabian Peninsula.

Table 1. Category description for bibliometric variables registered.

Variable	Type	Levels	
		Camel Urine's Bioactivity	**Camel Urine Metabolome**
Journal	Nominal	10 Scientific Journals	7 Scientific Journals and 1 International Conference Paper
Year of publication	Ordinal	1996 to 2021	1925 to 2019
JCR Impact Factor per paper publication year	Numeric	0 to 3.014	0 to 3.138
Total number of citations per paper	Numeric	0 to 47	0 to 46
Number of authors	Numeric	1 to 12	1 to 4
Country of corresponding author	Nominal	Algeria, Canada, Malaysia, and Saudi Arabia	China, Denmark, Saudi Arabia, and Sudan
Camel species	Nominal	*Camelus dromedarius* and Not indicated [1]	*Camelus dromedarius*, *Camelus bactrianus*, and Not indicated [1]
Camels' breeding location	Nominal	Algeria, Egypt, Saudi Arabia, Somaliland, and Not indicated [1]	China, Egypt, Saudi Arabia, and Not indicated [1]
Sample size	Numeric	3 to 67 (Not indicated in 7 documents) [2]	1 to 23 (Not indicated in 4 documents [2])
Sex of sampled animals	Nominal	Male, female, and Not indicated [1]	Female and Not indicated [1]
Mean age of sampled animals (years)	Numeric	3.5 to 6 (Not indicated in 7 documents [2])	2.5 to 6 (Not indicated in 6 documents [2])
Physiological status of sampled animals	Nominal	Lactating females, Physiological status cluster 1 (virgin, pregnant, and lactating females), and Not indicated [1]	Lactating females, pregnant females, Physiological status cluster 2 (virgin and lactating females), and Not indicated [1]

[1] Qualitative data not detailed;[2] Quantitative data not detailed. When testing the statistics' parametric preliminary assumptions, 'Not indicated' data for nominal variables were considered as a different category, while 'Not indicated' data for ordinal and numeric variables were treated as missing values.

Table 2. Summary statistics for the ordinal and numeric variables.

Camel Urine's Bioactivity			
Normally distributed variable	**Mean**	**Standard deviation**	**Min/Max**
JCR Impact Factor per paper publication year	1.2	1.1	0/3.014
Number of authors	5	3	1/12
Sample size	25	27	3/67
Non-normally distributed variable	**Median**	**Mode**	**Interquartile range**
Year of publication	2016	2011	25.00
Total number of citations per paper	7.0	1.0	3.0
Mean age of sampled animals (years)	6.0	6.0	2.5
Camel Urine Metabolome			
Normally distributed variable	**Mean**	**Standard deviation**	**Min/Max**
Number of authors	2.9	1.1	1/4
Non-normally distributed variable	**Median**	**Mode**	**Interquartile range**
Year of publication	2015	2016	94.00
JCR Impact Factor per paper publication year	0.0	0.0	3.1
Total number of citations per paper	3.0	0.0	46.0
Sample size	1.0	1.0	22.0
Mean age of sampled animals (years)	4.2	2.5	3.5

As suggested by Iglesias Pastrana et al. (2020), the relative economic and demographic importance of camels across countries translates into the greater or lesser attention paid by academicians and researchers to the study of the camel species. In this regards, in terms of internationalization, seven countries around the world have been involved in the research of camel urine's bioactivity and/or its metabolomic profile, namely, Saudi Arabia (n = 13), Sudan (n = 2), and one paper per country in Algeria, China, Denmark, Canada, and Malaysia, respectively. The articles included in the present review were published in 17 different journals and one international conference. Most of

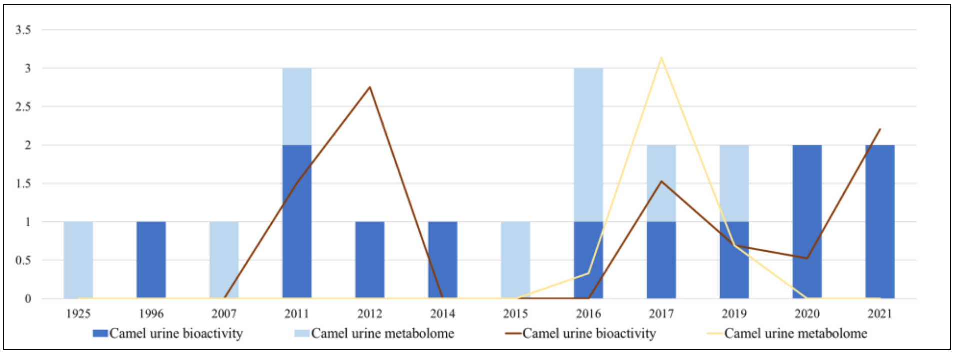


Figure 2. Number and impact factor of camel urine- and metabolome-related publications from 1925 to 2021. Bars represent the number of documents published per topic and year, while straight lines depict each year's respective mean JCR impact index.

the journals had an ethnopharmacology and biological chemistry background scope. The average number of authors per publication was five for camel urine's bioactivity and three for its metabolomic profile. When the journal impact factor was considered, seven and three journals were indexed in JCR in the year in which the camel urine bioactivity and camel urine metabolome papers were published, respectively.

The maximum JCR impact factor for the papers reviewed on camel urine's bioactivity was 3.014, which was reached by an article focusing on camel urine's inhibition of cytochrome P450 1a1 gene expression in murine hepatoma. This article was published in 2011 in the *Journal of Ethnopharmacology* (Alhaider et al., 2011). On the other hand, the lowest JCR impact factor (0.692) was reached by an article published in 2019 in the *International Journal of Pharmacology*, which focused on the hepatoprotective effects of camel urine against carbon tetrachloride-induced liver toxicity (Mahmoud, Elsaed, & Gabr, 2019).

Regarding the papers dealing with the camel urine metabolome, the maximum (3.138) and minimum (0.660) JCR impact factors were reached by two articles published in the *Saudi Journal of Biological Sciences* (Ahamad et al., 2017) and the *Indian Journal of Pharmaceutical Sciences* (Khedr & Khorshid, 2017), respectively. Figure 2 illustrates the mean JCR impact index per topic reviewed and year. A parallel trend was described by the number of papers published and their academic impact.

The most highly cited paper on camel urine's bioactivity was an article dealing with the cytotoxic effects of camel urine towards different human cancer cell lines, which was published in 2012 in the *Journal of Ethnopharmacology* (Al-Yousef et al., 2012), with a total of 47 citations. This value was close to that of the most highly cited article on camel urine metabolome, with 46 citations. It may be worth mentioning that the publication of the latter took place in 1925 in the *Journal of Biological Chemistry* (Read, 1925) and constitutes the first simple analysis of some of the metabolites in camel urine.

Three of the documents published in 2020, 2011, and 2016, which were considered in the present study, had not been cited at the moment in which the data collection carried out in the present study was finished, with respect to both camel urine's bioactivity and metabolome-related literature.

In summary, despite the time gap mentioned above, research efforts towards deepening the knowledge of camel urine's bioactivity have been comparatively more regular in time and relevant in terms of the scientific impact of the publications that eventually were published than those focused on the metabolomic profile of this organic substrate. Indeed, although the first quantification of a discrete number of target metabolites in camel urine was published in 1925, no further research had followed until after almost one century. Indirectly, this provides evidence for the fact that there is a lack of a consistent time-overlap between both research topics. This, in turn, may have conditioned the interpretation and applicability of the results published, given the metabolomic profile and existing variability of the urines sampled had been barely known prior to bioactivity testing. Furthermore, a huge proportion of the papers reviewed were published in non-indexed journals, often resulting in a lack of peer-reviewed processes, which translated into poor scientific standards being applied.

Regarding the number of authors involved in the studies, although the difference between camel urine's bioactivity and metabolome is not large, the authors of the papers on camel urine's bioactivity were more numerous. This finding could be explained on the basis that researchers of a wider range of disciplines are needed to properly investigate the bioactive effects of camel urine from a biomedical perspective. That is, specialists in molecular biology, physiology, biotechnology, and pharmaceutics usually congregate to contribute to the development of such studies. As it could be expected, the main authors of the literature reviewed are affiliated to academic institutions set in countries where camel production is well-established and the Muslim religion is practiced, i.e., where there is a local interest in valuing the camel urine.

Relevant data are frequently missing, namely, regarding the total number of animals sampled (documents not reporting the information; n = 11), their mean age (documents not reporting the information; n = 13), physiological status (documents not reporting the information; n = 10), camel species (documents not reporting the information; n = 8), animal- breeding location (documents not reporting the information; n = 7), and sex (documents not reporting the information; n = 4). As a result, the potential variability in urine's bioactive effects and metabolome, which could be ascribed to an animal's intrinsic and extrinsic factors, cannot be determined and compared across studies. In general, adult virgin, pregnant, and lactating female dromedaries raised in Arabian countries are the most prevalent constituents of animal samples in the literature consulted for both topics, while males continue to be somehow avoided, possibly for socio-cultural preferences biased towards female urine (Haroun, 2015). Furthermore, there is a bias towards the use of dromedary camels rather than Bactrian camels, with just one report on the camel urine metabolome using urine from a female Bactrian camel (Read, 1925).

Overall, the results of the bibliometric analysis illustrate that the sampling methodology is generally limited and the omission of information when publishing results in camel urine-focused research affects the interpretation, reproducibility, and replicability of scientific data (McAlinden, Khadka, & Pesudovs, 2015).

The bioactive effects of camel urine: current status of knowledge

Several studies conducted mainly during the last three decades have provided evidence for the anticancer, cardiovascular, gastroprotective, hepatoprotective, and antimicrobial effects of camel urine (Alebie, Yohannes, & Worku, 2017; Ali, Baby, & Vijayan, 2019; Alkhamees & Alsanad, 2017; Gader & Alhaider, 2016). In this context, although the majority of the analyses have been performed *in vitro*, studies on living subjects also exist (Salamt et al., 2021).

Among the papers considered, five studies tested the *in vitro* effects of camel urine toward murine (Alhaider et al., 2011) and human cell lines (Alhaidar, Abdel Gader, & Mousa, 2011; Alyahya, Gader, & Alhaider, 2016; Al-Ghumlas, 2020; Al-Yousef et al., 2012) and multidrug-resistant strains of *E. coli* (Elbehiry et al., 2021); four research works involved living mice (Alhaider et al., 2014; Al-Harbi et al., 1996; Hu et al., 2017; Mahmoud, Elsaed, & Gabr, 2019); one paper combined *in vitro* and *in vivo* experiments (Anwar et al., 2021); and a theoretical review reported the traditional use of camel urine for the treatment of cancer in a local Algerian population (Taïbi et al., 2020).

The biomedical application that was more frequently investigated was the potential use of camel urine for the treatment of oncological pathologies (n = 4). Still, other properties such as antiplatelet (n = 3), gastro- and hepatoprotective (n = 2), anticlastogenic (n = 2), and antimicrobial (n = 1) effects were also approached. These studies have shown that camel urine has cytotoxic effects against different human (Al-Yousef et al., 2012; Taïbi et al., 2020) and murine (Alhaider et al., 2011) cancer cell lines, in addition to presenting potential towards regulatory-related inflammatory angiogenesis (Alhaider et al., 2014). Moreover, camel urine was reported to inhibit platelet aggregation (Alhaidar, Abdel Gader, & Mousa, 2011; Alyahya, Gader, & Alhaider, 2016; Al-Ghumlas, 2020), to protect against hepatic dysfunction (Mahmoud, Elsaed, & Gabr, 2019), to prevent gastric ulceration (Hu et al., 2017), to act as an anti-clastogenic factor (Anwar et al., 2021; Al-Harbi et al., 1996), and to aid the treatment of certain infectious diseases (Elbehiry et al., 2021).

All the aforementioned studies used whole camel urine as their bioactive substrate, with differences being mainly ascribed to sample processing: raw unprocessed urine (n = 9), lyophilized urine resuspended in PBS immediately before utilization (n = 2), and fresh sterilized urine mixed with distilled water (n = 1).

Anecdotally, the bioactivity of other substrates was also referenced or tested in literature. For instance, Al-Yousef et al. (2012) cited that some patients drink camel urine mixed with camel milk as an unconventional chemotherapeutic regimen for cancer treatment in the Arabian Peninsula, which would be later supported by Gupta et al. (2021) who recently demonstrated the anticancer properties of this traditional practice. Additionally, the bioactive fraction PMF (Prophet Medicine Fraction) and subfraction PMF-K, obtained by fractioning previously lyophilized camel urine (PM701), have been highlighted as selective anticancer (Khorshid, Osman, A.-M.M.; & Abdel-Sattar, 2009; Noor et al., 2015) and antimicrobial (Bakhsh et al., 2019) agents. In line with this, the registered patents for these pharmaceutical formulations state that the fractionation of the total urine will strengthen the efficacy of this animal-derived substance but also its preparation into capsules or combination with nanoparticles so as to help target the cancer tissues without harming the normal ones (Ahmed et al., 2015; Khorshid, 2020). In this regard, the authors also discuss and address the implications of formulation in the enhancement or deterioration of camel urine's bioactivity. Similarly, cow urine has been granted US Patents for its antibiotic, antifungal, and anticancer properties (Mahajan et al., 2020), and human urine is processed to obtain a peptide fraction that is used in the treatment of allergic diseases and autoimmune processes (Márquez-García et al., 2021). In general, the acknowledged bioactive effects of camel urine are hypothetically ascribed to the bioactive compounds present in the desert plants upon which these animals feed (Alkhamees & Alsanad, 2017; Kaul, 1976; Zaki et al., 1984). In parallel, the research postulates that the single-domain antibodies found in camel blood, which present rapid renal clearance, are the main responsible elements for the presumable bioactivity of camel urine (Alhaider et al., 2012; Hamers-Casterman et al., 1993).

Still, these hypotheses need to be further tested through the active work of research groups on camel urine's bioactivity and metabolome. Among other factors, specific attention must be paid to record the information related to the breeding location, production system, and diet of the animals whose urine is intended to be tested for bioactivity and/or characterized for its metabolomes, which is supported by the preliminary conclusions drawn by Ali et al. (2012) and Elkhair (2019), who reported that the free or restricted access to feed and water as well as the nutritional status of the animals may more greatly influence renal function and urine excretion than other factors such as age.

Another methodology-related bias that may extensively affect research outcomes is the lack of knowledge regarding the osmolarity of the camel urine before experimental testing. If we consider the physiological adaptation of camels to desert conditions, their renal physiology is well known to function in favor of water retention and urine concentration. Hence, when highly concentrated urines are tested for bioactivity, toxicity may arise from the osmolarity values that exceed the cells' tolerance limits (Kültz, 2004; Wang, 2015), and not from specific urine's bioactive compounds. Hence, given that the tolerability range to different osmolarity conditions is expected to vary across cell lines (Price, 2017), it can be crucially important to measure urine's osmolarity before experimental testing and to pre-process the samples as needed to adapt the osmotic concentration to the specific cell(s) line(s) under study. Contextually, the evaluation of camel urine prior to studying its properties and inner characteristics such its osmolarity, together with a deeper knowledge of the metabolomic profile, may help researchers study the substrates that better suit the subsequent aims of research and may enhance the development of strategies aimed at functionally valorizing the use of camel urine as an alternative source of potential drugs' discovery and isolation.

Camel urine metabolome: a detailed overview and future prospects for biomedical research

Once the biological activities of whole camel urine are tested and confirmed under the experimental assumptions described in the previous subsection, the following step is the understanding of the relationship between the chemical composition and bioactivity patterns of each urine tested.

Although the use of web-based platforms for the prediction of bioactivity and the associated beneficial effects of chemicals can support the process of new drugs' discovery, it is highly recommended to additionally perform evaluations of key biochemical parameters (i.e., permeability) and design functional assays (*in vitro/in vivo*) given the intrinsic limitations of prediction rates that can sometimes arise from in silico results when approached separately (Johansson et al., 2011; Kumar et al., 2021).

Table 3 lists the metabolites whose presence in camel urine has been reported to date. Generally, urine samples were extracted with organic solvents (Ahamad et al., 2017; El-Nadi & Torki, 2007; Mahmoud, Elsaed, & Gabr, 2019). After derivatization with a silylating reagent, the analytes were identified through GC-MS analysis by comparison with the spectra included in the National Institute of Standard and Technology (NIST) (Ahamad et al., 2017; Salwa et al., 2016) based on a comparison of the unknown analytes' mass spectrum's peaks to those of the peaks in the library's spectra (Match factor > 800) (Khogali et al, 2011). Careful inspection of the analytical methods used (generally roughly described in most of the cited papers) compelled the exclusion of several compounds that were "found" in urine. which were likely food contaminants, artifactual derivatives,

Table 3. List of major metabolites reported to be present in camel urine.

IUPAC Name	References
2-Methylbutanedioic acid	Ahamad et al., 2017; Emwas, Al-Talla, & Kharbatia, 2015; Mahmoud, Elsaed, & Gabr, 2019
Propanedioic acid	Ahamad et al., 2017; Mahmoud, Elsaed, & Gabr, 2019
2-Aminopropanedioic acid	Ahamad et al., 2017; Emwas, Al-Talla, & Kharbatia, 2015; Mahmoud, Elsaed, & Gabr, 2019
(2S,3R)-Butane-1,2,3,4-tetrol	Ahamad et al., 2017; Emwas, Al-Talla, & Kharbatia, 2015; Mahmoud, Elsaed, & Gabr, 2019
(2S)-2-Amino-4-(diaminomethylideneamino)oxybutanoic acid	Ahamad et al., 2017; Mahmoud, Elsaed, & Gabr, 2019
2-Amino-3-methyl-4H-imidazol-5-one	Ahamad et al., 2017; Mahmoud, Elsaed, & Gabr, 2019; Read, 1925
(3R,4S,5R,6R)-6-(Hydroxymethyl)oxane-2,3,4,5-tetrol	Ahamad et al., 2017; Mahmoud, Elsaed, & Gabr, 2019
(2S,4R)-Pentane-1,2,3,4,5-pentol	Ahamad et al., 2017; Mahmoud, Elsaed, & Gabr, 2019
Nonanedioic acid	Ahamad et al., 2017; Khogali et al., 2011; Mahmoud, Elsaed, & Gabr, 2019
2-Benzamidoacetic acid	Ahamad et al., 2017; Emwas, Al-Talla, & Kharbatia, 2015; Mahmoud, Elsaed, & Gabr, 2019; Read, 1925
2-(*N*-Acetylanilino)acetate *	Ahamad et al., 2017; Mahmoud, Elsaed, & Gabr, 2019
(2*R*)-2-[(2*S*,3*R*,4*S*)-3,4-Dihydroxy-5-oxooxolan-2-yl]-2-Hydroxyacetaldehyde	Ahamad et al., 2017; Mahmoud, Elsaed, & Gabr, 2019
Hexadecanoic acid	Ahamad et al., 2017; Mahmoud, Elsaed, & Gabr, 2019
3-Phenylpropanoic acid	Ahamad et al., 2017; Mahmoud, Elsaed, & Gabr, 2019
7-[3,5-Dihydroxy-2-(3-hydroxyoct-1-enyl)cyclopentyl]heptanoic acid	Ahamad et al., 2017; Mahmoud, Elsaed, & Gabr, 2019
5-[(2*S*,3*R*,4*S*,5*R*)-3,4-Dihydroxy-5-(hydroxymethyl)oxolan-2-yl]-1*H*-pyrimidine-2,4-dione	Ahamad et al., 2017; Emwas, Al-Talla, & Kharbatia, 2015; Mahmoud, Elsaed, & Gabr, 2019

Table 3. *Cont.*

IUPAC Name	References
(3*R*,4*S*,5*S*,6*R*)-6-[[(2*S*,3*R*,4*S*,5*R*,6*R*)-3,4,5-Trihydroxy-6-(hydroxymethyl)oxan-2-yl]oxymethyl]oxane-2,3,4,5-tetrol	Ahamad et al., 2017; Mahmoud, Elsaed, & Gabr, 2019
(4*R*,5*R*,6*R*)-6-(Hydroxymethyl)oxane-2,4,5-triol	Ahamad et al., 2017; Mahmoud, Elsaed, & Gabr, 2019
(*E*)-Octadec-9-enoic acid	Ahamad et al., 2017; Khogali et al., 2011; Mahmoud, Elsaed, & Gabr, 2019
2-Hydroxypropanoic acid	Emwas, Al-Talla, & Kharbatia, 2015
Acetic acid	Emwas, Al-Talla, & Kharbatia, 2015; Khogali et al., 2011; Salwa et al., 2016
(2*S*)-2-Aminopropanoic acid	Emwas, Al-Talla, & Kharbatia, 2015
2-Aminoacetic acid	Emwas, Al-Talla, & Kharbatia, 2015
Oxalic acid	Emwas, Al-Talla, & Kharbatia, 2015
2-Methylphenol;3-methylphenol;4-methylphenol	Emwas, Al-Talla, & Kharbatia, 2015
2-Hydroxy-2-methylpropanoic acid	Emwas, Al-Talla, & Kharbatia, 2015
3-Hydroxy-3-methylbutanoic acid	Emwas, Al-Talla, & Kharbatia, 2015
Urea	Emwas, Al-Talla, & Kharbatia, 2015; Read, 1925
Benzoic acid	Emwas, Al-Talla, & Kharbatia, 2015; Khogali et al., 2011; Salwa et al., 2016
2-Phenylacetic acid	Emwas, Al-Talla, & Kharbatia, 2015
Benzene-1,2-diol	Emwas, Al-Talla, & Kharbatia, 2015
2-Hydroxybenzoic acid	Emwas, Al-Talla, & Kharbatia, 2015; Khogali et al., 2011
3-Methylhexanedioic acid	Emwas, Al-Talla, & Kharbatia, 2015

Table 3. *Cont.*

IUPAC Name	References
1-Methylimidazol-2-amine	Emwas, Al-Talla, & Kharbatia, 2015
3-Hydroxybenzoic acid	Emwas, Al-Talla, & Kharbatia, 2015
3-Hydroxy-3-(3-hydroxyphenyl)propanoic acid	Emwas, Al-Talla, & Kharbatia, 2015
Heptanedioic acid	Emwas, Al-Talla, & Kharbatia, 2015
2-[(2-Hydroxybenzoyl)amino]acetic acid	Emwas, Al-Talla, & Kharbatia, 2015
7,9-Dihydro-3*H*-purine-2,6,8-trione	Emwas, Al-Talla, & Kharbatia, 2015
2-[(3-Hydroxybenzoyl)amino]acetatic acid **	Emwas, Al-Talla, & Kharbatia, 2015
(3*S*,4*R*,5*S*)-5-[(1*R*)-1,2-Dihydroxyethyl]oxolane-2,3,4-triol	Emwas, Al-Talla, & Kharbatia, 2015
(2*S*,3*S*,4*S*,5*R*,6*S*)-3,4,5-trihydroxy-6-(4-methylphenoxy)oxane-2-carboxylic acid	Emwas, Al-Talla, & Kharbatia, 2015; Khogali et al., 2011
(2*S*,3*R*,4*S*,5*R*)-3,4,5,6-Tetrahydroxyoxane-2-carboxylic acid	Emwas, Al-Talla, & Kharbatia, 2015
3-Methylheptan-4-one	Khogali et al., 2011; Salwa et al., 2016
Butyl butanoate	Khogali et al., 2011; Salwa et al., 2016
1-*N*,1-*N*,2-*N*,2-*N*-Tetrafluoro-2-methylpropane-1,2-diamine	Salwa et al., 2016
1,1-Dibutoxybutane	Khogali et al., 2011; Salwa et al., 2016
Pentanoic acid	Salwa et al., 2016
Butyl 4-hydroxybenzoate	Salwa et al., 2016
Hydroxylamine	Salwa et al., 2016
(9Z,12Z,15Z)-octadeca-9,12,15-trienoic acid	Salwa et al., 2016
Creatine	Read, 1925
9-Methylanthracene	El-Nadi & Al-Torki, 2007

Table 3. *Cont.*

IUPAC Name	References
1-Methyl-7-propan-2-ylphenanthrene	El-Nadi & Al-Torki, 2007
5-Methyl-6-phenylpyrazine-2,3-dicarbonitrile	El-Nadi & Al-Torki, 2007
1,2-Dichloro-4-ethylbenzene	El-Nadi & Al-Torki, 2007
6,15-Dimethyltricyclo [10.4.0.04,9]hexadeca-1(12),4(9),5,7,13,15-hexaene	El-Nadi & Al-Torki, 2007
2,3,5-Trimethylphenanthrene	El-Nadi & Al-Torki, 2007
1-(2-Hydroxyphenyl)-3-phenylpropane-1,3-dione	El-Nadi & Al-Torki, 2007
1,1-Diphenylprop-1-ene-2-thiol	El-Nadi & Al-Torki, 2007
2,5-Dimethyl-4-oxidopyrazin-1-ium 1-oxide	El-Nadi & Al-Torki, 2007
1-Isothiocyanato-2-methylsulfanylbenzene	El-Nadi & Al-Torki, 2007
Benzo[*f*][1]benzothiole	El-Nadi & Al-Torki, 2007
4-Methyldibenzothiophene	El-Nadi & Al-Torki, 2007
(3*S*,3a*S*,5a*S*,9b*S*)-7-Chloro-3,5a,9-trimethyl-3a,4,5,9b-tetrahydro-3*H*-benzo[*g*][1]benzofuran-2,8-dione	El-Nadi & Al-Torki, 2007
1-Methyl-3,7-dihydropurine-2,6-dione	El-Nadi & Al-Torki, 2007
Bicyclo [4.2.0]octa-1,3,5-triene	El-Nadi & Al-Torki, 2007
9-Azatricyclo [10.4.0.02,7]hexadeca-1(16),2,4,6,12,14-hexaene	El-Nadi & Al-Torki, 2007
1,2,3,4,6,7,8,11,12,12b-Decahydrobenzo[*a*]anthracene	El-Nadi & Al-Torki, 2007
Phenol	Khogali et al., 2011
(E)-3-phenylprop-2-enoic acid	Khogali et al., 2011
Butyl hexadecanoate	Khogali et al., 2011

Compounds in italics are known to have bioactive properties with applications in human health and therapeutics. * As its trimethylsilyl ester; ** Found as its bis-trimethylsilyl derivative.

or compounds coming from the partial degradation of the stationary phases (Si-containing compounds). Only organic compounds were reported, and the heavy metal complexes reported in the original papers as "found" were excluded.

As expected, many of the enlisted metabolites are relatively hydrophilic with their corresponding calculated partition coefficient (cLog*P*) values often being ≤ 0 (Figure 3, panel A; Table S2). This should prevent any systemic pharmacological effect for most of them since cLog*P* values of pharmacologically relevant compounds generally fall within the 0 to 3 cLog*P* range (Oprea, 2000). This inference is in agreement with the very low drug-likeness shown by most of the major constituents in camel urine (cf. Table S2 and panels B and C in Figure 3; Oprea, (2000), Ghose et al. (1999)). A fraction ≥ 75% of the stated metabolites should be endowed with good oral bioavailability since they do not violate the 'Rule of Five' (Ro5) test (Lipinski et al., 1997) and Veber's filter for oral absorption (Veber et al., 2002) (Table S2 and panels D and E in Figure 3). The major components found in camel urine are small molecules (MW = 200±100; Table S2) and 38% of them could be considered as useful fragments to develop rather complex derivatives with good expectations for biological activity since they fulfil the 'Rule of Three' (Ro3) proposed for fragment-based lead discovery (Congreve et al. (2003); panel F in Figure 3). The quality of those fragments is high in most cases as may be inferred from the high fraction of sp^3-hybridized carbon atoms (Fsp^3) found in most of them and the frequent presence of chirality centers. High Fsp^3 and chirality are positively related to the rate of success in clinical development (Panels G and H in Figure 3, and Table S2; Lovering et al. (2009)).

In total, seventy-two compounds detected in camel urine were assumed to be highly abundant. Out of these, twenty-seven were found in at least two of the studies examined. This indicates that these compounds may be present across different urine samples regardless of the intrinsic and extrinsic (dietary and environmental, among others) factors that vary between animals and across species, and thus probably arising from common metabolic pathways.

The evaluation of the urinary metabolomic profile of other species is scarce, specifically if we aim at finding resources in which the bioactive role of urine metabolites is evaluated. Among those twenty-seven metabolites common to camel urine metabolomics studies, seven bioactive compounds are shared with cattle (propanedioic acid, hippuric acid, butanedioic acid, ribitol, D-glucuronic acid, hexadecenoic acid, and prostaglandin f1*α*) (Johansson et al., 2011), two with goats (hippuric acid and glycine) (Contreras-Jodar et al., 2019), one with sheep (creatinine) (Marsden et al., 2020), and four with giraffes (methylsuccinate, benzoate, hippuric acid, and creatinine) (Zhu et al., 2020).

On the other hand, the fact that certain chemicals could only be exclusively found in one study may reflect the potential variability in urine composition and bioactive effects

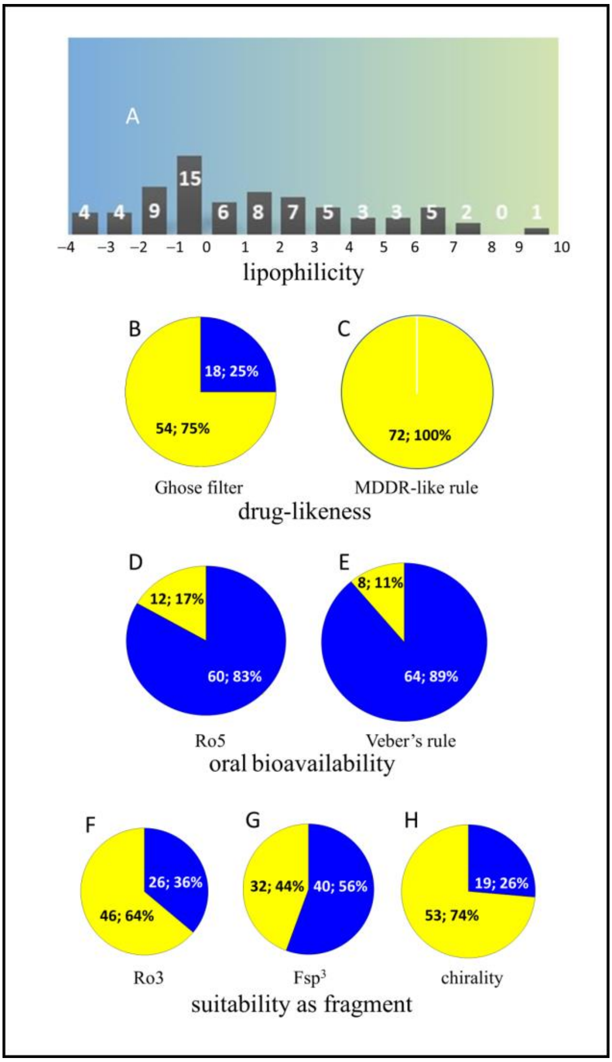


Figure 3. A: distribution of cLogP (ACD/Labs 2020.1.0) in camel urine metabolome; B: number and percentage of camel urine chemicals violating the drug-like Ghose filter [−0.4 < cLog*P* < 5.6, 160 < MW < 480, 40 < molar refractivity (Khogali et al., 2011) < 130, 20 < number of atoms < 70 (Oprea, 2000), yellow sector]; C: number and percentage of camel urine chemicals violating the MACCS-II Drug Data Report (MDDR)-like rule [ring number (RN) ≥ 3, rigid bonds (RBs) ≥ 6, RBs ≥ 18 (Khogali et al., 2011)] for drug-like compounds (yellow area); D: number and percentage of camel urine chemicals fulfilling the Rule of Five's (Ro5) requirements [hydrogen bond donors (HBDs) ≤ 5, hydrogen bond acceptors (HBAs) ≤ 10, MW ≤ 500 Da, cLog*P* ≤ 5 (Ghose, Viswanadhan, & Wendoloski, 1999) for oral bioavailability (blue sector); E: number and percentage of camel urine chemicals fulfilling Veber's rule [polar surface area (PSA) ≤ 140 Å2, rotatable bonds (RBs)≤ 10, HBDs + HBAs ≤ 12 (Lipinski et al., 1997)] for oral bioavailability (blue sector); F: number and percentage of camel urine chemicals fulfilling the Rule of Three's (Ro3) requirements [hydrogen bond donors (HBDs) ≤ 3, hydrogen bond acceptors (HBAs) ≤ 3, MW < 300 Da, cLog*P* ≤ 3 (Veber et al., 2002)] for fragments (blue sector); G: number and percentage of camel urine compounds with a fraction of sp^3-hybridized carbon atoms (Fsp^3) > 0.2 (Congreve et al., 2003) (blue sector); H: number and percentage of chiral compounds found in camel urine.

across different camel subjects, breeds, and populations for animal-related factors influencing metabolism such as sex (Rettenbacher et al., 2004; Touma et al., 2003), age (Poureslami et al., 2010), diet (Contreras-Jodar et al., 2019; Morrow et al., 2022), environmental seasonality (Kuntz et al., 2006; McNab, 2002), composition of gut microbiome (Goymann, 2012; Pusateri et al., 1990), and the kinetics of the reactions leading to the production of metabolites or the time course of metabolism (Jacobson & Gerig, 1988). For these reasons, it is strongly recommended that details on the animals' sex, age, physiological status, rearing conditions (desert-living vs. farming), and diet formulation/composition are provided alongside the animal subjects or groups from which the urine was collected.

Moreover, the compounds detected depend on the analytical strategy employed, from sample preparation to the technique used for compositional profiling (Chetwynd, Dunn, & Rodriguez-Blanco, 2017; Laparre et al., 2017; Sykes, 2007). In the metabolomics studies reviewed, the sample preparation methods included liquid–liquid extraction with organic solvents, such as dichloromethane (Elbehiry et al., 2021; Johansson et al., 2011), diethyl ether (Ahamad et al., 2017), chloroform, and ethanol (Emwas, Al-Talla, & Kharbatia, 2015), or solid phase extraction (Khedr & Khorshid, 2017). Additionally, some studies employed enzymatic treatments to remove urea (Lovering, Bikker, & Humblet, 2009) or to hydrolyze glucuronides and sulphate-conjugated compounds (Khedr & Khorshid, 2017). Naturally, the conditions used in the extraction procedure will significantly affect the obtained compounds. For instance, Ahamad et al. (2017) optimized the extraction solvent and identified several carboxylic acids from which hippuric acid appears in higher concentrations. It should be highlighted that the authors did not perform a quantitative analysis. On the other hand, El-Nadi and Al-Torki (2007) used a less polar solvent and naturally identified less polar compounds, mainly aromatic derivatives. Additionally, knowing that some more abundant compounds can hinder the observation of other metabolites, some authors employed enzymatic treatments to remove urea (Lovering, Bikker, & Humblet, 2009) or to hydrolyze glucuronides and sulphate-conjugated compounds (Khedr & Khorshid, 2017). One of those examples is the work of Khedr and Khorshid (2017), where the authors were able to quantify some phenolic compounds, including interesting bioactive compounds such as salicylic and cinnamic acids, in camel urine after a pre-treatment with β-glucuronidase aryl-sulphatase.

Regarding the analytical platform used, all studies employed gas chromatography coupled with mass spectrometry (GC-MS). Some studies analyzed only volatile compounds (Elkhair, 2019; Khogali et al., 2011), whereas others included a derivatization step, mostly silylation, to detect less volatile metabolites such as amino acids and phenolic compounds (Johansson et al., 2011; Khedr & Khorshid, 2017; Lovering, Bikker, & Humblet, 2009). An important limitation of these works is that they did not report accurate quantification data. Indeed, as far as we could perceive, none used the internal standard method, which is the most recommended approach in MS-based analysis to compensate for variable response factors arising from matrix effects.

As mentioned before, sample derivatization prior to GC-MS enables the range of detected compounds to be enlarged. However, it often implies the use of lengthy procedures, which may hinder reproducibility and introduce artifacts that complicate data analysis. Techniques such as LC-MS and NMR spectroscopy represent attractive alternatives for analyzing the urinary non-volatile metabolic profile. To our knowledge, their application to the study of camel urine has not been reported yet, although they have been widely employed in the analysis of human urine, as recently reviewed elsewhere (Silva et al., 2020; Rodriguez-Morato, Pozo, & Marcos, 2018). Benefiting from important advances in separation technologies, such as HILIC (hydrophilic chromatographic separation), which allows for the improved separation of highly polar compounds, and UPLC (ultra-performance LC), which enables significant improvements in sensitivity, LC-MS offers great advantages for urinary analysis. As for NMR, although it has lower sensitivity (sub-mM) than MS-based methods (<pM) (and thus a lower metabolome coverage), its associated simple sample preparation protocols, non-destructive nature, unparalleled reproducibility, and inherently quantitative power represent attractive features that justify its continued application in the metabolic profiling of complex biofluids such as urine. Hence, future applications of LC-MS and/or NMR profiling to the study of camel urine are expected to significantly complement the GC-MS studies already reported and to disclose significant new information on urinary metabolites.

In this context, the standardization of the techniques used for the study of the metabolomic profile of camel urine, linked to the increase in the sample variability, would allow for the statistical analysis of the potential influence of the different abovementioned animal-related factors on the excreted metabolites. Concerning diet, given that the majority of the studies that report a significant effect of diet on the metabolites excreted are performed under laboratory conditions with animals fed with relatively standardized diets, it can be expected that there will be pronounced differences found regarding the kind and proportion of metabolites excreted in animals that are allowed to freely graze and thus have more variable diets (Pusateri et al., 1990), such as camels. Similar to the recently published review on camel milk's bioactive peptides (Redha et al., 2021), we explored the literature on the main sources and biological effects for each chemical found in camel urine (Supplementary Table S2). The most-reported compounds are plant structural compounds or metabolites and products of bacterial metabolism. Their main applications can be summarized under the following categories: plastic fabrics, cosmetics, food additives/preservatives, anticancer agents, analgesic/anti-inflammatory compounds, and biocides. In general, the most commonly reported uses can be classified within the first three categories. Nonetheless, more *in vivo* evidence is needed to further recognize the potential industrial/pharmacological uses of all these chemicals, together with a wider knowledge of the possible interactions/interferences between urine compounds.

To the best of our knowledge, the metabolomic profiling of camel urine followed by bioactive testing has only been performed in one study, which addressed the protective role of camel urine against carbon tetrachloride-induced liver toxicity (Elbehiry et al., 2021). Instead, the seven additional papers considered were isolated evaluations of the metabolomic profile of camel urine, without a posterior evaluation of its potential bioactive effects. It is also interesting to note that, as for urine bioactivity-related research, a sex bias is widely present in metabolomic studies, since the majority (n = 6) of these studies characterized female camel urine, and the rest (n = 2) did not indicate the sex of the sampled animals.

Furthermore, taking into consideration the reported absence of genetic toxicity related to the intake of camel urine (Alhaider et al., 2014; Khorshid et al., 2015; Osman, 2010), its low content of urea and ammonia (the main compounds responsible for the characteristic odor of the biofluid), and its rich mineral salt composition and higher concentration in comparison with the urine from other mammals (Al-Yousef et al., 2012), the exploration of the unique chemical constituents of camel urine and their different molecular mechanisms of action against different pathological conditions should be considered as an emerging strategy deserving further study concerning the assessment of camel urine exploitation as a natural source for the discovery and isolation of new chemicals with valuable pharmaceutical potential.

The motivation of the present research is not to promote the consumption of raw camel urine, but to value its role as a source for specific molecules with bioactive potential, which can also be safety-evaluated with respect to medicinal chemistry and drug discovery in a public health scenario. Indeed, the Shia code explicitly asks for caution in the consumption of urine from animals. According to Islamic laws in reference to the use of medicines from halal sources, “it is haraam to drink the urine of all haraam animals, and also of those whose meat is halal to eat, including, as an obligatory precaution, that of a camel. However, the urine of a camel, a cow or a sheep can be consumed, if recommended for any medical treatment” (Alim, Marselina, & Rais, 2020; Kashim et al., 2019).

This is supported by the fact that camel urine has been compared to other drugs since more than a decade ago. Contextually, Kabarity et al. (1988) reported camel urine’s cytotoxic effect to be comparable with that of cyclophosphamide, a standard drug used in cancer chemotherapy. However, these and other authors reported the absence of a significant clastogenic effect from consuming camel urine, namely, a mitodepressive effect. Indeed, as suggested before by Anwar et al. (2021) the lack of such a clastogenic effect may be dose-dependent in light of their finding of 25 and 50 mL/kg of camel urine treatment significantly improving the cyclophosphamide-induced clastogenic effect, while the mitodepressive effect may necessitate a rather reduced concentration.

Additionally, regarding the protective effects of camel urine against peptic ulcers, Salamt et al. (2021) suggested that a treatment of 5 mL/kg of camel urine results in 100% ulcer inhibition in HCl/EtOH and WRS models, which was reduced to 66.7% in an indomethacin model. Furthermore, there was a 100% healing rate (no ulcers observed) in indomethacin-induced gastric damage (healing model) compared with cimetidine, which only resulted in a 60.5% healing rate. However, the doses of camel urine currently suggested as effective cannot be accurate since the methodological approaches have been a single run instead of an iterative process (five steps or phases), which is the accepted standardized strategy for drug development in medicinal chemistry.

Thus, despite the aforementioned assessment of the bioactivity and putative beneficial effects of camel urine towards oncological, cardiovascular, digestive, and infectious pathologies, substantial knowledge gaps have been identified within the scientific literature on the subject. The reduced sample size and high variability, along with the non-indication of specific intrinsic and extrinsic factors and the disregard for urine's properties such as its osmolarity, could lead to the misinterpretation of the bioactive effects of camel urine, hence leading researchers to formulate biased conclusions. Furthermore, as the metabolome of this animal-derived secretion is hardly determined before bioactivity assays, potentially bioactive small molecules cannot be proposed and used for validation tests. Among other factors, the preliminary physical–chemical status of the urines when used for bioactivity or metabolomics analysis (i.e., lyophilized) should be further studied and considered as an influencing factor given its potential conditioning effects on research outputs. Consequently, future research initiatives should focus on disentangling the multi-etiological background of the camel urine metabolome and its specific potential implications for public health promotion through preclinical studies aimed at testing the bioactivity of the individual molecules contained in the urine of these animals but that, in any case, do not promote the consumption of this biological fluid in a raw status. Different approaches may be useful in this respect, including tandem metabolite profiling and bioactivity screening of whole urines or their selected fractions to identify bioactive candidates. Ideally, this should then be followed by assessments of individual compounds to validate their putative biological effects *in vitro* and *in vivo*. This may allow for the determination of dose-dependent effects, safety levels, and the potential inclusion of specific metabolites in the formulation of new drugs.

Conclusions

Although the research addressing camel urine has existed for more than a century, large time gaps have occurred until the present. The clear lack of connection between metabolomics strategies and camel urine's composition and bioactivity has translated into the limited knowledge of this important biological matrix. Most of the scarce articles published in this context have emerged from few countries and have been published in journals with ethnopharmacology and biological chemistry scopes. Still, the importance of the subject has been duly recognized; as such, the publications have tended to reach high impact levels. According to the current knowledge, a considerably larger number of bioactive metabolites can be found in camel urine compared to that of other affine species. This explains the patent interest in the topic within the scientific community, especially in fields related to potential human benefits or drawbacks derived from the use of camel urine (e.g., anticancer, cardiovascular, gastroprotective, hepatoprotective, and antimicrobial effects, among others). Among the main limitations of the research work developed to date, sampling-related problems and the omission of information have been identified as significantly affecting the interpretation, reproducibility, and replicability of data. In addition, a larger number of *in vivo* studies may need to be implemented in contrast to *in vitro* studies. Particularly, osmolarity and alkalinity parameters need to be controlled prior to the undertaking of research aiming at testing bioactivity. All in all, enhanced multidisciplinary, comprehensive studies are required to evaluate the implication of intrinsic and extrinsic factors in camel urine's composition and properties, thus enabling the determination of the conditions and levels at which bioactivity is developed to ensure future reliable applications of camel urine's components in biomedicine.

Supplementary materials: The supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/ijms232315024/s1. (See Royston (1991)).

Author contributions: Conceptualization, L.G and E.C.; methodology, C.I.P., M.N.S. and G.L.; software, C.I.P., M.N.S. and G.L.; validation, J.V.D.B., F.J.N.G., E.C., L.G., D.C.G.A.P., A.M.G. and I.F.D.; formal analysis, C.I.P., F.J.N.G. and G.L.; investigation, C.I.P., M.N.S., L.G., D.C.G.A.P., A.M.G., I.F.D. and G.L.; resources, C.I.P., J.V.D.B., F.J.N.G., E.C., L.G. and G.L.; data curation, C.I.P., M.N.S., F.J.N.G. and G.L.; writing—original draft preparation, C.I.P., M.N.S., I.F.D. and G.L.; writing—review and editing, J.V.D.B., F.J.N.G., L.G., E.C., I.F.D. and G.L.; visualization, E.C., L.G., I.F.D. and G.L.; supervision, J.V.D.B., F.J.N.G., E.C., L.G. and G.L.; project administration, J.V.D.B., E.C., I.F.D. and G.L.; funding acquisition, J.V.D.B., E.C. and I.F.D. All authors have read and agreed to the published version of the manuscript.

Funding: The present research was carried out in the financing framework of the international project CA.RA.VA.N–"Toward a Camel Transnational Value Chain" (Reference APCIN-2016-00011-

00-00) and during the covering period of a predoctoral contract (FPU Fellowship) funded by the Spanish Ministry of Science and Innovation. This work was also developed within the scope of the projects CICECO-Aveiro Institute of Materials (UIDB/50011/2020, UIDP/50011/2020 & LA/P/0006/2020) and LAQV-REQUIMTE (UIDB/50006/2020), financed by national funds through the FCT/MEC (PIDDAC).

Data availability statement: The data presented in this study are available on request from the first author.

Conflicts of interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Abdelzaher, H.M., Alsuhaymi, M., Alshammari, F.M., Alshammari, S.A., & Alshammari, Z.M. (2020). Evaluation of the effectiveness of virgin camel's urine as antifungal agents. *Journal of Bacteriology and Mycology*, 8, 124–128.

Ahamad, S.R., Alhaider, A.Q., Raish, M., & Shakeel, F. (2017). Metabolomic and elemental analysis of camel and bovine urine by GC–MS and ICP–MS. *Saudi Journal of Biological Sciences*, 24, 23–29.

Ahmed, G.A., Khorshid, F.A., Khedr, A., El-Hamidy, S.M., & Salah, N.A. (2015). The effect of PMF Camel Urine Nanoparticles on A549 Cells: The Mechanism of Action and Drug Delivery. *Life Sciences*, 12, 63–75.

Ajiboye, T.O., Ogunbiyi, O.D., Omotola, E.O., Adeyemi, W.J., Agboola, O.O., & Onwudiwe, D.C. (2022). Urine: Useless or useful "waste"? *Results in Engineering*, 16, 100522.

Alebie, G., Yohannes, S., & Worku, A. (2017). Therapeutic applications of camel's milk and urine against cancer: Current development efforts and future perspectives. *Journal of Cancer Sciences and Therapy*, 9, 468–478.

Alhaidar, A., Abdel Gader, A.G.M., & Mousa, S.A. (2011). The antiplatelet activity of camel urine. *Journal of Alternative and Complementary Medicine*, 17, 803–808.

Alhaider, A.A., El Gendy, M.A., Korashy, H.M., & El-Kadi, A.O. (2011). Camel urine inhibits the cytochrome P450 1a1 gene expression through an AhR-dependent mechanism in Hepa 1c1c7 cell line. *Journal of Ethnopharmacology*, 133, 184–190.

Alhaider, A.A., Bayoumy, N., Argo, E., Gader, A.G., & Stead, D.A. (2012). Survey of the camel urinary proteome by shotgun proteomics using a multiple database search strategy. *Proteomics*, 12, 3403–3406.

Alhaider, A.A., Gader, A.G.M.A., Almeshal, N., & Saraswati, S. (2014). Camel urine inhibits inflammatory angiogenesis in murine sponge implant angiogenesis model. *Biomedicine & Aging Pathology*, 4, 9–16.

Ali, A., Baby, B., & Vijayan, R. (2019). From desert to medicine: A review of camel genomics and therapeutic products. *Frontiers in Genetics*, 10, 17.

Ali, M.A., Adem, A., Chandranath, I.S., Benedict, S., Pathan, J.Y., Nagelkerke, N., Nyberg, F., Lewis, L.K., Yandle, T.G., & Nicholls, G.M. (2012). Responses to dehydration in the one-humped camel and effects of blocking the renin-angiotensin system. *PLoS ONE*, 7, e37299.

Alim, A.P., Marselina, T., & Rais, Z. (2020). The Advantages of Wudhu for Some Contemporary Problems. *Maddika: Journal of Islamic Family Law*, 1, 25–38.

Alkhamees, O.A., & Alsanad, S.M. (2017). A review of the therapeutic characteristics of camel urine. *African Journal of Traditional, Complementary and Alternative Medicines*, 14, 120–126.

Alyahya, A.M., Gader, A.G.M.A., & Alhaider, A.A. (2016). Characterization of inhibitory activity of camel urine on human platelet function. *Journal of Taibah University Medical Sciences*, 11, 26–31.

Al-Abdalall, A.H.A. (2010). The inhibitory effect of camels urine on mycotoxins and fungal growth. *African Journal of Agricultural Research*, 5, 1331–1337.

Al-Ghumlas, A.K. (2020). Camel platelet aggregation responses and the antiplatelet effect of camel urine: Comparison between black and white camels. *Heliyon*, 6, e05353.

Al-Harbi, M., Qureshi, S., Ahmed, M., Raza, M., Baig, M., & Shah, A. (1996). Effect of camel urine on the cytological and biochemical changes induced by cyclophosphamide in mice. *Journal of Ethnopharmacology*, 52, 129–137.

Al-Yousef, N., Gaafar, A., Al-Otaibi, B., Al-Jammaz, I., Al-Hussein, K., & Aboussekhra, A. (2012). Camel urine components display anti-cancer properties in vitro. *Journal of Ethnopharmacology*, 143, 819–825.

Anwar, S., Ansari, S.A., Alamri, A., Alamri, A., Alqarni, A., Alghamdi, S., Wagih, M.E., Ahmad, A., & Rengasamy, K.R. (2021). Clastogenic, anti-clastogenic profile and safety assessment of Camel urine towards the development of new drug target. *Food and Chemical Toxicology*, 151, 112131.

Armstrong, J.W. (1944). *The Water of Life: A Treatise on Urine Therapy*: Health Science Press, Elsevier.

Bakhsh, R.S., Noor, S.O., Khorshid, F.A.R., Ahmed, F., Alsulaimany, A.A., Najjar, A.A., & Al-Hejin, A. (2019). The antibacterial activity of a fraction extracted from camel urine against mycobacterium tuberculosis isolated from tuberculosis patients in Jeddah City. *Advances in Environmental Biology*, 13, 1–6.

Beacock, M. (2012). Does eating placenta offer postpartum health benefits? *British Journal of Midwifery*, 20, 464–469.

Booth, A., Sutton, A., & Papaioannou, D. (2016). *Systematic Approaches to a Successful Literature Review*: SAGE.

Campbell, N., He, F., Cappuccio, F., & MacGregor, G. (2021). Dietary Sodium 'Controversy'—Issues and Potential Solutions. *Current Nutrition Reports*, 10, 188–199.

Casquero, M.A.M. (2005). Virtudes mágicas y medicinales de la orina según los escritores latinos (1ª parte). *Estudios Humanísticos-Filología*, 27, 139–170.

Casquero, M.A.M. (2006). Virtudes mágicas y medicinales de la orina según los escritores latinos (2ª parte). *Estudios Humanísticos-Filología*, 28, 49–72.

Chetwynd, A.J., Dunn, W.B., & Rodriguez-Blanco, G. (2017). Collection and preparation of clinical samples for metabolomics. *Metabolomics: from fundamentals to clinical applications*, 965, 19–44.

Christy, M. (1994). *Your Own Perfect Medicine*: Scottsdale Arizona, Inc.

Congreve, M., Carr, R., Murray, C., & Jhoti, H. (2003). A 'rule of three' for fragment-based lead discovery? *Drug Discovery Today*, 8, 876–877.

Contreras-Jodar, A., Nayan, N.H., Hamzaoui, S., Caja, G., & Salama, A.A. (2019). Heat stress modifies the lactational performances and the urinary metabolomic profile related to gastrointestinal microbiota of dairy goats. *PLoS ONE*, 14, e0202457.

Corp., I. (2017). *IBM SPSS Statistics for Windows (Version 25.0)*. Armonk, NY: IBM Corp.

Cuenca-Estrella, M., & Martín, R.B. (2004). *La medicina en el Antiguo Egipto*: Alderabán Ediciones.

Eldor, J. (1997). Urotherapy for patients with cancer. *Medical Hypotheses*, 48, 309–315.

Elbehiry, A., Marzouk, E., Moussa, I.M., Alenzi, A., Al-Maary, K.S., Mubarak, A.S., Alshammari, H.D., Al-Sarar, D., Alsubki, R.A., & Hemeg, H.A. (2021). Multidrug-resistant *Escherichia coli* in Raw Milk: Molecular Characterization and the potential impact of camel's Urine as an Antibacterial Agent. *Saudi Journal of Biological Sciences*, 28, 2091–2097.

Elkhair, N.M. (2019). Effect of age on certain urine parameters of young camels (*Camelus dromedarius*). *Online Journal of Animal and Feed Research*, 9, 33–37.

El-Nadi, A., & Al-Torki, A. (2007). Chemical and biochemical composition of pregnant camel urine (*Camelus dromedarius*). *International Journal of Biotechnology*, 4, 433–434.

El-Reash, A.A., Hamama, H., Eldars, W., Lingwei, G., Zaen El-Din, A.M., & Xiaoli, X. (2019). Antimicrobial activity and pH measurement of calcium silicate cements versus new bioactive resin composite restorative material. *BMC Oral Health*, 19, 235.

Emwas, A.-H.M., Al-Talla, Z.A., & Kharbatia, N.M. (2015). Sample collection and preparation of biofluids and extracts for gas chromatography–mass spectrometry. In *Metabonomics* (pp. 75–90): Springer.

Faye, B. (2013). Camel farming sustainability: The challenges of the camel farming system in the XXIth century. *Journal of Sustainable Development*, 6, 74.

Gader, A.G.M.A., & Alhaider, A.A. (2016). The unique medicinal properties of camel products: A review of the scientific evidence. *Journal of Taibah University Medical Sciences*, 11, 98–103.

García, A.F. (2006). La orina en las recetas de los alquimistas griegos: Papiro X de Leiden y Papiro de Estocolmo. *Estudios Clásicos*, 48, 65–78.

Garfield, E. (2006). The history and meaning of the journal impact factor. *Journal of the American Medical Association*, 295, 90–93.

Ghose, A.K., Viswanadhan, V.N., & Wendoloski, J.J. (1999). A knowledge-based approach in designing combinatorial or medicinal chemistry libraries for drug discovery. 1. A qualitative and quantitative characterization of known drug databases. *Journal of Combinatorial Chemistry*, 1, 55–68.

Gole, F.A., & Hamido, A.J. (2020). Review on health benefits of camel urine: Therapeutics effects and potential impact on public health around east hararghe district. *American Journal of Pure and Applied Biosciences*, 2, 183–191.

Goymann, W. (2012). On the use of non-invasive hormone research in uncontrolled, natural environments: The problem with sex, diet, metabolic rate and the individual. *Methods in Ecology and Evolution*, 3, 757–765.

Gupta, I., Shanmuganathan, S., Al-Abri, H., & Ouhtit, A. (2021). Molecular evidence of anticancer activity of camel milk combined with camel urine. *Austin Journal of Cancer and Clinical Research*, 8, 1093.

Gusenbauer, M., & Haddaway, N.R. (2020). Which academic search systems are suitable for systematic reviews or meta-analyses? Evaluating retrieval qualities of Google Scholar, PubMed, and 26 other resources. *Research Synthesis Methods*, 11, 181–217.

Hamers-Casterman, C., Atarhouch, T., Muyldermans, S.a., Robinson, G., Hammers, C., Songa, E.B., Bendahman, N., & Hammers, R. (1993). Naturally occurring antibodies devoid of light chains. *Nature*, 363, 446–448.

Haroun, E.M.H.K. (2015). *Effects of Type of Nutrition on the Chemical Composition of Camel Milk and Urine*: University of Gezira, Wad Madani, Republic of the Sudan.

Hernandes, V.V., Barbas, C., & Dudzik, D. (2017). A review of blood sample handling and pre-processing for metabolomics studies. *Electrophoresis*, 38, 2232–2241.

Hu, Z., Chang, X., Pan, Q., Gu, K., & Okechukwu, P.N. (2017). Gastroprotective and ulcer healing effects of camel milk and urine in HCl/EtOH, non-steroidal anti-inflammatory drugs (indomethacin), and water-restraint stress-induced ulcer in rats. *Pharmacognosy Magazine*, 13, 559.

Iglesias Pastrana, C., Navas González, F.J., Ciani, E., Barba Capote, C.J., & Delgado Bermejo, J.V. (2020). Effect of research impact on emerging camel husbandry, welfare and social-related awareness. *Animals*, 10, 780.

Jacobson, A., & Gerig, J. (1988). Metabolism of profluralin in rats. 1. Identification of metabolites. *Chemical Research in Toxicology*, 1, 304–311.

Johansson, U., Sönströd, C., Norinder, U., & Boström, H. (2011). Trade-off between accuracy and interpretability for predictive in silico modeling. *Future Medicinal Chemistry*, 3, 647–663.

Joseph, S., Karnik, S., Nilawe, P., Jayaraman, V.K., & Idicula-Thomas, S. (2012). ClassAMP: A prediction tool for classification of antimicrobial peptides. *EEE/ACM Transactions on Computational Biology and Bioinformatics*, 9, 1535–1538.

Kabarity, A., Mazrooei, S., & Elgindi, A. (1988). Camel urine as a possible anticarcinogenic agent. *Arab Gulf Journal of Scientific Research*, 6, 55.

Kashim, M., Mohamad, M.N., Sukor, A.S.A., Adnan, N.I.M., Safiai, M.H., & Jamsari, E.A. (2019). Animal urine therapy according to Islamic and scientific perspectives. *International Journal of Civil Engineering and Technology*, 10, 2280–2286.

Kaul, V. (1976). Antimicrobial activities of the essential oils of *Artemisia absinthium* Linn, *Artemisia vestita* Wall, and *Artemisia vulgaris* Linn. *Indian Journal of Pharmacology*, 38, 21–22.

Khedr, A., & Khorshid, F. (2017). Characterization and Determination of Major Bioactive Acids in Camel Urine Using Gas Chromatography Mass-spectrometry. *Indian Journal of Pharmaceutical Sciences*, 78, 680–687.

Khogali, S.M., Abdalrahman, S.H., Musa, E.M., & El, A.M. (2011). Gas chromatography mass spectrophotometry (gc-ms) analysis of female camel urine extracts. Proceedings of the Camel Conference, SOAS.

Khorshid, F.A., Osman, A.-M.M., & Abdel-Sattar, E. (2009). Cytotoxic activity of bioactive fractions from pm 701. *Electronic Journal of Environmental, Agricultural and Food Chemistry*, 8, 1091–1098.

Khorshid, F., Rabah, S., Abuaraki, H., Ali, A., Noor, S., & Alkabkaby, H. (2015). Safety of Oral Administration of PMF a Fraction Derived From Camel Urine: Acute Study on Mice. *International Journal of Emerging Technology and Advanced Engineering*, 5, 365–370.

Khorshid, F.A. (2020). *Separation and Formulation of Bioactive Fraction and Subfraction from Camel Urine Works as Anticancer Agent*. United States patent US, 10, 624, 927.

Khoruts, A., & Brandt, L.J. (2019). Fecal microbiota transplant: A rose by any other name. *Official journal of the American College of Gastroenterology*, 2019, 114, 1176.

Kültz, D. (2004). Hyperosmolality triggers oxidative damage in kidney cells. *Proceedings of the National Academy of Sciences*, 101, 9177–9178.

Kumar, R., Ali, S.A., Singh, S.K., Bhushan, V., Kaushik, J.K., Mohanty, A.K., & Kumar, S. (2021). Peptide profiling in cow urine reveals molecular signature of physiology-driven pathways and in-silico predicted bioactive properties. *Scientific Reports*, 11, 12427.

Kuntz, R., Kubalek, C., Ruf, T., Tataruch, F., & Arnold, W. (2006). Seasonal adjustment of energy budget in a large wild mammal, the Przewalski horse (*Equus ferus przewalskii*) I. Energy intake. *Journal of Experimental Biology*, 209, 4557–4565.

Laparre, J., Kaabia, Z., Mooney, M., Buckley, T., Sherry, M., Le Bizec, B., & Dervilly-Pinel, G. (2017). Impact of storage conditions on the urinary metabolomics fingerprint. *Analytica Chimica Acta*, 951, 99–107.

Lipinski, C.A., Lombardo, F., Dominy, B.W., & Feeney, P.J. (1997). Experimental and computational approaches to estimate solubility and permeability in drug discovery and development settings. *Advanced Drug Delivery Reviews*, 23, 3–25.

Lovering, F., Bikker, J., & Humblet, C. (2009). Escape from flatland: Increasing saturation as an approach to improving clinical success. *Journal of Medicinal Chemistry*, 52, 6752–6756.

Mahajan, S.P., Chavan, S.A., Shinde, S.A., & Narkhede, M.B. (2020). Miraculous Benefits of Cow Urine: A Review. *Journal of Drug Delivery and Therapeutics*, 10, 275–281.

Mahmoud, H.S., Elsaed, W.M., & Gabr, S.A. (2019). Camel urotherapy and hepatoprotective effects against carbon tetrachloride-induced liver toxicity. *International Journal of Pharmacology*, 15, 696–705.

Márquez-García, J., Hernández-Doño, S., Ceja-Mendoza, M., Pedraza-Jiménez, M., García-Rivas, M., Martínez-Escobar, L., Fragoso-Sánchez, A., de la Cruz, L.M., & Granados, J. (2021). Cytokines and growth factors in a biologic product obtained from patients' urine as immune-modulators to treat autoimmune and allergic diseases. *Cytokine*, 141, 155427.

Marsden, K.A., Lush, L., Holmberg, J.A., Whelan, M.J., King, A.J., Wilson, R.P., Charteris, A.F., Cardenas, L.M., Jones, D.L., & Chadwick, D.R. (2020). Sheep urination frequency, volume, N excretion and chemical composition: Implications for subsequent agricultural N losses. *Agriculture, Ecosystems & Environment*, 302, 107073.

McAlinden, C., Khadka, J., & Pesudovs, K. (2015). Precision (repeatability and reproducibility) studies and sample-size calculation. *Journal of Cataract & Refractive Surgery*, 41, 2598–2604.

McLean, A.K., & Gonzalez, F.J.N. (2018). Can scientists influence donkey welfare? Historical perspective and a contemporary view. *Journal of Equine Veterinary Science*, 65, 25–32.

McNab, B.K. (2002). *The Physiological Ecology of Vertebrates: A View from Energetics*: Cornell University Press.

Mills, M., & Faunce, T. (1991). Melatonin supplementation from early morning auto-urine drinking. *Medical Hypotheses*, 36, 195–199.

Mok, C.K.P., Zhu, A., Zhao, J., Lau, E.H., Wang, J., Chen, Z., Zhuang, Z., Wang, Y., Alshukairi, A.N., & Baharoon, S.A. (2021). T-cell responses to MERS coronavirus infection in people with occupational exposure to dromedary camels in Nigeria: An observational cohort study. *Lancet Infectious Diseases*, 21, 385–395.

Morrow, C.J., Kolver, E.S., Verkerk, G.A., & Matthews, L.R. (2002). Fecal glucocorticoid metabolites as a measure of adrenal activity in dairy cattle. *General and Comparative Endocrinology*, 126, 229–241.

Nalbantoglu, S. (2019). Metabolomics: Basic principles and strategies. *Molecular Medicine*, 10.

Noor, S.O., AlAttas, S.G., Khorshid, F.K., Elsourojy, Y.A., & Tawfik, N. (2015). In vitro Evaluation of Cytotoxicity, Antiviral and Activity of PMF Derived from Camel Urine. Proceedings of the International Conference on Energy, Environment and Material Science (EEMAS).

Oprea, T.I. (2000). Property distribution of drug-related chemical databases. *Journal of Computer-Aided Molecular Design*, 14, 251–264.

Osman, A.-M. (2010). Dose escalation phase I study in healthy volunteers to evaluate the safety of a natural product PM701. *Journal of Pharmacology and Toxicology*, 5, 91–97.

Page, M.J., McKenzie, J.E., Bossuyt, P.M., Boutron, I., Hoffmann, T.C., Mulrow, C.D., Shamseer, L., Tetzlaff, J.M., Akl, E.A., Brennan, S.E., Chou, R., Glanville, J., Grimshaw, J.M., Hróbjartsson, A., Lalu, M.M., Li, T., Loder, E.W., Mayo-Wilson, E., McDonald, S., McGuinness, L.A., Stewart, L.A., Thomas, J., Tricco, A.C., Welch, V.A., Whiting, P., & Moher, D. (2021). The PRISMA 2020 statement: An updated guideline for reporting systematic reviews. *International Journal of Surgery*, 10, 1–11.

Patwardhan, B., & Khambholja, K. (2011). Drug discovery and Ayurveda: Win-win relationship between contemporary and ancient sciences. In *Drug Discovery and Development–Present and Future*: IntechOpen.

Piasecki, J., Waligora, M., & Dranseika, V. (2018). Google search as an additional source in systematic reviews. *Science and Engineering Ethics*, 24, 809–810.

Plinio. (2007). *Historia Natural* (2nd ed.) (Cantó, J., Santamaria, I.G., Marín, S.G., Tarriño, E., Eds.): Cátedra.

Poureslami, R., Turchini, G., Raes, K., Huyghebaert, G., & De Smet, S. (2010). Effect of diet, sex and age on fatty acid metabolism in broiler chickens: SFA and MUFA. *British Journal of Nutrition*, 104, 204–213.

Price, P.J. (2017). Best practices for media selection for mammalian cells. *In Vitro Cellular & Developmental Biology - Animal*, 53, 673–681.

Pusateri, D.J., Roth, W.T., Ross, J.K., & Shultz, T.D. (1990). Dietary and hormonal evaluation of men at different risks for prostate cancer: Plasma and fecal hormone-nutrient interrelationships. *American Journal of Clinical Nutrition*, 51, 371–377.

Read, B.E. (1925). Chemical constituents of camel's urine. *Journal of Biological Chemistry*, 64, 615–617.

Redha, A.A., Valizadenia, H., Siddiqui, S.A., & Maqsood, S. (2021). A state-of-art review on camel milk proteins as an emerging source of bioactive peptides with diverse nutraceutical properties. *Food Chemistry*, 273, 131444.

Rettenbacher, S., Möstl, E., Hackl, R., Ghareeb, K., & Palme, R. (2004). Measurement of corticosterone metabolites in chicken droppings. *British Poultry Science*, 45, 704–711.

Rodriguez-Morato, J., Pozo, Ó.J., & Marcos, J. (2018). Targeting human urinary metabolome by LC–MS/MS: A review. *Bioanalysis*, 10, 489–516.

Royston, P. (1991). Estimating departure from normality. *Statistics in Medicine*, 10, 1283–1293.

Ridley, D. (2012). *The Literature Review: A Step-by-Step Guide for Students*: SAGE.

Salamt, N., Idrus, R.B.H., Kashim, M.I.A.M., & Mokhtar, M.H. (2021). Anticancer, antiplatelet, gastroprotective and hepatoprotective effects of camel urine: A scoping review. *Saudi Pharmaceutical Journal*, 29, 740–750.

Salwa, M., Bdalla, E., Mohamed, S., & Barajob, A. (2016). Novel Compounds in Lyophilized Female Camel Urine. *Journal of Infectious Diseases & Therapy*, 4, 296.

Savica, V., Calò, L.A., Santoro, D., Monardo, P., Mallamace, A., & Bellinghieri, G. (2011). Urine therapy through the centuries. *Journal of Nephrology*, 24, S123–S125.

Sharma, A., Gupta, P., Kumar, R., & Bhardwaj, A. (2016). dPABBs: A novel in silico approach for predicting and designing anti-biofilm peptides. *Scientific Reports*, 6, 21839.

Silva, J.A.M. (2010). A medicina na Mesopotâmia antiga (2ª parte). *Acta Médica Portuguesa*, 23, 125–140.

Silva, R.A., Pereira, T.C., Souza, A.R., & Ribeiro, P.R. (2020). 1H NMR-based metabolite profiling for biomarker identification. *Clinica Chimica Acta*, 502, 269–279.

Stanhope, K.L. (2016). Sugar consumption, metabolic disease and obesity: The state of the controversy. *Critical Reviews in Clinical Laboratory Sciences*, 53, 52–67.

Suarez, M., Caimari, A., del Bas, J.M., & Arola, L. (2017). Metabolomics: An emerging tool to evaluate the impact of nutritional and physiological challenges. *Trends in Analytical Chemistry*, 96, 79–88.

Suhre, K., & Gieger, C. (2012). Genetic variation in metabolic phenotypes: Study designs and applications. *Nature Reviews Genetics*, 13, 759–769.

Sykes, B.D. (2007). Urine stability for metabolomic studies: Effects of preparation and storage. *Metabolomics*, 3, 19–27.

Taïbi, K., Abderrahim, L.A., Ferhat, K., Betta, S., Taïbi, F., Bouraada, F., & Boussaid, M. (2020). Ethnopharmacological study of natural products used for traditional cancer therapy in Algeria. *Saudi Pharmaceutical Journal*, 28, 1451–1465.

Thakur, A. (2004). Therapeutic Use of Urine in Early Indian Medicine. *Indian Journal of History of Science*, 39, 415–427.

Touma, C., Sachser, N., Möstl, E., & Palme, R. (2033). Effects of sex and time of day on metabolism and excretion of corticosterone in urine and feces of mice. *General and Comparative Endocrinology*, 130, 267–278.

Vaidya, A., Vaidya, R., Vaidya, V., Joshi, B., Mody, J., Joshi, J., Amonkar, A., & Sirsat, S. (2003). Spontaneous or induced regression of cancer a novel research strategy for ayurvidya. *Ancient Science of Life*, 22, 75.

Vartanian, L.R., Schwartz, M.B., & Brownell, K.D. (2007). Effects of soft drink consumption on nutrition and health: A systematic review and meta-analysis. *American Journal of Public Health*, 97, 667–675.

Veber, D.F., Johnson, S.R., Cheng, H.-Y., Smith, B.R., Ward, K.W., & Kopple, K.D. (2002). Molecular properties that influence the oral bioavailability of drug candidates. *Journal of Medicinal Chemistry*, 45, 2615–2623.

Vuorela, P., Leinonen, M., Saikku, P., Tammela, P., Rauha, J.-P., Wennberg, T., & Vuorela, H. (2004). Natural products in the process of finding new drug candidates. *Current Medicinal Chemistry*, 11, 1375–1389.

Wang, W. (2015). Tolerability of hypertonic injectables. *International Journal of Pharmaceutics*, 490, 308–315.

Wu, D., Fan, Y., Liu, S., Woollam, M.D., Sun, X., Murao, E., Zha, R., Prakash, R., Park, C., & Siegel, A.P. (2020). Loading-induced anti-tumor capability of murine and human urine. *Journal of the Federation of American Societies for Experimental Biology*, 34, 7578.

Zaki, D., Abd-El-Aziz, M., El-Gengeihy, S., & Morsi, N. (1984). Antimicrobial potentialities of some Egyptian desert plants. *Herba Hungarica*, 23, 73–84.

Zhang, X., Chen, F., & Wang, M. (2015). Bioactive substances of animal origin. In *Handbook of Food Chemistry* (pp. 1099-1033): Springer.

Zhao, S., & Li, L. (2020). Chemical Derivatization in LC-MS Based Metabolomics Study. *Trends in Analytical Chemistry*, 131, 115988.

Zhu, C., Fasoli, S., Isani, G., & Laghi, L. (2020). First insights into the urinary metabolome of captive giraffes by Proton Nuclear Magnetic Resonance Spectroscopy. *Metabolites*, 10, 157.

7.4 Osmolarity-dependent modulation of cell viability by camel urine: implications for assessing bioactive properties

Carlos Iglesias Pastrana[1], Maria Noemi Sgobba[2], Francisco Javier Navas González[1], Juan Vicente Delgado Bermejo[1], Ciro Leonardo Pierri[3], Giovanni Lentini[3], Biagia Musio[4], Taher Kamal Sayed Osman[5], Vito Gallo[4,6], Iola F. Duarte[7], Lorenzo Guerra[2] and Elena Ciani[2]

[1]Department of Genetics, Faculty of Veterinary Sciences, University of Córdoba, 14014 Cordoba, Spain

[2]Department of Biosciences, Biotechnologies and Environment, University of Bari 'Aldo Moro', 70121 Bari, Italy

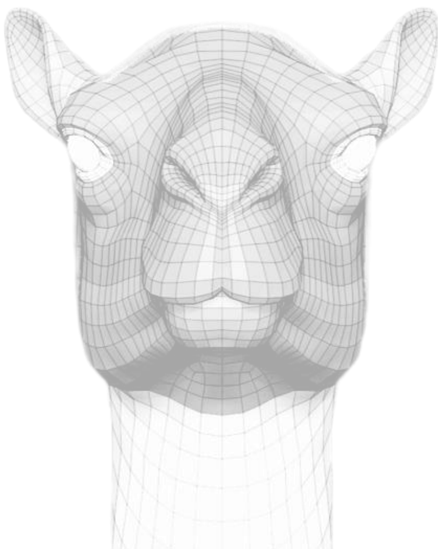
[3]Department of Pharmacy-Pharmaceutical Sciences, University of Bari 'Aldo Moro', 70125 Bari, Italy

[4]Department of Civil, Environmental, Land, Construction Engineering and Chemistry (DICATECh), Polytechnic University of Bari, 70125 Bari, Italy

[5]Salam Veterinary Group, Kingdom of Saudi Arabia

[6]Innovative Solutions S.r.l, Spin Off Company at Polytechnic University of Bari, 70015 Noci (Bari), Italy

[7]Department of Chemistry, CICECO Aveiro Institute of Materials, University of Aveiro, 3810-193 Aveiro, Portugal



Quality indicator information provided on the publication
Latest information available (2022)

Status of the manuscript: Submitted

Journal (year, volume, page(s)): *Journal of Cellular Biochemistry*

International database in which it is indexed: Journal of Citation Reports (JCR)

Thematic area in the reference database: Biochemistry & Molecular Biology

Impact index of the journal in the year of the article's publication: 4

Rank/number of thematic area journals: 119/285 (Q2)

Abstract

The widespread ethnomedical practice of dromedary urinotherapy as a remedy against various illnesses, including cancer, is well recognized in traditional dromedary countries, and multiple researchers tried to unravel its antiproliferative bioactive potential and provide scientific evidence through *in vitro* experiments. The physico-chemical properties of urines, such as osmolarity could deeply influence the results of *in vitro* tests, although seldom considered. In the present study, we assessed the osmolarity-dependent modulation of cell viability by dromedary urine in human renal cell lines recognized as valuable models in toxicological research. The effect of hyperosmolar mannitol-composed solutions and dromedary urine on human non-tumor (HK2) and tumor renal cells (Caki-1) viability and morphology has been assessed through resazurin-based assay and microscopy analysis. Mannitol-induced hyperosmolarity up to 500 mOsm/L did not significantly affect cell viability nor morphology in both HK2 and Caki-1. When exposed to urine solutions (diluted to <500 mOsm/L) significant antiproliferative effects were observed almost exclusively in Caki-1 cells (in two out of the ten tested samples), while effects on cell morphology (elongation) were observed only in HK2 cells (in six samples). A preliminary Nuclear Magnetic Resonance (NMR) metabolic profiling of the tested camel urine samples was performed and a comprehensive list of the identified compounds is provided. Our study reveals that high osmolarity levels exceeding 500 mOsm/L result in cell death in the investigated cell lines. These findings underscore the critical role of osmotic conditions in mediating the observed cellular responses and emphasize the need for careful consideration of osmolarity when evaluating *in vitro* the bioactive properties of camel urine. Moreover, we found that the observed effects of camel urines are evident when cells are exposed to solutions with osmolarity below the aforementioned threshold, suggesting the presence of bioactive compounds. Further investigation are needed to elucidate the possible role of the small molecules contained in urines in the observed effects on cell viability and morphology.

Keywords

Camel urine, osmolarity, human proximal tubule epithelial cell line HK2, human renal carcinoma cell line Caki-1, cell viability, cell morphology

Introduction

Multiple research studies echo the popular belief within Islamic prophetic medicine that oral administration of *Camelus dromedarius* (hereinafter simply referred to as camel) urine, either alone or mixed with milk, is an effective and safe therapeutic remedy against various ailments (Abdel Gader and Alhaider, 2016; Iglesias Pastrana et al., 2022). Reports on the use of this animal product as a therapeutic agent in humans (Anwar et al., 2021) and on its multiple bioactivities, including cytotoxic effects towards different tumor cell lines (Al-Yousef et al., 2012), inhibition of platelet aggregation, protection of gastric (Al-Ghumlas, 2020; Hu et al., 2017) and hepatic epithelia (Hany S. Mahmoud, Wael M. Elsaed, & Sami A. Gabr, 2019), anticlastogenic activity (Anwar et al., 2021) and antimicrobial properties (Elbehiry et al., 2021), provide some scientific elements in support of its putative therapeutic potential. In particular, the anticancer properties of camel urine, tested mainly *in vitro*, have harnessed increasing interest (Alebie et al., 2017; Iglesias Pastrana et al., 2022).

Nevertheless, some critical methodological gaps could be limiting the pharmaceutical and clinical application of the documented results (Iglesias Pastrana et al., 2022). First, urine osmolarity is never measured prior to bioactivity testing and this could deeply influence the results of *in vitro* tests. Indeed, it is unknown whether the reported antiproliferative effects of camel urine could be related to the high osmolarity values (up to 3200 mOsm/L) of this animal fluid (Attas et al., 2020; Gaughan, 2011). Additionally, the chemical composition of the urine(s) tested is hardly analyzed and this second issue hinders the identification of specific chemicals as candidates with bioactive potential (Atanasov et al., 2021). Furthermore, the production of such chemicals could be influenced by multiple animal intrinsic and extrinsic factors such as sex, age, physiological status, or diet (Bollard et al., 2005; Abdelzaher et al., 2020; Schreier et al., 2013), and this variability is seldom considered. For instance, most studies have focused on the urine from female camels due to the popular belief that it is the most effective (Iglesias Pastrana et al., 2022; Vogt et al., 2016), thus overlooking possible gender-related effects.

In this work, we tested the bioactivity of a set of camel urines, derived from animals of different sex, age, and physiological status, while taking into account the possible influence of the samples' osmolarity. In particular, we assessed the antiproliferative activity of camel urine solutions towards human non-tumor and tumor renal cells, via microscopic examination and cell viability measurements. The two cell lines considered, HK2 and Caki-1 cells, are valuable models in toxicological research (Brodaczewska et al., 2019; Chae et al., 2020; García-Pérez et al., 2021; Hua et al., 2017; Lee et al., 2021; Mossoba & Sprando, 2020; Zhao et al., 2020), and, to the best of our knowledge, their response to camel urine exposure is here reported for the first time. In addition, we performed a preliminary Nuclear Magnetic Resonance (NMR) metabolic profiling on the tested urine samples in order to identify candidate metabolites possibly responsible for the observed effects on the adopted cellular models.

Material and methods

Urine collection and processing

All the animals included in this study are cohoused in a farm located in the Doñana National Park (southwestern Spain) and are fed on the same diet (alfalfa, beet pulp, calcium carbonate, salt, and selenium). Experimental conditions for urine sampling were adjusted following the recommendations by Emwas et al. (2016). For each animal, a sterile, single-use plastic bag was placed in a collection cone holder to recover mid-stream, first-morning-void urine when naturally peeing. Samples from 10 dromedary camels (Table 1) were collected on a single day in February 2020. Immediately after collection, urine was transferred to 15-mL tubes and centrifuged at 2,500 × g for 5 min at 4°C. Once recovered, the supernatant was filtered using a 0.22 μm filter and aliquoted. The preservative sodium azide (NaN_3) is then added at a final concentration of 0.05% wt/vol in the aliquots to be used for NMR analysis. For safe long-term storage, all aliquots were stored at -80°C until *in vitro* bioactivity experiments and metabolic profiling were carried out.

Table 1. Urine samples categorical description.

ID	Gender	Age (years)	Physiological status
01FD	Female	35	Not neutered
02MF	Male	1.5	Bull
03MH	Male	14	Bull
04MM	Male	28	Neutered
05MP	Male	32	Neutered
06FP	Female	4	Pregnant
07MR	Male	4	Bull
08FS	Female	19	Not neutered
09MS	Male	30	Neutered
10MT	Male	20	Neutered

Osmolarity assessment of camel urine samples

The osmolarity of camel urine samples was measured by a VAPRO® vapor pressure osmometer 5600 (Wescor, Inc., Logan, UT, USA) with fresh 290 mmol/kg, 1000 mmol/kg and 100 mmol/kg standard solutions, following the manufacturer's instructions. A single Whatman filter paper disc (Wescor, ss-033) was placed in the central depression of the holder by metal forceps, and 10 μl of the samples diluted 1:2 with ultrapure water was expelled onto the disc. Saturated discs were rapidly transferred to the vapor pressure osmometer sample holder, and osmolarity was determined. All samples were analyzed in triplicate.

Cell cultures

The human proximal tubule epithelial cell line (HK2) (Ryan et al., 1994) and the human renal carcinoma cell line (Caki-1) (Glube et al., 2007), proposed as a model system of proximal tubule epithelium, were purchased from the American Type Culture Collection (ATCC, Manassas, VA, USA). Both cell lines were cultured in Dulbecco's modified Eagle's medium high glucose (Elabscience Biotechnology Inc., USA, EP-CM-L0032), supplemented with 10% foetal bovine serum (Euroclone S.p.A., Milan, Italy), in 25 cm^2 culture flasks and were maintained at 37°C and 5% CO_2, regularly passaged on reaching 90% confluency using a 0.25% trypsin-EDTA solution (Elabscience Biotechnology Inc., USA, EP-CM-L0446).

Hyperosmolar solutions preparation for in vitro testing

Increasing media osmolarity conditions adjusted with mannitol were evaluated to determine the osmotic range at which no significant decrement in the viability of cells is produced. Mannitol, a cell membrane-impermeable, non-metabolizable sugar (Kinsman et al., 2017), was used as a reference osmolyte to study the tolerance limits of cultured cells to osmotic stress. Hyperosmolar solutions were prepared by the addition of the proper weighted powder of D (—) mannitol (Riedel-de Haën, cat. no. 33440) in the complete culture medium (whose osmolarity was 290 mOsm/L) to reach 400, 450, 500, 600, 700 and 800 mOsm/L respectively. After mannitol was dissolved, the solutions were sterilized using 0.22 μm filters.

Urine samples preparation for in vitro testing

All the urine samples were first diluted 1:10 using the complete culture medium. The osmolarity of diluted urines was assessed as previously described, and urine samples exceeding the 500 mOsm/L value were further diluted adopting the minimum possible dilution ratio (max 1:15, final dilution ratio) necessary to keep osmolarity values below that threshold, thus trying to avoid excessive dilution of the potentially bioactive molecules present in urine samples. The 500 mOsm/L threshold was adopted since it was shown in our experiments (see the 3.2. Results section) to be a non-toxic osmolarity value.

Cell viability assay

HK2 and Caki-1 cells were seeded in 96 multi-well plates at a density of 15,000 cells/well in the growth medium and allowed to attach overnight. Then, cells were incubated with hyperosmolar media adjusted with mannitol or with urine-composed solutions for 24, 48, and 72 hours at 37°C, 5% CO_2. Cell viability was evaluated in the control condition (cells grown in the complete medium) and in the test conditions (cells grown in the hyperosmolar media or urine-composed media) via a resazurin-based assay (Biotium, Inc., Fremont, CA, USA) performed according to the manufacturer's instructions. The assay is based on the ability of living cells to reduce oxidized non-fluorescent blue resazurin to a red fluorescent dye (resorufin) by a mitochondrial reductase. At the end of the resazurin incubation time (2 hours), resorufin fluorescence was recorded at $\lambda_{Ex/Em}$ 535/590nm in a FLUOstar® Omega microplate reader (BMG LABTECH GmbH, Ortenberg, Germany).

Correlation of resazurin-based fluorescence with cell number

HK2 and Caki-1 cells were seeded in triplicate in 96 multi-well plates, to reach 5000, 7500, 10000, 12500, 15000, 20000, 25000, and 30000 cells/well (Balbaied & Moore, 2020). Cells were incubated in the complete culture medium for 12 hours to allow them to attach and then the resazurin-based assay was performed following the manufacturer's instructions. At the end of the resazurin incubation time (2 hours), fluorescence was recorded as described above. The correlation between cell numbers and resazurin fluorescence was examined and the resulting linear equations (Supplementary Figures S1-S2) were used to estimate the number of cells, based on the fluorescent signals, for the conditions applied in our *in vitro* viability assays.

Statistical analysis

Data are presented as the means ± standard errors (S.E.M.). The effect of the treatments ((i) hyperosmotic media and (ii) urine solutions) was analyzed with GraphPad Prism 9.5.1 software using a one-way analysis of variance (ANOVA). Dunnett's *post hoc* test was performed. Dunnett's test compares the means from several experimental groups against the mean of a control group in order to see if there is a difference. Differences were considered statistically significant at $P < 0.05$.

Optical microscopy analysis

Before undergoing the resazurin-based cell viability assay, HK2 and Caki-1 cells were seeded in 96 multi-well plates at a density of 15,000 cells/well in the growth medium and allowed to attach overnight. After treatment with hyperosmolar solutions or with camel urine-composed solutions, cells were monitored via optical microscopy analysis. Brightfield images were acquired through a Nikon Digital SIGHT camera and the NIS Elements software (version 3.00 SP7; Nikon, Turin, Italy), with 100x magnification (TE2000 inverted microscope by Nikon, Turin, Italy) to evaluate cell morphology evolution over time (at 24, 48 and 72 hours).

Nuclear Magnetic Resonance (NMR) analysis

Freeze-dried urine samples were reconstituted in deuterated phosphate buffer (100 mM, pH 7.4), containing 0.1 mM TSP-d4, and 550 μL were transferred into 5 mm NMR tubes. ^{1}H NMR spectra were acquired on a Bruker Avance III HD 500 spectrometer (University of Aveiro, PTNMR network) operating at 500.13 MHz for proton (^{1}H) observation, at 298 K, using a 5 mm TXI probe. One-dimensional (1D) ^{1}H spectra were acquired using a standard Bruker pulse program ('noesypr1d'), with an acquisition time of 2.3 s, relaxation delay of 4s, 32768 data points, a spectral width of 14.00 ppm and 128 scans. Two-dimensional (2D) spectra, namely ^{1}H-^{1}H total correlation (TOCSY), ^{1}H-^{13}C heteronuclear single quantum correlation (HSQC) and J-resolved spectra were recorded to aid spectral assignment (Mitschke et al., 2022).

Results

Osmolarity of camel urine samples

Considering the strong water reabsorption capacity of camel kidneys, and the highly concentrated urines that this species can eliminate, the osmolarity of tested camel urine samples was measured before cell exposure. We found great variability in the urine concentration, with all the samples showing values far from the physiological osmolarity of the extracellular environment (about 300 mOsm/L), as reported in Table 2.

Mannitol induces a dose- and time-dependent cytotoxicity on human renal cells

The exposure of cells to hyperosmotic stress triggers cell shrinkage, oxidative stress, protein carbonylation, mitochondrial depolarization, DNA damage, and cell cycle arrest, thus reducing cell proliferation and increasing the susceptibility of cells to apoptosis (Chen et al., 2015; Grauso et al., 2019; Hosseiniyan Khatibi et al., 2019). As such,

Table 2. Measurements of camel urine samples osmolarity.

ID	Urine osmolarity (mOsm/L)
01FD	1315
02MF	1696
03MH	2391
04MM	1376
05MP	1595
06FP	770
07MR	730
08FS	1328
09MS	2060
10MT	1859

a preliminary evaluation of the effect of increasing osmolarity values (above the physiological condition) on cell viability was conducted to unravel the tolerance limits of the tested cell lines (non-tumor HK2 and tumor Caki-1 human renal cell lines) in *in vitro* experiments. To simulate hyperosmolarity conditions, we used D (−) mannitol as organic cell-impermeable osmolyte (Bálint et al., 2007), dissolved, at different concentrations, in the complete cell culture medium, thus increasing medium osmolarity from 290 mOsm/L (complete culture medium) up to 400, 450, 500, 600, 700, and 800 mOsm/L. Both cell lines were seeded in 96 multi-well plates and were exposed to the complete culture medium (control) and to the six different hyperosmolar solutions for 24, 48, and 72 hours, respectively. Optical microscope (100x) observation of treated and control cells was performed at each time point to evaluate the cellular morphology in response to the hyperosmolarity. As shown in Figure 1A (HK2) and Figure 1B (Caki-1), neither cell line presented any remarkable morphological change up to the 500 mOsm/L conditions, at all the time points considered. On the contrary, higher osmolarity conditions were associated with a clear decrease in the cellular volume (and cellular density), likely due to cellular death, as also suggested by the resazurin-based cell viability assay (Figure 2A and Figure 2B, respectively).

Indeed, both Caki-1 and HK2 cells showed a significant decrease in cell viability at 600, 700, and 800 mOsm/L after 24, 48, and 72 hours of incubation. In particular, strong toxicity was observed at the highest concentration and the longest time of incubation, with 94.3% and 85% of HK2 and Caki-1 cell death, respectively. On the other hand, cell viability was not significantly altered, compared to control conditions, at 400, 450, and 500 mOsm/L in both our models.

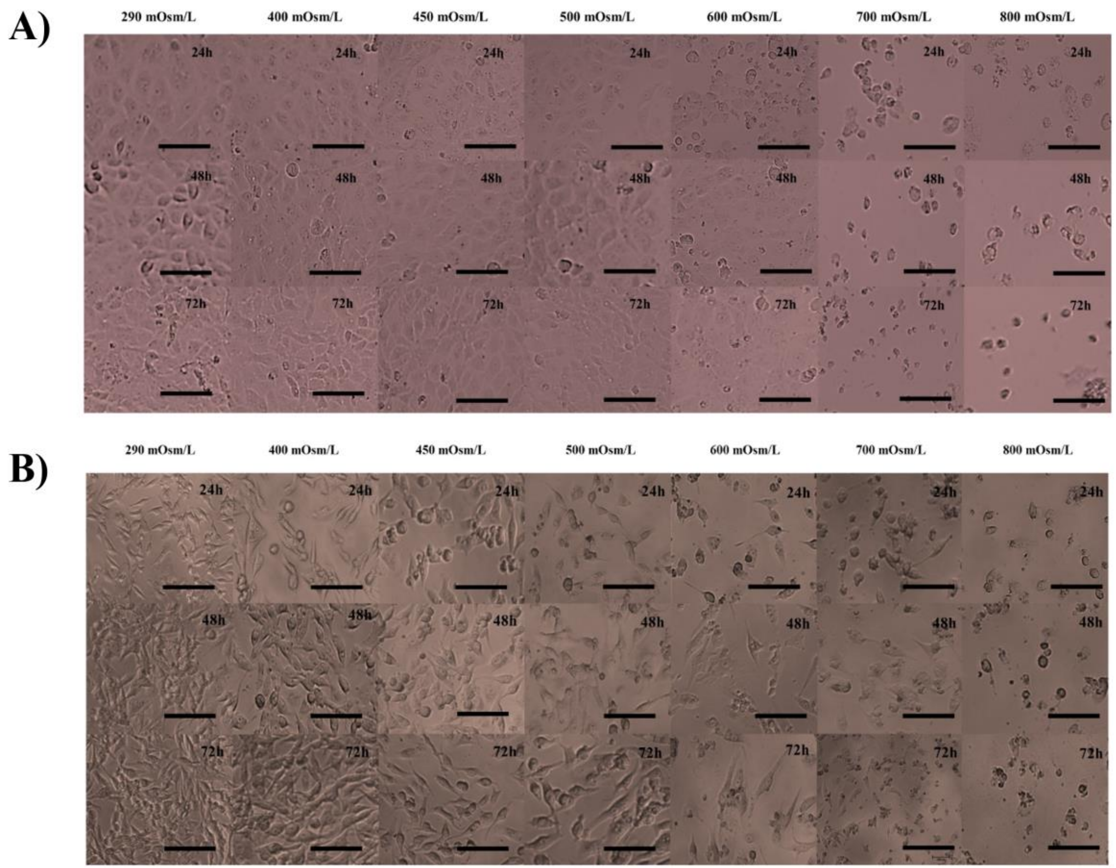


Figure 1. Brightfied images (100x magnification) of renal cells after exposure to hyperosmolar solutions.

(**A**) Optical microscopy analysis of human kidney (HK2) cells exposed to D (–) mannitol-composed medium. Hyperosmolarity does not significantly affect cell morphology up to 500 mOsm/L. An important and time-dependent reduction in cellular volume and cellular density was observed at 600, 700, and 800 mOsm/L.

(**B**) The human renal carcinoma (Caki-1) cell line exhibits the same behavior as HK2, when exposed to identical experimental conditions, with nearly no effect on cellular morphology and cellular density up to 500 mOsm/L.

Scale bar: 100 μm.

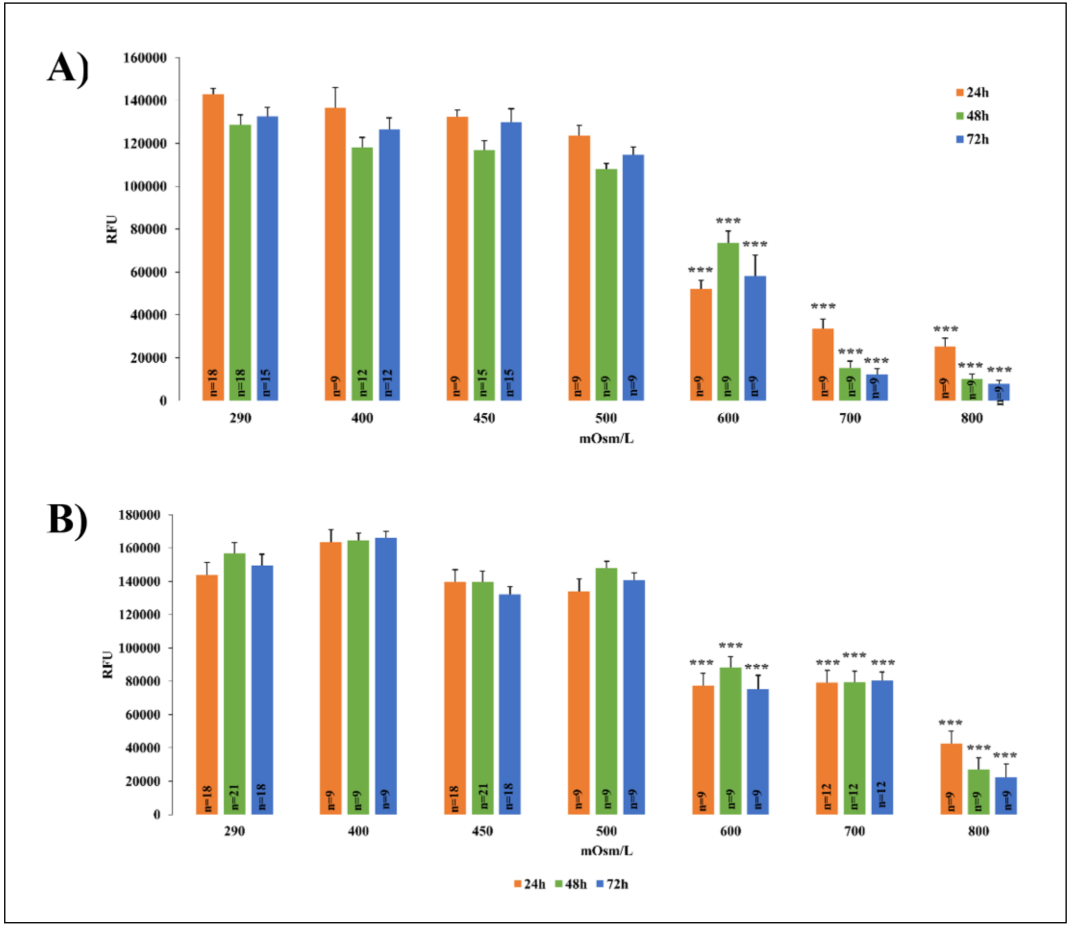


Figure 2. Resazurin-based cell viability assay to assess hyperosmolarity tolerance of the adopted cell lines.

(**A**) The non-tumor HK2 cells exposed to D (–) mannitol-composed medium for 24, 48 and 72 hours exhibit a good tolerance to hyperosmolarity up to 500 mOsm/L, while 600, 700, and 800 mOsm/L cause a progressive and statistically significant decrease in cell viability.

(**B**) The tumor Caki-1 cells, when exposed to identical experimental conditions as HK2, showed a slightly higher hyperosmolarity tolerance, compared to HK2.

*** $P<0.001$; n = number of observations.

Caki-1 and HK2 cell lines display dissimilar response to the tested urines

Considering the above results and the urine osmolarity (Table 2), all urine samples were diluted with the complete cell culture medium to obtain final urine solutions with an osmolarity lower than 500 mOsm/L (see 2.6. Materials and Methods section). Cells were then exposed to urine solutions at the same three time points used for the osmolarity assessments. In Caki-1 cells, for all the camel urine solutions and all the tested time points, no significant effects were detected using the resazurin-based cell viability assay, except for the urine solutions from the 02MF and 09MS camels. For these samples, a statistically significant viability decline was observed compared to controls at 24 hours (02MF), 48 hours (09MS) and 72 hours (02MF and 09MS). At the longest time of incubation (72 hours), we observed, respectively for the 02MF and 09MS urine solutions, a decrease in cell number from about 20,700 to about 13,000 cells and from about 20,700 to 8,100 cells, compared to the control (Figure 3).

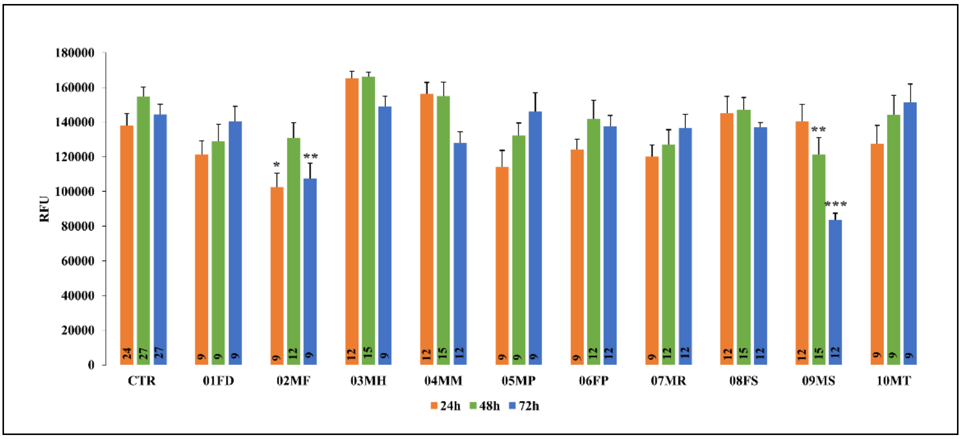


Figure 3. Camel urine solutions effects on tumor renal cells viability. The tumor Caki-1 cells were exposed to the complete culture medium (CTR) and the camel urine solutions for 24, 48, and 72 hours, and the resazurin-based cell viability assay was performed at each time point. A statistically significant decrease in cell viability was observed, compared to the control condition, only for solutions containing urine coming from two male camels: at 24 hours, when cells were treated with urine from 02MF, and, at 72 hours, when treated with urines from 02MF and 09MS.
* $P<0.05$, ** $P<0.01$, *** $P<0.001$; n = number of observations.

Statistically significant reduction in cell viability was not observed for the non-tumor cell line (HK2) in none of the urine solutions when exposed to the same experimental conditions described above for Caki-1, except for the urine solution from the 09MS camel after 72 hours of exposure, when a roughly 32% reduction of HK2 cell viability was observed (Figure 4).

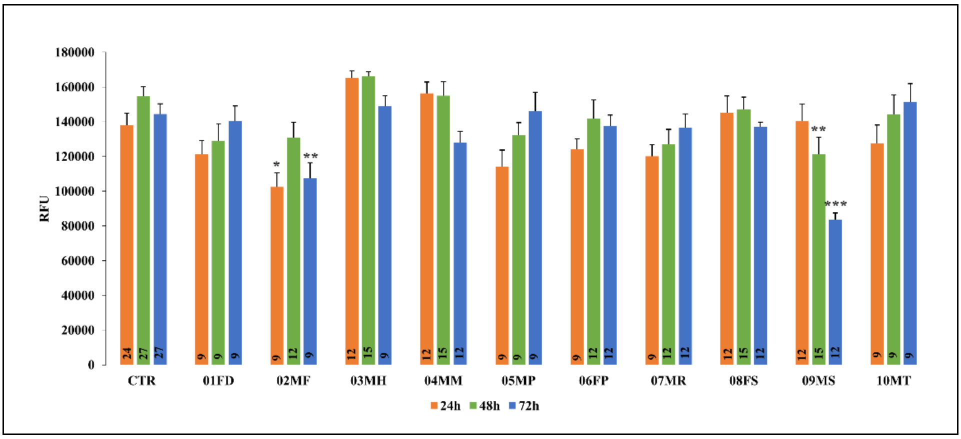


Figure 4. Camel urine solutions effects on non-tumor renal cells viability. The non-tumor HK2 cells were exposed to the complete cell culture medium (CTR) and to camel urine solutions for 24, 48, and 72 hours and the resazurin-based cell viability assay was performed at each time point. A statistically significant decrease in cell viability was observed, compared to the control condition, only after 72h of incubation with 09MS urine solutions.

*** $P<0.001$; n = number of observations.

In what concerns cell morphology, HK2 cells appeared more elongated when incubated with six (01FD, 02MF, 04MM, 05MP, 08FS, and 09MS; Figure 5, Supplementary Figures S3-S7) out of ten samples compared to the control cobblestone shape. On the contrary, brightfield images did not show any clear modification in the Caki-1 cell shape, as reported in Supplementary Figures S8-S11.

Metabolites identified in camel urine samples through NMR analysis

A preliminary NMR spectroscopic investigation was applied to the tested urine samples in order to obtain information on the pool of metabolites most represented in their aqueous extracts (see Table 1). The metabolites identified by 1D ^{1}H NOESY experiments on the aqueous extracts of the analyzed urine samples are shown in Table 3. The nature of such metabolites was confirmed through homo- and hetero-nuclear 2D NMR experiments. The urine samples from 02MF and 09MS camels showed a higher amount of N-acetylglucosamine, pyruvic acid and trigonelline, and a lower amount of lactic acid, allantoin and hippuric acid, compared to the other tested urine samples (data not shown).

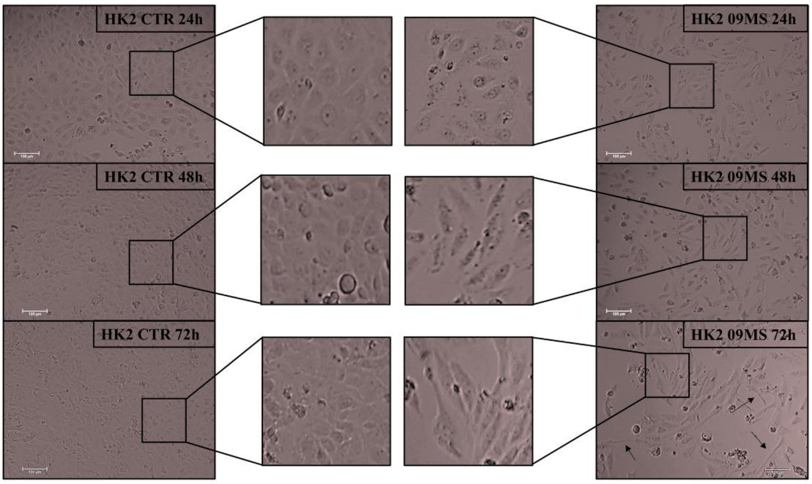


Figure 5. Morphological changes in non-tumor renal cells exposed to 02MF urine solution. HK2 cells were exposed for 24, 48, and 72 hours (right panel) to the solution containing urine from the 09MS sample (100x magnification). Clear and time-dependent morphological changes were observed, with HK2 becoming more elongated compared to the control (CTR) cobblestone-shaped cells (left panel). The insets of each panel represent 3x magnification of the corresponding brightfield image. The black arrows indicate cell protrusions. Scale bar: 100 µm.

Table 3. List of metabolites contained in the aqueous extracts of the analyzed urine samples.

Metabolite	**δ (ppm) and multiplicity details**
Lactic acid	1.34 (d, 6.9 Hz); 4.14 (q)
N-Acetylglucosamine (NAG)	1.93 (s)
Pyruvic acid	2.34 (s)
Succinic acid	2.41 (s)
Creatine/creatinine	3.02 (s); 4.01 (s)
Malonic acid	3.15 (s)
Carnitine	3.19 (s)
Trimethylamine *N*-oxide (TMAO)	3.26 (s)
Glycine	3.56 (s)
Allantoin	5.37 (s)
Fumaric acid	6.53 (s)
Phenylalanine	7.38 (m); 3.29 (dd); 3.13 (dd)
Hippuric acid	7.55 (m); 7.63 (m); 7.83 (m); 3.96 (s)
Benzoic acid	7.88 (m); 7.56 (m); 7.49 (m)
Trigonelline	8.09 (m); 8.85 (dd, 8.6, 4.4 Hz)
Hypoxanthine	8.14 (s); 8.16(s)
Formic acid	8.47 (s)
1-Methylnicotinamide	8.92 (dd); 8.70 (dd)

The resonance frequencies of the signals are indicated as delta (δ) and the units are given in part per million (ppm); multiplicity patterns are described as: (s) singlet, (d) doublet, (q) quartet, (m) multiplet, (dd) doublet of doublets.

Discussion

The currently available literature on the bioactivity of camel urine reports a plethora of potential therapeutic effects related to the inhibition of platelet aggregation (Al-Ghumlas, 2020; Alhaidar et al., 2011; Alhaider et al., 2014), hepatoprotective (Hany S. Mahmoud, Wael M. Elsaed, & Sami A. Gabr, 2019) and gastroprotective (Hu et al., 2017) effects, together with antibacterial (Elbehiry et al., 2021; Rofaei et al., 2022) and antifungal activities (Al-Abdalall, 2010; Abdelzaher et al., 2020), and also anticancer activity (Alhaidar et al., 2011; Al-Yousef et al., 2012; Romli et al., 2017; Salamt et al., 2021), which have been assessed *in vitro* and/or *in vivo*. On the contrary, a recent research has reported that camel urine had no clinical benefits in 20 cancer patients undergoing urinotherapy up to 6 months (Al Zahrani A et al., 2023). In all the *in vitro* studies which reported the effectiveness of camel urine, used as (i) fractions (PMF) (Khorshid et al., 2015), (ii) raw urines, or (iii) lyophilized urines (resuspended in PBS or in distilled water), the physical-chemical properties, namely osmolarity, of camel urines had been neglected, with possible misinterpretation of the test results (Iglesias Pastrana et al., 2022). Moreover, none of these works addressed issues related to possible morphological changes of cells after exposure to camel urines, suggesting that information may be missing, albeit useful. Another weakness of these studies is the poor characterization of the chemical composition of the camel urine. Taken together, these considerations point to the need for a "good practice" shared by researchers in this field, in order to reduce the variability of the *in vitro* testing of camel urine bioactivity.

Osmolarity effects on human renal cells

In the camel species, the kidney presents peculiar anatomical features conferring a strong capacity for water reabsorption and the faculty to eliminate very concentrated urine, up to 3200 mOsm/L (Abdalla, 2020; Gaughan, 2011; Ouajd & Kamel, 2009). Urine osmolarity is a multifactorial parameter that also depends on, other than the species, the sex, and the physiological status of the animals (intrinsic factors), the geo-climatic area where camels live, their diet, access to water, and even the time of sampling during the day (extrinsic factors) (Dubost et al., 2021; Ghamdi & Khorshid, 2012; Elkhair, 2019; Porowski et al., 2019; van Vonderen et al., 1997; Yagil & Berlyne, 1978). It is well known that *in vitro* exposure to hyperosmotic stress represents a challenge for cell survival (Hosseiniyan Khatibi et al., 2019). This can be particularly limiting when addressing *in vitro* studies involving the effects of camel urine, as disentangling the contribution of hyperosmolarity vs. the contribution ascribable to a given treatment could be very cumbersome. Under this scenario, we intentionally exposed our cellular models to hyperosmolarity up to 800 mOsm/L using the metabolically inert mannitol for 24, 48, and

72 hours, to test their tolerance to hyperosmotic stress. Indeed, both HK2 (non-tumor) and Caki-1 (tumor) cell lines, as a model for the human renal proximal tubule (Glube et al., 2007; Ryan et al., 1994), are not physiologically exposed to hyperosmolar environments. In our experimental conditions, both cell lines seemed to tolerate well hyperosmolarity values up to 500 mOsm/L. At higher osmolarity levels, a progressive drop in cell viability was observed, with almost complete mortality (about 95%) at 800 mOsm/L after 72 hours of exposure. In general, the trend observed in our work is consistent with that reported in different cell lines (Chen et al., 2015; Fujisawa et al., 2012; Guo et al., 2017; Kim et al., 2021), and by Shi et al. (Shi et al., 2018) who assessed the cytotoxicity of mannitol-induced hyperosmolarity on human tubular renal cells (HK2), detecting a dose- and time-dependent effect. In our experimental conditions, viability levels significantly different from the control were observed at 600 mOsm/L, while in the above study viability levels significantly different from the control had been already observed when 100 mM mannitol were added to their complete culture medium (roughly corresponding to 400 mOsm/L). Dissimilarity in the adopted complete culture medium composition, as well as in the number of replicates (and, consequently, in the captured biological variability, possibly impacting statistical significance) may explain the observed differences.

Effects of camel urines on human renal cells viability and morphology

We then exposed cells to camel urines that had been diluted to maintain osmolarity levels below the non-toxic threshold (500 mOsm/L), defined on the basis of our experimental results. Interestingly, two of the ten tested samples showed cytotoxicity toward tumor cells. Since all samples were adjusted to a similar osmolarity, other factors, possibly related to the chemical composition of urines, must be responsible for their bioactivity. The animals included in this study were reared under rather homogenous conditions, hence, the contribution of extrinsic factors to urine compositional variability, such as diet composition, should be minimal. Regarding intrinsic factors, our dataset included three females and seven males of different ages and physiological statuses. The two bioactive samples were from two males, one being among the oldest neutered subjects (09MS), and the other being the youngest animal, and one out of the three not neutered bulls (02MF). Hence, there appears to be no direct correlation between the sample bioactivity hereby examined and the animals' age, sex, or neutering status, although the low number of animals per category limits the sample representativeness. An interesting aspect is that the viability of non-tumor renal cells was not affected upon exposure to any of the tested camel urines, except for the urine solution from 09MS sample, only at the longest time of incubation. This is in line with other studies showing the different behavior of tumor vs. non-tumor cell lines (Al-Yousef et al., 2012; Gorshkov et al., 2019; Kritis et al., 2015; Moon et al., 2019; Pham et al., 2018) and represents a positive outcome in view of possible future investigation in the antiproliferative research field. On the other hand, only non-tumor renal cells were prone to morphological changes, observed upon exposure to urine solutions from two females (01FD and 08FS) and four males (02MF, 04MM, 05MP and 09MS). The above changes were gradual over time, thus suggesting that the observed morphological alterations may represent an early event in the progression towards cell death (Tian et al., 2003). In addition, peculiar protrusions were observed (Fig 5 and Figs S3-S6), possibly corresponding to echinoid spikes known to be related with the apoptotic process (Alrumaihi et al., 2021; Syed Abdul Rahman et al., 2013).

The preliminary NMR spectroscopic study, performed on the tested urine samples, provided insights into their chemical composition. Among the pool of compounds identified as present in the urine aqueous extracts (Table 3), the antioxidant N-acetylglucosamine, pyruvic acid and trigonelline (Azam et al., 2014; Chowdhury et al., 2018; Ramos-Ibeas et al., 2017) were found to be present in higher amount in the two significantly antiproliferative urine samples (02MF and 09MS), compared to the other tested urines, thus suggesting a possible involvement of these molecules in the observed renal cells viability patterns. While it is possible to provide some interpretations based on the knowledge of metabolic pathways, it is essential to note that, without specific experimental data on the effect of the single cited molecules, or their combination, on the investigated cell lines, any conclusion remains speculative.

In the context of a possible interpretation, the observed antiproliferative effects on tumor cells (Caki-1), compared to non-cancer cells (HK2), could be indicative of a negative modulation of critical metabolic pathways, i.e. glycolytic pathways upregulated in renal cancer cells (Trisolini et al., 2021), necessary for cancer cell growth and division (see Figure 6). On this concern, pyruvic acid, trigonelline, and N-acetylglucosamine, and/or their derivatives can enter the investigated cells through already characterized transporters (Akella et al., 2019; Emami Riedmaier et al., 2012; Liang et al., 2015; Ma et al., 2019; Shikhman et al., 2009; Sprowl-Tanio et al., 2016). Thus, the three molecules can participate to the modulation of glycolysis and hexosamine biosynthetic pathway, and/or mitochondrial function (Akella et al., 2019). N-acetylglucosamine can be involved in modifications of serine/threonine residues of nuclear or cytoplasmic proteins. The resulting O-linked-N-acetylglucosaminylation couples the processes of nutrient sensing, metabolism, signal transduction and transcription, and plays important roles in the development, physiology and physiopathology (Chang et al., 2020). Alternatively, N-acetylglucosamine can undergo deacetylation supplying the cell with glucosamine, which can impact glucose metabolism by promoting or inhibiting glycolysis, depending on specific cell needs or growth contexts, leading to changes in energy production (Akella et al., 2019; Lee et al., 2019; Zhang et al., 2021). For example, N-acetylglucosamine

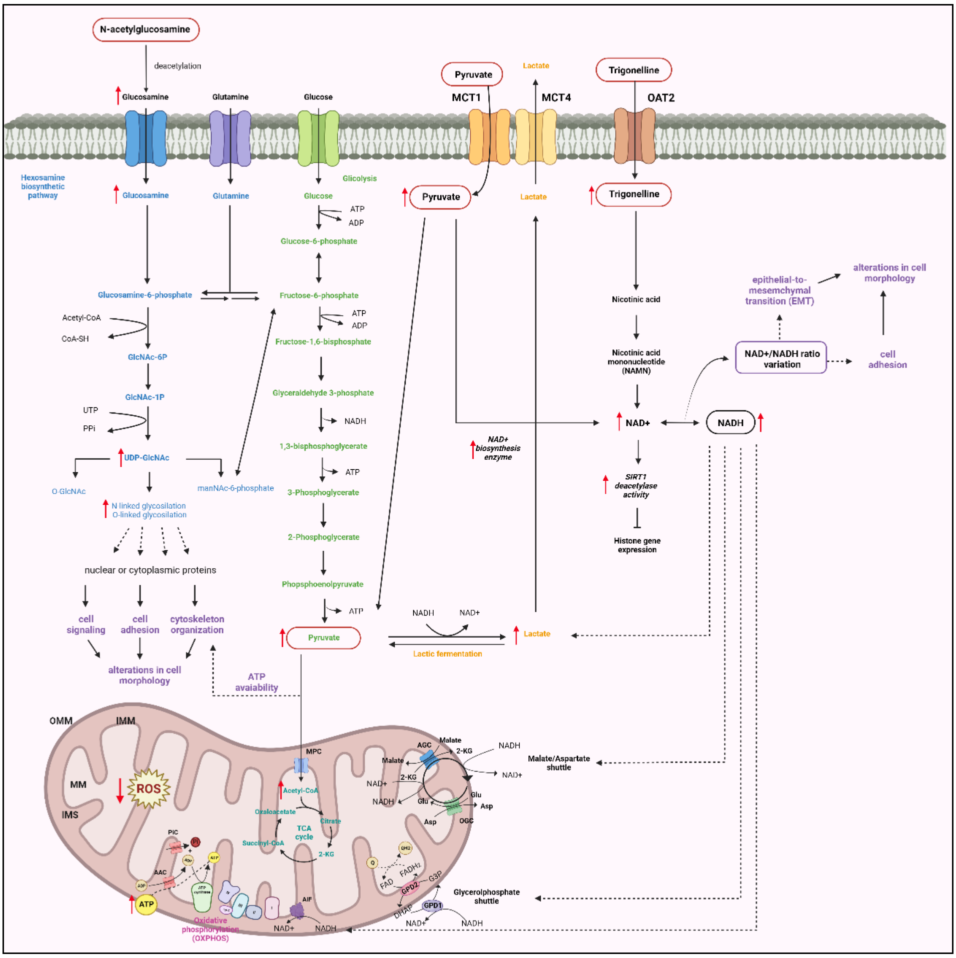


Figure 6. Proposed effects of the compounds identified in camel urines on cell viability and morphology. N-acetylglucosamine, pyruvic acid, and trigonelline can all be related to glycolysis and mitochondrial function. The increase of N-acetylglucosamine can rise the rate of post-translational modifications (N-acetylglucosaminylation), involving cytoskeleton remodeling proteins; by deacetylation, it can supply cells with glucosamine, impacting glucose metabolism. The pyruvic acid accumulation may result in an increased lactate production and can repress histone gene expression via histone deacetylase activity of SIRT1; it can also impact ATP availability, thus affecting cytoskeleton reorganization. The increase of trigonelline can affect the NAD^+/NADH ratio, thus impacting on cellular energetic metabolism and influencing either the epithelial-mesenchymal transition or cell adhesion, leading to cell morphology and motility alterations. Abbreviations: OMM, outer mitochondrial membrane; IMS, intermembrane space; IMM, inner mitochondrial membrane; MM, mitochondrial matrix; AAC, ADP/ATP carrier; PiC, phosphate carrier; TCA, tricarboxylic acid cycle; MPC, mitochondrial pyruvate carrier; AIF, apoptosis-inducing factor; AGC, aspartate/glutamate carrier; OGC, 2-oxoglutarate/malate carrier; 2-KG, 2-ketoglutarate; Glu, glutamate; Asp, aspartate; GPD1, glycerol-3-phosphate dehydrogenase 1; GPD2, glycerol-3-phosphate dehydrogenase 2; G3P, glycerol-3-phosphate; DHAP, dihydroxyacetone phosphate; MCT1, monocarboxylate transporter 1; MCT4, monocarboxylate transporter 4; OAT, organic anion transporters. Created with BioRender.

can be metabolized to fructose-6-phosphate, a key intermediate in glycolysis, or it can also work as a precursor for the hexosamine biosynthetic pathways, which produces UDP-N-acetylglucosamine. On the other hand, an increased flux through the hexosamine biosynthetic pathway has been associated with cell proliferation and survival in some cancer types (Akella et al., 2019; Lee et al., 2019; Zhang et al., 2021). Similarly, pyruvic acid represents a master molecule of several metabolic pathways, from Krebs cycle to lactate production. An excess of pyruvic acid accumulation in glycolytic cancer cells showing impaired mitochondria may result in the upregulation of lactate production, as observed in patients affected by mitochondrial diseases (Laera et al., 2020; Punzi et al., 2018; Todisco et al., 2023; Tragni et al., 2022). Lactate accumulation can stimulate cell proliferation (Sharma et al., 2022). However, it was recently observed that exogenous pyruvate can inhibit the proliferation of different types of cancer cells (Ma et al., 2019). The role of exogenous pyruvate on cancer cells proliferation is still a matter of debate, also considering the more glycolytic or oxidative metabolism that may characterize specific cancer types (Diers et al., 2012; Trisolini et al., 2020). Moreover, it was proposed that pyruvate can repress histone gene expression by inducing the expression of NAD+ biosynthesis enzyme, which then increases NAD^+ levels and activates the histone deacetylase activity of SIRT1 (Ma et al., 2019). Finally, trigonelline is a derivative of nicotinic acid (niacin or vitamin B3) and can be metabolized into nicotinamide, a precursor for the synthesis of NAD^+, which can impact NAD^+/NADH ratio. An increase of NAD^+ may improve mitochondrial function and redox homeostasis, further impaired in kidney cancer cells. The rescued mitochondrial activity reduces ROS and affects cancer cells proliferation, typically favored by redox stress (Zahra et al., 2021). The last observation is coherent with what observed following the addition of the exogenous antioxidant pyruvate and N-acetylglucosamine (Azam et al., 2014; Chowdhury et al., 2018; Ma et al., 2019; Ramos-Ibeas et al., 2017; Todisco et al., 2023; Tragni et al., 2022).

Concerning the morphological changes observed in non-tumor kidney cells (HK2), it is expected that N-acetylglucosamine can provide GlcNAcyl moieties for post-translational modifications, which can affect cell signaling and cytoskeleton leading to alterations in cell shape and motility (Xu et al., 2019). In addition, N-acetylglucosamine has been implicated in cell adhesion and migration processes through the regulation of the expression and/or activity of adhesion molecules and integrins, which may cause an increase in cell elongation in those cells that do not use N-acetylglucosamine as fuel for other pathways (Xu et al., 2019). Similarly, pyruvic acid can impact the availability of ATP, which is essential for actin filament dynamics and actin is a major cytoskeletal component whose rearrangement can determine changes in cell shape and elongation (DeWane et al., 2021). Finally, trigonelline, by affecting NAD^+/NADH ratio, may influence either the epithelial-mesenchymal transition or cell adhesion leading to changes in cell morphology and motility (Thomson et al., 2019).

Conclusions

This study highlights the critical importance of determining non-toxic osmolarity threshold levels specific to each cell model when evaluating the cytotoxicity of camel urine *in vitro*. Our methodological approach provides valuable guidance for future research in this multidisciplinary field. While we observed detectable effects of camel urine on cellular attributes, it is important to interpret the observed antiproliferative effects in the tumor cell line with caution, as they may be influenced by various factors. Another notable limitation of our study is the relatively small number of tested samples, which may limit the generalizability of our findings to the broader camel population. Future studies should aim to address this limitation by including a larger and more diverse sample size, encompassing camels from different geographic regions and reared under varying production systems. Moreover, comprehensive characterization of the composition of camel urine from different individuals is crucial to understand potential variations in bioactive components. Additionally, in-depth investigations are warranted to explore the *in vitro* effects of individual or combined molecules identified in camel urine, using techniques such as *in silico* testing to prioritize their evaluation.

By addressing these aspects, future research can further elucidate the mechanisms underlying the effects of camel urine and the specific bioactive molecules that may improve cell viability and expand our understanding of the potential pharmaceutical applications of the highlighted bioactive molecules. This will contribute to the advancement of knowledge in this emerging field.

List of abbreviations

HK2 (Human Kidney 2)

NMR (Nuclear Magnetic Resonance)

ATCC (American Type Culture Collection)

EDTA (Ethylenediaminetetraacetic acid)

TSP-D4 (3-(Trimethylsilyl)propionic-2,2,3,3 acid sodium salt D4)

TXI (Triple Resonance Probe)

TOCSY (Total Correlation Spectroscopy)

HSQC (Heteronuclear Single Quantum Correlation)

Ethics statement: No ethical assessment and permit were specifically required for sampling because the collection of urine occurred when animals naturally peed (article 1, section 5 of the Directive 2010-63-EU). Animals were not restrained for sampling, neither physically nor chemically. Nevertheless, procedures to avoid any possible animal distress during the samples' collection were put in place, according to local consolidated practices, in compliance with the Directive 2010-63-EU.

Author contributions: Conceptualization: L.G. Data curation: C.I.P.; M.N.S.; B.M. Formal analysis: C.I.P.; M.N.S.; B.M.; I.F.D.; V.G. Funding acquisition: E.C. Investigation: C.I.P.; M.N.S.; L.G.; B.M; I.F.D. Methodology: C.I.P.; M.N.S.; L.G.; I.F.D. Project administration: L.G.; E.C.; V.G.;C.L.P. Resources: C.I.P.; L.G.; T.K.S.O.; I.F.D. Software: C.I.P.; M.N.S.; B.M.;C.L.P. Supervision: L.G.; E.C.; F.J.N.G.; J.V.D.B.; V.G.; C.L.P. Validation: C.I.P.; M.N.S.; B.M.;C.L.P. Visualization: M.N.S. Writing – Original Draft: C.I.P.; M.N.S.; L.G.; E.C.; G.L.; C.L.P. Writing – Review & Editing: C.I.P.; M.N.S.; L.G.; F.J.N.G.; J.V.D.B.; I.F.D.; G.L.; T.K.S.O.; E.C.; C.L.P.; V.G. All authors read and approved the final manuscript.

Funding: This research did not receive any dedicated grant. However, the study was carried out in the framework of the EU-funded projects CA.RA.VA.N—'Toward a Camel Transnational Value Chain' (Reference APCIN-2016-00011-00-00) and CAMEL-SHIELD (Camel breeding systems: actors in the sustainable economic development of the northern Sahara territories through innovative strategies for natural resource management and marketing), that assured human, instrumental and biological resources necessary for this work. C.I.P. is granted with a predoctoral contract (FPU Fellowship) funded by the Spanish Ministry of Science and Innovation, and M.N.S. holds a PhD fellowship granted to the University of Bari (Italy) by the Italian Ministry of University and Research (MUR), XXXVII cycle (https://www.uniba.it/it/ricerca/dottorati/37-ciclo). Further acknowledgment is due to the project CICECO-Aveiro Institute of Materials (UIDB/50011/2020, UIDP/50011/2020 & LA/P/0006/2020), financed by national funds through the FCT/MEC (PIDDAC). The NMR spectrometer is part of the National NMR Network (PTNMR), partially supported by Infrastructure Project Nº 022161 (co-financed by FEDER through COMPETE 2020, POCI and PORL and FCT through PIDDAC). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Data availability statement: The data presented in this study are available on request from the first author.

Acknowledgments: The authors would like to thank the personnel of the Aires Africanos farm located in the Doñana National Park (southwestern Spain) for kind collaboration during urine collection.

Competing interest: The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Abdalla, M.A. (2020). Anatomical features in the kidney involved in water conservation through urine concentration in dromedaries (*Camelus dromedarius*). *Heliyon*, 6.

Abdel Gader, A.G.M., & Alhaider, A.A. (2016). The unique medicinal properties of camel products: A review of the scientific evidence. *Journal of Taibah University Medical Sciences*,11, 98–103.

Akella, N.M., Ciraku, L., & Reginato, M.J. (2019). Fueling the fire: emerging role of the hexosamine biosynthetic pathway in cancer. *BMC Biology*, 17, 52.

Al Zahrani, A., Alfakeeh, A., Alghareeb, W., Bakhribah, H., Basulaiman, B., & Alsuhail, A. (2023). Observational study and literature review of the use of camel urine for treatment of cancer patients. *Eastern Mediterranean Health Journal*, 29(8).

Al-Abdalall, A. (2010). The inhibitory effect of camels urine on mycotoxins and fungal growth. *African Journal of Agricultural Research*, 5, 1331–1337.

Alebie, G., Yohannes, S., & Worku, A. (2017). Therapeutic Applications of Camel's Milk and Urine against Cancer: Current Development Efforts and Future Perspectives. *Journal of Cancer Sciences and Therapy*, 9.

Al-Ghumlas, A.K. (2020). Camel platelet aggregation responses and the antiplatelet effect of camel urine: comparison between black and white camels. *Heliyon*, 6.

Alhaidar, A., Abdel Gader, A.G.M., & Mousa, S.A. (2011). The Antiplatelet Activity of Camel Urine. *Journal of Alternative and Complementary Medicine*, 17, 803–808.

Alhaider, A.A., Gader, A.G.M.A., Almeshal, N., & Saraswati, S. (2014). Camel urine inhibits inflammatory angiogenesis in murine sponge implant angiogenesis model. *Biomedicine & Aging Pathology*, 4, 9–16.

Alrumaihi, F.A., Khan, M.A., Allemailem, K.S., Alsahli, M.A., Almatroudi, A., Younus, H., Alsuhaibani, S.A., Algahtani, M., & Khan, A. (2021). Methanolic Fenugreek Seed Extract Induces p53-Dependent Mitotic Catastrophe in Breast Cancer Cells, Leading to Apoptosis. *Journal of Inflammation Research*, 14, 1511–1535.

Al-Yousef, N., Gaafar, A., Al-Otaibi, B., Al-Jammaz, I., Al-Hussein, K., & Aboussekhra, A. (2012). Camel urine components display anti-cancer properties in vitro. *Journal of Ethnopharmacology*, 143, 819–825.

Anwar, S., Ansari, S.A., Alamri, Abdulwahab, Alamri, Abdulhakeem, Alqarni, A., Alghamdi, S., Wagih, M.E., Ahmad, A., & Rengasamy, K.R. (2021). Clastogenic, anti-clastogenic profile and safety assessment of Camel urine towards the development of new drug target. *Food and Chemical Toxicology*, 151, 112131.

Atanasov, A.G., Zotchev, S.B., Dirsch, V.M., & Supuran, C.T. (2021). Natural products in drug discovery: advances and opportunities. *Nature Reviews Drug Discovery*, 20, 200–216.

Attas, A., Khorshid, F., Kao, M., & Bahieldin, A. (2020). Antiviral activity of extracted fraction from camel urine against corona and influenza a (H1N1) viruses. *Applied Ecology & Environmental Research*, 17(5).

Azam, M.S., Kim, E.J., Yang, H.-S., & Kim, J.K. (2014). High antioxidant and DNA protection activities of N-acetylglucosamine (GlcNAc) and chitobiose produced by exolytic chitinase from Bacillus cereus EW5. *SpringerPlus* 3, 354.

Balbaied, T., & Moore, E., 2020. Resazurin-Based Assay for Quantifying Living Cells during Alkaline Phosphatase (ALP) Release. *Applied Sciences*, 10, 3840.

Bálint, Z., Krizbai, I.A., Wilhelm, I., Farkas, A.E., Párducz, A., Szegletes, Z., & Váró, G. (2007). Changes induced by hyperosmotic mannitol in cerebral endothelial cells: an atomic force microscopic study. *European Journal of Biophysics*, 36, 113–120.

Bollard, M.E., Stanley, E.G., Lindon, J.C., Nicholson, J.K., & Holmes, E. (2005). NMR-based metabonomic approaches for evaluating physiological influences on biofluid composition. *NMR in Biomedicine*, 18, 143–162.

Brodaczewska, K.K., Bielecka, Z.F., Maliszewska-Olejniczak, K., Szczylik, C., Porta, C., Bartnik, E., & Czarnecka, A.M. (2019). Metastatic renal cell carcinoma cells growing in 3D on poly-D-lysine or laminin present a stem-like phenotype and drug resistance. *Oncology Reports*, 42, 1878–1892.

Chae, I.G., Song, N.-Y., Kim, D.-H., Lee, M.-Y., Park, J.-M., & Chun, K.-S. (2020). Thymoquinone induces apoptosis of human renal carcinoma Caki-1 cells by inhibiting JAK2/STAT3 through pro-oxidant effect. *Food and Chemical Toxicology*, 139, 111253.

Chang, Y.-H., Weng, C.-L., & Lin, K.-I. (2020). O-GlcNAcylation and its role in the immune system. *Journal of Biomedical Science*, 27, 57.

Chen, X., Zhou, C., Yan, C., Ma, J., & Zheng, W. (2015). Hyperosmotic stress induces cisplatin sensitivity in ovarian cancer cells by stimulating aquaporin-5 expression. *Experimental and Therapeutic Medicine*, 10, 2055–2062.

Chowdhury, A.A., Gawali, N.B., Munshi, R., & Juvekar, A.R. (2018). Trigonelline insulates against oxidative stress, proinflammatory cytokines and restores BDNF levels in lipopolysaccharide induced cognitive impairment in adult mice. *Metabolic Brain Disease*, 33, 681–691.

DeWane, G., Salvi, A.M., & DeMali, K.A. (2021). Fueling the cytoskeleton – links between cell metabolism and actin remodeling. *Journal of Cell Science*, 134.

Diers, A.R., Broniowska, K.A., Chang, C.-F., & Hogg, N. (2012). Pyruvate fuels mitochondrial respiration and proliferation of breast cancer cells: effect of monocarboxylate transporter inhibition. *Biochemical Journal*, 444, 561–571.

Dubost, J.-M., Kongchack, P., Deharo, E., Sysay, P., Her, C., Vichith, L., Sébastien, D., & Krief, S. (2021). Zootherapeutic uses of animals excreta: the case of elephant dung and urine use in Sayaboury province, Laos. *Journal of Ethnobiology and Ethnomedicine*, 17, 62.

Elbehiry, A., Marzouk, E., Moussa, I.M., Alenzi, A., Al-Maary, K.S., Mubarak, A.S., Alshammari, H.D., Al-Sarar, D., Alsubki, R.A., Hemeg, H.A., Kabli, S.A., & Attala, O.A. (2021). Multidrug-resistant Escherichia coli in Raw Milk: Molecular Characterization and the potential impact of camel's Urine as an Antibacterial Agent. *Saudi Journal of Biological Sciences*, 28, 2091–2097.

Elkhair, NM. (2019). Effect of age on certain urine parameters of young camels (*Camelus dromedarius*). *Online Journal of Animal and Feed Research*, 9(1): 33-37.

Emami Riedmaier, A., Nies, A.T., Schaeffeler, E., & Schwab, M. (2012). Organic Anion Transporters and Their Implications in Pharmacotherapy. *Pharmacological Reviews*, 64, 421–449.

Fujisawa, M., Tokuda, M., Morimoto-Yamashita, Y., Tatsuyama, S., Arany, S., Sugiyama, T., Kitamura, C., Shibukawa, Y., & Torii, M. (2012). Hyperosmotic stress induces cell death in an odontoblast-lineage cell line. *Journal of Endodontics*, 38, 931–935.

García-Pérez, E., Ryu, D., Kim, H.-Y., Kim, H.D., & Lee, H.J. (2021). Human Proximal Tubule Epithelial Cells (HK-2) as a Sensitive In Vitro System for Ochratoxin A Induced Oxidative Stress. *Toxins*, 13, 787.

Gaughan, J. (2011). Which physiological adaptation allows camels to tolerate high heat load – and what more can we learn? *Journal of Camelid Science*, 4.

Ghamdi, Z., & Khorshid, F. (2012). Cytotoxicity of the Urine of Different Camel Breeds on the Proliferation of Lung Cancer Cells, A549. *Journal of Natural Sciences Research*, 2.

Glube, N., Giessl, A., Wolfrum, U., & Langguth, P. (2007). Caki-1 Cells Represent an in vitro Model System for Studying the Human Proximal Tubule Epithelium. *Nephron Experimental Nephrology*, 107, e47–e56.

Gorshkov, K., Sima, N., Sun, W., Lu, B., Huang, W., Travers, J., Klumpp-Thomas, C., Michael, S.G., Xu, T., Huang, R., Lee, E.M., Cheng, X., & Zheng, W. (2019). Quantitative Chemotherapeutic Profiling of Gynecologic Cancer Cell Lines Using Approved Drugs and Bioactive Compounds. *Translational Oncology*, 12, 441–452.

Grauso, M., Lan, A., Andriamihaja, M., Bouillaud, F., & Blachier, F. (2019). Hyperosmolar environment and intestinal epithelial cells: impact on mitochondrial oxygen consumption, proliferation, and barrier function in vitro. *Scientific Reports*, 9, 11360.

Guo, M., Pegoraro, A.F., Mao, A., Zhou, E.H., Arany, P.R., Han, Y., Burnette, D.T., Jensen, M.H., Kasza, K.E., Moore, J.R., Mackintosh, F.C., Fredberg, J.J., Mooney, D.J., Lippincott-Schwartz, J., & Weitz, D.A. (2017). Cell volume change through water efflux impacts cell stiffness and stem cell fate. *Proceedings of the National Academy of Sciences*, 114, E8618–E8627.

Hany S. Mahmoud, Wael M. Elsaed, & Sami A. Gabr (2019). Camel urotherapy and hepatoprotective effects against carbon tetrachloride-induced liver toxicity. *International Journal of Pharmacology*, 15(6), 696-705.

Hosseiniyan Khatibi, S.M., Zununi Vahed, F., Sharifi, S., Ardalan, M., Mohajel Shoja, M., & Zununi Vahed, S. (2019). Osmolytes resist against harsh osmolarity: Something old something new. *Biochimie,* 158, 156–164.

Hu, Z., Chang, X., Pan, Q., Gu, K., & Okechukwu, P.N. (2017). Gastroprotective and ulcer healing effects of camel milk and urine in HCl/EtOH, non-steroidal anti-inflammatory drugs (indomethacin), and water-restraint stress-induced ulcer in rats. *Pharmacognosy Magazine*, 13, 559.

Hua, Y., Liang, C., Zhu, J., Miao, C., Yu, Y., Xu, A., Zhang, J., Li, P., Li, S., Bao, M., Yang, J., Qin, C., & Wang, Z. (2017). Expression of lactate dehydrogenase C correlates with poor prognosis in renal cell carcinoma. *Tumor Biology*, 39, 1010428317695968.

Iglesias Pastrana, C., Delgado Bermejo, J.V., Sgobba, M.N., Navas González, F.J., Guerra, L., Pinto, D.C.G.A., Gil, A.M., Duarte, I.F., Lentini, G., & Ciani, E., 2022. Camel (*Camelus* spp.) Urine Bioactivity and Metabolome: A Systematic Review of Knowledge Gaps, Advances, and Directions for Future Research. *International Journal of Molecular Sciences*, 23, 15024.

Khorshid, F., Emwas, A.-H., & Mahboub, F. (2015). The Cytotoxic Effect of Small and Large Molecules of PMF Fraction Extracted from Camel Urine on Cancer Cells. *British Journal of Medical and Health Research*, 6, 384–396.

Kim, G.-N., Hah, Y.-S., Seong, H., Yoo, W.-S., Choi, M.-Y., Cho, H.-Y., Yun, S.P., & Kim, S.-J. (2021). The Role of Nuclear Factor of Activated T Cells 5 in Hyperosmotic Stress-Exposed Human Lens Epithelial Cells. *International Journal of Molecular Sciences*, 22, 6296.

Kinsman, B.J., Browning, K.N., & Stocker, S.D. (2017). NaCl and osmolarity produce different responses in organum vasculosum of the lamina terminalis neurons, sympathetic nerve activity and blood pressure. *Journal of Physiology*, 595, 6187–6201.

Kritis, A.A., Stamoula, E.G., Paniskaki, K.A., & Vavilis, T.D. (2015). Researching glutamate – induced cytotoxicity in different cell lines: a comparative/collective analysis/study. *Frontiers in Cellular Neuroscience*, 9.

Laera, L., Punzi, G., Porcelli, V., Gambacorta, N., Trisolini, L., Pierri, C.L., & De Grassi, A. (2020). CRAT missense variants cause abnormal carnitine acetyltransferase function in an early-onset case of Leigh syndrome. *Human Mutation*, 41, 110–114.

Lee, C.-C., Huang, P.-Y., Hsieh, Y.-H., Chen, Y.-S., & Tsai, J.-P. (2021). Melatonin combined with sorafenib synergistically inhibit the invasive ability through targeting metastasis-associated protein 2 expression in human renal cancer cells. *Tzu Chi Medical Journal*, 34, 192–199.

Lee, S.-U., Li, C.F., Mortales, C.-L., Pawling, J., Dennis, J.W., Grigorian, A., & Demetriou, M. (2019). Increasing cell permeability of N-acetylglucosamine via 6-acetylation enhances capacity to suppress T-helper 1 (TH1)/TH17 responses and autoimmunity. *PLOS ONE* 14, e0214253.

Liang, Y., Li, S., & Chen, L., 2015. The physiological role of drug transporters. *Protein Cell* 6, 334–350.

Ma, R., Wu, Y., Zhai, Y., Hu, B., Ma, W., Yang, W., Yu, Q., Chen, Z., Workman, J.L., Yu, X., & Li, S. (2019). Exogenous pyruvate represses histone gene expression and inhibits cancer cell proliferation via the NAMPT–NAD+–SIRT1 pathway. *Nucleic Acids Research*, 47, 11132–11150.

Mitschke, N., Vemulapalli, S. P. B., & Dittmar, T. (2023). NMR spectroscopy of dissolved organic matter: a review. *Environmental Chemistry Letters*, 21(2), 689-723.

Moon, D., Kim, J., & Yoon, S.-P. (2019). Yeast extract inhibits the proliferation of renal cell carcinoma cells via regulation of iron metabolism. *Molecular Medicine Reports*, 20, 3933–3941.

Mossoba, M.E., & Sprando, R.L. (2020). In Vitro to In Vivo Concordance of Toxicity Using the Human Proximal Tubule Cell Line HK-2. *International Journal of Toxicology*, 39, 452–464.

Ouajd, S., & Kamel, B. (2009). Physiological particularities of dromedary (*Camelus dromedarius*) and experimental implications. *Scandinavian Journal of Laboratory Animal Science*, 36(1), 19-29.

Pham, H.N.T., Sakoff, J.A., Vuong, Q.V., Bowyer, M.C., & Scarlett, C.J. (2018). Comparative cytotoxic activity between kaempferol and gallic acid against various cancer cell lines. *Data Brief*, 21, 1033–1036.

Porowski, T., Kirejczyk, J.K., Mrozek, P., Protas, P., Kozerska, A., Łabieniec, Ł., Szymański, K., & Wasilewska, A. (2019). Upper metastable limit osmolality of urine as a predictor of kidney stone formation in children. *Urolithiasis*, 47, 155–163.

Punzi, G., Porcelli, V., Ruggiu, M., Hossain, M.F., Menga, A., Scarcia, P., Castegna, A., Gorgoglione, R., Pierri, C.L., Laera, L., Lasorsa, F.M., Paradies, E., Pisano, I., Marobbio, C.M.T., Lamantea, E., Ghezzi, D., Tiranti, V., Giannattasio, S., Donati, M.A., Guerrini, R., Palmieri, L., Palmieri, F., & De Grassi, A. (2018). SLC25A10 biallelic mutations in intractable epileptic encephalopathy with complex I deficiency. *Human Molecular Genetics*, 27, 499–504.

Ramos-Ibeas, P., Barandalla, M., Colleoni, S., & Lazzari, G. (2017). Pyruvate antioxidant roles in human fibroblasts and embryonic stem cells. *Molecular and Cellular Biochemistry*, 429, 137–150.

Rofaei, N.A.E., Balla, M.H., Mutwali, E.M., Elkhiry, H.B., Rofaei, N.A.E., Balla, M.H., Mutwali, E.M., & Elkhiry, H.B. (2022). In vitro assessment of antibacterial property of camel's urine against some isolated *Salmonella* strains. *GSC Advanced Research and Reviews*, 13, 109–114.

Romli, F., Abu, N., Khorshid, F.A., Syed Najmuddin, S.U.F., Keong, Y.S., Mohamad, N.E., Hamid, M., Alitheen, N.B., & Nik Abd Rahman, N.M.A. (2017). The Growth Inhibitory Potential and Antimetastatic Effect of Camel Urine on Breast Cancer Cells In Vitro and In Vivo. *Integrative Cancer Therapies*, 16, 540–555.

Ryan, M.J., Johnson, G., Kirk, J., Fuerstenberg, S.M., Zager, R.A., & Torok-Storb, B. (1994). HK-2: An immortalized proximal tubule epithelial cell line from normal adult human kidney. *Kidney International*, 45, 48–57.

Salamt, N., Idrus, R.B.H., Kashim, M.I.A.M., & Mokhtar, M.H. (2021). Anticancer, antiplatelet, gastroprotective and hepatoprotective effects of camel urine: A scoping review. *Saudi Pharmaceutical Journal*, SPJ 29, 740–750.

Schreier, C., Kremer, W., Huber, F., Neumann, S., Pagel, P., Lienemann, K., & Pestel, S. (2013). Reproducibility of NMR Analysis of Urine Samples: Impact of Sample Preparation, Storage Conditions, and Animal Health Status. *BioMed Research International*, 2013, e878374.

Sharma, D., Singh, M., Gupta, R., Kumar, Vivek, Kumar, Vinit, & Rani, R. (2022). Intervention on lactate in cancer: A promising approach for the development of cancer therapeutics. *Advances in Cancer Biology - Metastasis*, 5, 100058.

Shi, J., Qian, J., Li, H., Luo, H., Luo, W., & Lin, Z. (2018). Renal tubular epithelial cells injury induced by mannitol and its potential mechanism. *Renal Failure*, 40, 85–91.

Shikhman, A.R., Brinson, D.C., Valbracht, J., & Lotz, M.K. (2009). Differential metabolic effects of glucosamine and N-acetylglucosamine in human articular chondrocytes. *Osteoarthritis Cartilage,* 17, 1022–1028.

Sprowl-Tanio, S., Habowski, A.N., Pate, K.T., McQuade, M.M., Wang, K., Edwards, R.A., Grun, F., Lyou, Y., & Waterman, M.L. (2016). Lactate/pyruvate transporter MCT-1 is a direct Wnt target that confers sensitivity to 3-bromopyruvate in colon cancer. *Cancer & Metabolism*, 4, 20.

Syed Abdul Rahman, S.N., Abdul Wahab, N., & Abd Malek, S.N. (2013). In Vitro Morphological Assessment of Apoptosis Induced by Antiproliferative Constituents from the Rhizomes of Curcuma zedoaria. *Evidence-Based Complementary and Alternative Medicine*, 257108.

Thomson, T.M., Balcells, C., & Cascante, M. (2019). Metabolic Plasticity and Epithelial-Mesenchymal Transition. *Journal of Clinical Medicine*, 8, 967.

Tian, Y.-C., Fraser, D., Attisano, L., & Phillips, A.O. (2003). TGF-β1-mediated alterations of renal proximal tubular epithelial cell phenotype. *American Journal of Physiology-Renal Physiology*, 285, F130–F142.

Todisco, S., Musio, B., Pesce, V., Cavalluzzi, M.M., Petrosillo, G., La Piana, G., Sgobba, M.N., Schlosserová, N., Cafferati Beltrame, L., Di Lorenzo, R., Tragni, V., Marzulli, D., Guerra, L., De Grassi, A., Gallo, V., Volpicella, M., Palese, L.L., Lentini, G., & Pierri, C.L. (2023). Targeting mitochondrial impairment for the treatment of cardiovascular diseases: From hypertension to ischemia-reperfusion injury, searching for new pharmacological targets. *Biochemical Pharmacology*, 208, 115405.

Tragni, V., Primiano, G., Tummolo, A., Cafferati Beltrame, L., La Piana, G., Sgobba, M.N., Cavalluzzi, M.M., Paterno, G., Gorgoglione, R., Volpicella, M., Guerra, L., Marzulli, D., Servidei, S., De Grassi, A., Petrosillo, G., Lentini, G., & Pierri, C.L. (2022). Personalized Medicine in Mitochondrial Health and Disease: Molecular Basis of Therapeutic Approaches Based on Nutritional Supplements and Their Analogs. *Molecules*, 27, 3494.

Trisolini, L., Laera, L., Favia, M., Muscella, A., Castegna, A., Pesce, V., Guerra, L., De Grassi, A., Volpicella, M., & Pierri, C.L. (2021). Differential Expression of ADP/ATP Carriers as a Biomarker of Metabolic Remodeling and Survival in Kidney Cancers. *Biomolecules*, 11, 38.

Trisolini, L., Laera, L., Favia, M., Muscella, A., Castegna, A., Pesce, V., Guerra, L., De Grassi, A., Volpicella, M., & Pierri, C.L. (2020). Differential Expression of ADP/ATP Carriers as a Biomarker of Metabolic Remodeling and Survival in Kidney Cancers. *Biomolecules*, 11, 38.

van Vonderen, I.K., Kooistra, H.S., & Rijnberk, A. (1997). Intra- and Interindividual Variation in Urine Osmolality and Urine Specific Gravity in Healthy Pet Dogs of Various Ages. *Journal of Veterinary Internal Medicine*, 11, 30–35.

Vogt, K., Boos, S., Breitenmoser, U., & Kölliker, M. (2016). Chemical composition of Eurasian lynx urine conveys information on reproductive state, individual identity, and urine age. *Chemoecology*, 26, 205–217.

Xu, Z., Isaji, T., Fukuda, T., Wang, Y., & Gu, J. (2019). O-GlcNAcylation regulates integrin-mediated cell adhesion and migration via formation of focal adhesion complexes. *Journal of Biological Chemistry*, 294, 3117–3124.

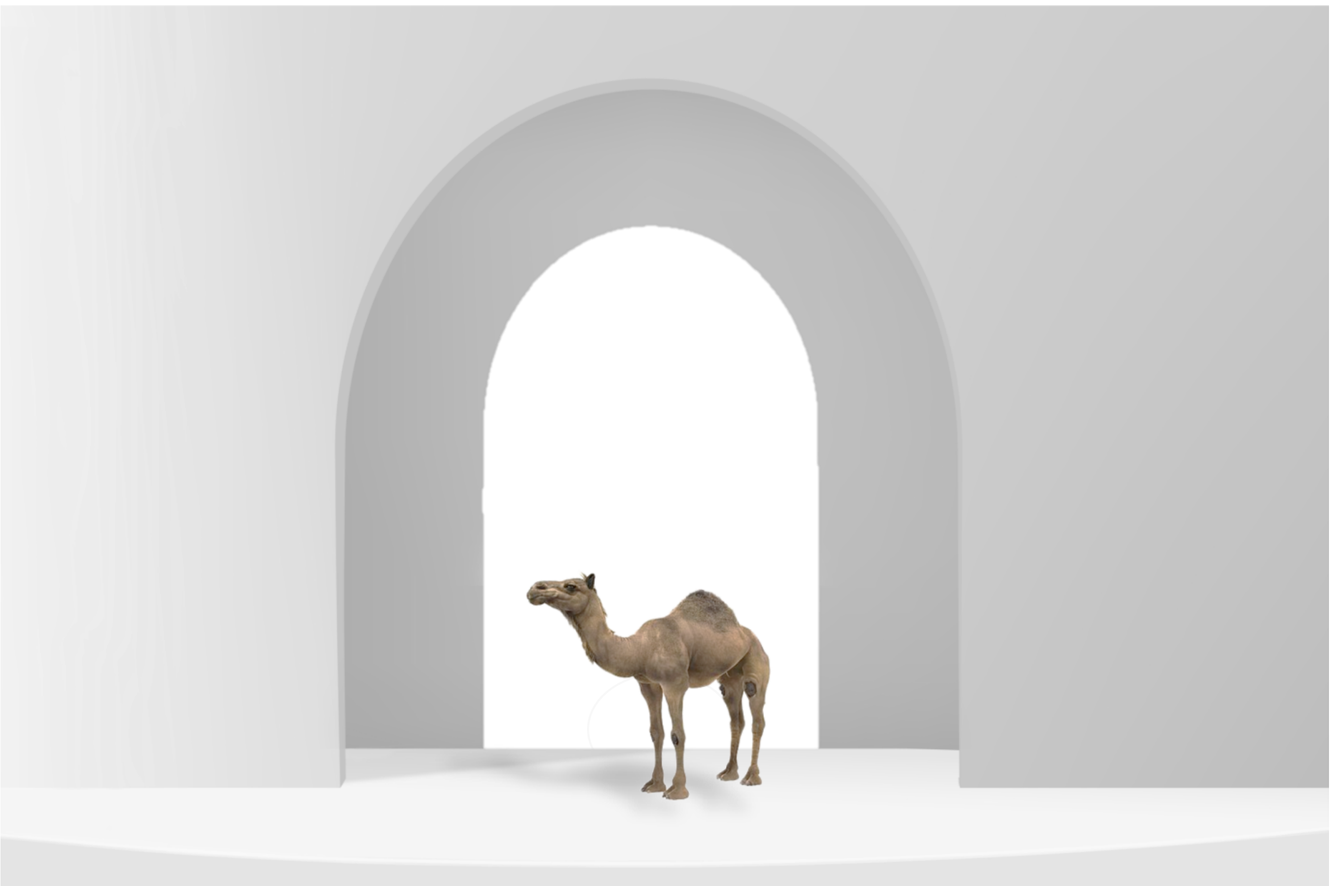
Yagil, R., & Berlyne, G.M. (1978). Glomerular Filtration Rate and Urine Concentration in the Dromedary Camel in Dehydration. *Kidney and Blood Pressure Research*, 1, 104–112.

Zahra, K.F., Lefter, R., Ali, A., Abdellah, E.-C., Trus, C., Ciobica, A., & Timofte, D. (2021). The Involvement of the Oxidative Stress Status in Cancer Pathology: A Double View on the Role of the Antioxidants. *Oxidative Medicine and Cellular Longevity*, 2021, 9965916.

Zhang, X., Alshakhshir, N., & Zhao, L. (2021). Glycolytic Metabolism, Brain Resilience, and Alzheimer's Disease. *Frontiers in Neuroscience*, 15, 662242.

Zhao, P., Chen, X., Wang, Q., Zou, H., Xie, Y., Liu, H., Zhou, Y., Liu, P., & Dai, H. (2020). Differential toxicity mechanism of gold nanoparticles in HK-2 renal proximal tubular cells and 786-0 carcinoma cells. *Nanomedicine*, 15, 1079–1096.

CONCLUSIONS



General conclusion

Natural/rearing environment and animal-based factors (phaneroptics and sex) differentially regulate body morphology, biomechanics, and behaviour related traits in the 'Canarian Camel' breed, which constitutes the only genetic resource of such nature in Europe, officially cataloged at risk of extinction and mainly relegated to leisure riding. The knowledge of the specific influence of each factor on the abovementioned traits' phenotypic variability, together with the identification of the genomic regions underlying such variability, the study of the socio-cultural dimensions of camelback leisure riding tours, and the exploration of new potential functional niches, will further inform future programs for the long-term, sustainable conservation and genetic improvement of this camel breed.

Specific conclusions

Chapter 1

- Although a contemporaneous, parallel evolution between socio-economic interests for the rearing and production of camel species and camel science progress is patent, topics such as camel handling, nutrition, ecology, genetic management, and production, are scarcely approached. This situation is limiting the enforcement of mandatory regulations to ensure sustainable camel breeding practices under the scope of animal welfare, being this subject particularly relevant for endangered genetic resources.

Chapter 2

- Despite the low intensity of artificial selection and limited pedigree management, substantial phenotypic diversification does exist for zoometric traits between and within subpopulations of the 'Canarian Camel' breed. This extant diversity, along with the significant influence of sex, physiological status, and coat colour on body morphology traits for this camel breed, will inform and predict the success of future breeding strategies.

- Mathematical modeling and linear appraisal scales constitute contactless, reliable methodologies for the zoometric characterization of dromedaries based on digital images and on-site visual evaluation, respectively.

Chapter 3

- Being a highly conserved ancestral trait, biomechanical performance in 'Canarian Camel' breed significantly depends on angularity and mechanical forces at the distal fore and rear extremity areas, the inclination of the pelvis, specific morphological proportionalities affecting the general balance of the body, neutering status, and the velocity, acceleration, spatial position, and displacement of scapula, shoulder, carpus, hip, and foot.

- Sex, castration, age, iris pigmentation, and the local variability for surface temperature at the cornea, withers, shoulder, pectoral muscles, semimembranosus-semitendinosus muscles, rump, and hind fetlock, serve for the prediction of thermophysiological response and tolerance to physical exercise in the 'Canarian Camel' breed.

Chapter 4

- New moon and ambient air predict the onset of spontaneous parturition depending on the sex of offspring in Canarian dromedary camels. This phenology can be interpreted as a manifestation of phenotypic adaptation that involves species-specific social ecology and body-fluid balance features to maximize parent fitness and offspring survival.

- Negative reinforcement strategies and the use of a combination of visual and auditory stimuli are the most optimal tools to increase camels' approaching behaviour towards new, unknown stimuli. Additionally, sex and interspecific communication signals (ear position) can serve to predict the proactive and reactive responses in the 'Canarian Camel' breed.

- Dromedary camels can be accurately assessed for cognitive traits underlying intelligence and general cognition processes by using a human-analogous, validated IQ (Intelligence Quotient) scoring method.

- The comfortability when separated from the main herd is the most distinguishing factor between Canarian dromedary camels for their Intelligence Quotient (IQ). This can be a reflection of the social character and hierarchy of the camels, thus a reliable indicator of the existence of a group intelligence for this animal species.

- In regards to the effects of different environment and animal-dependent factors (sex, phaneroptics, owner, and training regime) on cognitive performance, concentration, dependence on the group, docility, and ease of handling are the processes that best discriminate among qualitative categories for each influencing factor, therefore the best criteria for selection of dromedaries according to their cognitive abilities.
- Body morphology and weight, neutering status, age, coat colour and particularities, and iris colour significantly condition the probability of an individual camel emerging as a leader of group movements. Routine intraherd handling practices will be improved in efficiency and security through the identification and selection of the best leader camel(s).

Chapter 5

- Genotypic clustering further evidences the divergence and slight introgression between subpopulations of the 'Canarian Camel' breed, and suggests a human-driven selection of Canarian dromedaries for the maintenance of the size- and behaviour-assortative natural mating.

- Seventy different candidate genes have been identified to be controlling the extant phenotypic variability for zoometrics, biomechanics, and behaviour-related traits in leisure dromedary camels. Ten out of these seventy candidate genes were significantly associated with various traits, which suggests that the interindividual variability that exists for zoometrical, biomechanical, and behavioural phenotypes in leisure dromedary camels is regulated by determinants of polygenic nature.

- Candidate genes associated with zoometrics, biomechanics, and behaviour-related traits in Canarian dromedary camels are largely involved in the control of several neurodevelopmental processes, and visual, hearing and vestibular systems' function. Such findings fit the 'domestication syndrome' hypothesis and will assist the definition of future marker-assisted selection schemes for dromedaries.

Chapter 6

- Staff performance, cultural geography, diverse and animal-friendly, close interaction with camels, camel behaviour and performance, socio-temporal context, and positive previous experiences in camelback leisure riding contribute to increasing both customer general satisfaction and return intention probability in camel-riding tourist walks.

- Concerning camel behaviour and performance during leisure riding tours, animals' indifference towards humans is linked to user dissatisfaction. In addition, as the camel's environmental curiosity increases, full concentration is potentially reduced, and the level of customer satisfaction progressively decreases. Negative selection approaches against such behavioural features may be encouraged.

Chapter 7

- The great average diameter and its lower variation within small fragments along the snippet, confer camel hair fiber prominent resistance to industrial processing (spinning performance). Furthermore, the ability to reflect light and the internal medullation makes camel-origin fiber a valuable textile material for the lightness and heat-insulating properties of final textile products.
- From the mid-region to the back of the animal, the diameter at the base of the hair fiber increases for adult dromedary camels. Notable variability does also exist for both staple length and mean diameter of hair fibers from the regions of the shoulder and hump of this animal species. However, coat colour and particularities are unlikely to significantly affect fiber diameter and strength but the light reflection capacity of camel hair fibers.
- The empirical, standardized demonstration of the biomedical applications of the molecules contained in camel urine comprises the control and adjustment of urine osmolarity before *in vitro*/*in vivo* testing, and the ulterior association of bioactive effects with the metabolomic profile of urines. Under these assumptions, Canarian dromedary camel's urine has been demonstrated to limit proliferation and modify cell morphology in human renal tumoral and non-tumoral cells, respectively. The urine metabolite N-acetylglucosamine may play a role in the observed cell viability patterns.

Where we were

i. Unique European recognized camel breed ('Canarian Camel'), officially listed as endangered autochthonous livestock, and linked to the development of the socio-economic and cultural heritage of the Canary Islands (Spain) since the beginning of the 15th century, reproductively isolated for health reasons from camel populations of third countries, and lacking regulate, standardized phenotypic/functional characterization for those traits involved in their main functional performance (leisure tourism) as well as rigorous genealogical control.

ii. Imperative need to valorize and highlight the richness of this unique genetic resource as a measure of protection of the socio-cultural heritage and biodiversity of the Canary Islands.

Where we are

i. Implementation, optimization and validation of different methodologies for the zoometric, biomechanical and behavioural characterization of the 'Canarian Camel' breed, since these phenotypic/functional traits are those that largely influence its main functionality (leisure tourism). All the methodologies are translatable to other camel populations and species.

ii. Identification of genomic regions underlying the phenotypic variability for zoometric, biomechanics and behaviour related traits in leisure dromedary camels.

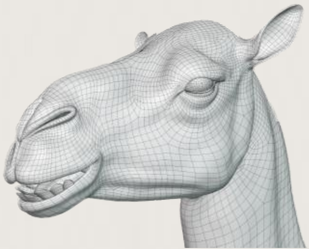
iii. Preliminary exploration of the potentialities of additional functional niches (textile fiber production and applied biomedicine) to be converted into economic, sustainable revenues for the conservation of the 'Canarian Camel' breed.

i. Since the Canary Islands constitutes the largest biological reserve of the 'Canarian Camel' breed, the technical training in the fields of animal phenotyping (based on the methodologies presented in the current doctoral thesis) and efficient management of the studbook becomes fundamental for local breeders, technicians, and other personalities involved and interested in the selective breeding and conservation of the Canarian camel breed.

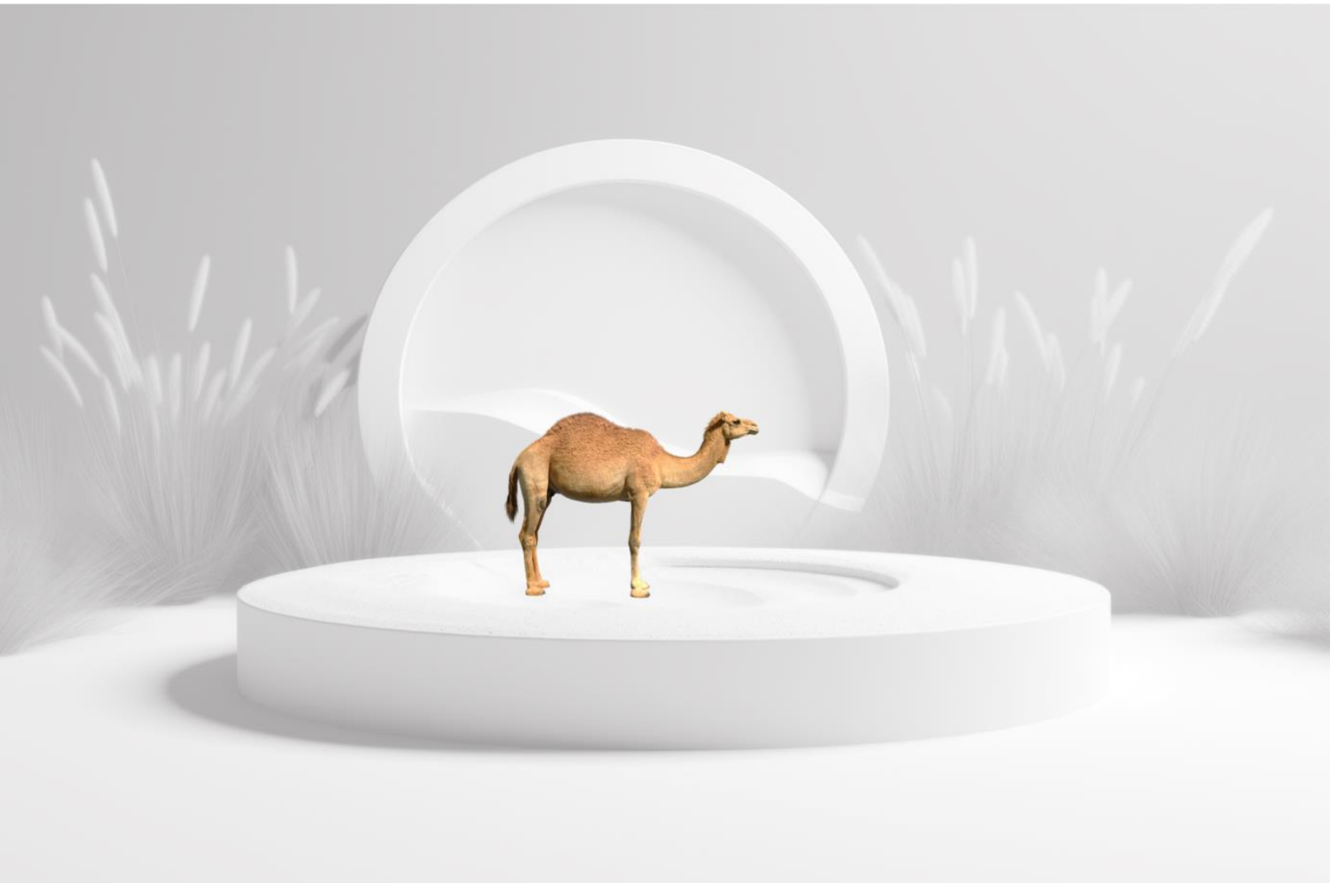
ii. The fact that the greatest effective population of 'Canarian Camel' breed inhabits a relatively reduced geographical range (Canary Islands) is a risk factor that can aggravate the conservation status of the breed in the face of stochastic phenomena. Therefore, their introduction in other geographical areas along Europe that potentially reunite the geo-climate conditions and specialized human resources for their sustainable breeding and survival, can help minimize this risk situation.

iii. The knowledge of the genomic regions that are controlling the phenotypic traits that largely influence the main functionality of 'Canarian Camel' breed, will aid at designing effective, marker-assisted selection schemes. These programmes can overcome, in the short to mid-term, the possible limitations that may arise from traditionally selection based on phenotypic and pedigree information (e.g., increase the rate of genetic gain).

iv. The evaluation of opportunities for sustainable exploitation of 'Canarian Camel' breed as food provider (milk and meat) at an European market -similarly to other camel breeds and populations worldwide- could be feasible in the short term as soon as local, specific facilities (technified milking parlours and specialized slaughterhouses) and a considerable number of producing camels are available.



OTHER RESULTS DERIVED FROM THE DOCTORAL THESIS



A. Scientific papers

a. Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S. and Delgado, J. V. (2020). Zoometric characterization and body condition score in Canarian camel breed. *Archivos de zootecnia*, 69(265), 14-21.

b. Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S. and Delgado, J. V. (2020). Biokinematics and applied thermography in the Canarian camel breed. *Archivos de zootecnia*, 69(265), 102-107.

c. Iglesias, C., Navas, F. J., Ciani, E., Arando, A., González, A., Marín, C., Nogales, S. and Delgado, J. V. (2020). Ethological characterization of the Canarian camel breed. *Archivos de zootecnia*, 69(265), 108-115.

d. Alary, V., Amsidder, L., Araba, A., Capote, C. B., Bedhiaf-Romdhani, S., Bensalem, W., Boujenane, I., Ciani, E., Letaief, N., Faye, B., Suheil Gaouar, S.B., Iglesias Pastrana, C., Nogales Baena, S., Amin Laridji, M.A. and Amine, L. (2021). Social network analysis of the stakeholders involved in the dromedary sector in the Mediterranean region. *Sustainability*, 13(21), 12127.

e. Iglesias, C., Navas, F. J., Ciani, E., Barba, C. J. and Delgado, J. V. (2022). Sociological profile of touristic camel rides users: a tool to contribute to the sustainable use of native camel genetic resources. *Options Méditerranéennes*, p.85.

B. Book chapters

a. Benaissa, M.H. and Iglesias Pastrana, C. (2023). Good Health: recognition and prevention of disease and pain. In *Dromedary Camel Behavior and Welfare: Camel-friendly Management Practices*. B. Padalino and B. Faye (Eds). Springer Nature. *Accepted for publication*.

b. Faraz, A., Maryam Hussain, S., Iglesias Pastrana, C. and Zappaterra, M. (2023). Good Camel Housing: camels and their interaction with the environment. In *Dromedary Camel Behavior and Welfare: Camel-friendly Management Practices*. B. Padalino and B. Faye (Eds). Springer Nature. *Accepted for publication*.

c. Ciani, E., Burger, P., Zappaterra, M. and Iglesias Pastrana, C. (2023). How early domestication and modern genomics contribute to camel welfare. In *Dromedary Camel Behavior and Welfare: Camel-friendly Management Practices*. B. Padalino and B. Faye (Eds). Springer Nature. *Accepted for publication*.

C. Contributions to national and international congresses and webinars

a. ***Keynote speech***:

   i. An overview on the use of dromedaries in tourism and assisted therapies. *Final Meeting of the EU-funded CARAVAN Project*. On-line, 9th-10th June 2021.

   ii. Pain assessment in animals through species-specific rating scales. *1st International Day (1st JISPA) on Animal Health and Welfare*. Animal Health & Production, National High School of Veterinary Medicine, Algiers (Algeria). On-line, 4th June 2022.

iii. Multiple phenotype collection in dromedary camels: zoometrics, kinetics and behavior. *The Sixth Conference of ISOCARD (The International Society of Camelid Research and Development)*. Al-Hofuf (Saudi Arabia), 12th-16th March 2023.

b. ***Oral communication***:

i. Carlos Iglesias Pastrana, Francisco Javier Navas González and Juan Vicente Delgado Bermejo. Dimensiones socio-culturales de los paseos turísticos en camello: beneficios de su conocimiento para la conservación de la biodiversidad. *II Congreso Internacional Multidisciplinar de Investigadores en Formación (CIMIF-20)*. On-line, 30th November-4th December 2020.

ii. Carlos Iglesias Pastrana, Francisco Javier Navas González, Elena Ciani, Sergio Nogales Baena and Juan Vicente Delgado Bermejo. Principales motivaciones del usuario cliente de paseos turísticos en camello: hacia un modelo integral de turismo sostenible para la conservación de la biodiversidad. *XXI Simposio Iberoamericano sobre conservación y utilización de Recursos Zoogenéticos*. On-line, 15th-16th December 2020.

iii. Carlos Iglesias Pastrana, Francisco Javier Navas González, Elena Ciani, Sergio Nogales Baena and Juan Vicente Delgado Bermejo. Conducta y desempeño del camello: factores condicionantes de la satisfacción general del cliente en paseos turísticos en camello. *XXI Simposio Iberoamericano sobre conservación y utilización de Recursos Zoogenéticos*. On-line, 15th-16th December 2020.

iv. Carlos Iglesias Pastrana, Francisco Javier Navas González, Elena Ciani, Sergio Nogales Baena and Juan Vicente Delgado Bermejo. Capacitación del factor humano prestador: garantía de la calidad del servicio y la satisfacción del cliente en paseos turísticos en camello. *XXI Simposio Iberoamericano sobre conservación y utilización de Recursos Zoogenéticos*. On-line, 15th-16th December 2020.

v. Carlos Iglesias Pastrana, Francisco Javier Navas González, Elena Ciani, Cecilio Barba Capote and Juan Vicente Delgado Bermejo. Bienestar animal en ganaderías camellares: correlaciones entre progreso científico y cobertura legislativa. *XXI Simposio Iberoamericano sobre conservación y utilización de Recursos Zoogenéticos*. On-line, 15th-16th December 2020.

vi. Iglesias Pastrana, C., Navas González, F.J., Delgado Bermejo, J.V., Araujo, R., Duarte, D., Pereira, E., Gil, A.M., Pinto, D., Duarte, I.F. and Ciani, E. Metabolomic analysis of camel urine towards the identification of bioactive compounds. *CARAVAN Project Final Meeting*. On-line, 9th-10th June 2021.

vii. Iglesias Pastrana, C., Sgobba, M.N., Navas González, F.J., Delgado Bermejo, J.V., Duarte, I.F., Lentini, G., Kamal Sayed Osman, T., Guerra, L. and Ciani, E. Dromedary camel urine limits proliferation and modifies cell morphology in human renal tumor and normal cells. *ICAR 2020+2 Satellite Meeting on Camelid Reproduction*. Bologna (Italy), 1st-3rd July 2022.

viii. Sgobba, M.N., Iglesias Pastrana, C., Lentini, G., Duarte, I.F., Navas González, F.J., Delgado Bermejo, J.V., Topputi, R., Kamal Sayed Osman, T., Ciani, E. and

Guerra, L. 2-PBA, a small molecule observed in dromedary urine, induces morphological changes in secondary human renal cell lines. *ICAR 2020+2 Satellite Meeting on Camelid Reproduction*. Bologna (Italy), 1st-3rd July 2022.

ix. Carlos Iglesias Pastrana, Francisco Javier Navas González, Elena Ciani, Beatriz López de los Santos and Juan Vicente Delgado Bermejo. Descripción fenotípica comparada de parámetros físico-mecánicos de pelo de camello según la región corporal y la edad. *XXIII Simposio Iberoamericano sobre conservación y utilización de Recursos Zoogenéticos/XIII Congreso Ibérico SERGA-SPREGA sobre Recursos Genéticos Animales*. Cordoba (Spain), 21th-23th October 2022.

x. Carlos Iglesias Pastrana, Francisco Javier Navas González, Elena Ciani, Beatriz López de los Santos and Juan Vicente Delgado Bermejo. Análisis discriminante y comparativo de parámetros físico-mecánicos relacionados con la calidad en fibras textiles: pelo de camello vs. lana ovina. *XXIII Simposio Iberoamericano sobre conservación y utilización de Recursos Zoogenéticos/XIII Congreso Ibérico SERGA-SPREGA sobre Recursos Genéticos Animales*. Cordoba (Spain), 21th-23th October 2022.

xi. Bruno, S., Senczuk, G., Landi, V., Di Civita, M., Brooks, S., Almathen, F., Faye, B., Gaouar, S.B.S., Piro, M., Kim, K-S., Dadi, H., Iglesias Pastrana, C., Al-Haddad, H., Al-Abri, M., David, X., Eggen, A., Burger, P. and Ciani, E. An extensive world-wide *Camelus dromedarius* genetic diversity study using whole-genome sequence data. *The Plant & Animal Genome Conference (PAG)*. San Diego (California, USA), 13th-18th January 2023.

xii. C. Iglesias Pastrana, F.J. Navas González, E. Ciani, M.E. Camacho Vallejo and J.V. Delgado Bermejo. Desarrollo de un modelo matemático para la extracción de medidas zoométricas lineales y tridimensionales a partir de fotografías 2D en dromedarios. *III Congreso Anual Internacional de Estudiantes de Doctorado (CAIED)*. Online, 2nd-3rd February 2023.

xiii. Bruno, S., Senczuk, G., Landi, V., Di Civita, M., Brooks, S., Almathen, F., Faye, B., Gaouar, S.B.S., Piro, M., Kim, K-S., Dadi, H., Iglesias Pastrana, C., Al-Haddad, H., Al-Abri, M., David, X., Eggen, A., Burger, P. and Ciani, E. The Illumina® Agricultural Greater Good Initiative: development of a medium-density SNP chip for camels. *The Sixth Conference of ISOCARD (The International Society of Camelid Research and Development)*. Al-Hofuf (Saudi Arabia), 12th-16th March 2023.

xiv. M.N. Sgobba, C. Iglesias Pastrana, N. Schlosserová, F.J. Navas González, J.V. Delgado Bermejo, T.O. Kamal Sayed, L. Guerra and E. Ciani. Camel urine impacts on human renal cell lines viability in serum-reduced media. *The Sixth Conference of ISOCARD (The International Society of Camelid Research and Development)*. Al-Hofuf (Saudi Arabia), 12th-16th March 2023.

xv. C. Iglesias Pastrana, F.J. Navas González, T. Kamal Sayed Osman, E. Ciani and J.V. Delgado Bermejo. Optimization and validation of a linear appraisal scoring system for physical fitness-linked zoometric traits in dromedary camels. *The Sixth Conference of ISOCARD (The International Society of*

Camelid Research and Development). Al-Hofuf (Saudi Arabia), 12th-16th March 2023.

xvi. P. A. Burger, E. Ciani, C. Iglesias Pastrana, H. Alhaddad and J.M. Astruc. The Sheep, Goats and Camelids Working Group at ICAR (International Committee of Animal Recording) and its opportunities for advanced performance recording. *The Sixth Conference of ISOCARD (The International Society of Camelid Research and Development)*. Al-Hofuf (Saudi Arabia), 12th-16th March 2023.

xvii. G. Senczuk, S. Bruno, M. Di Civita, V. Landi, S. Brooks, F. Almathen, B. Faye, S.B.S. Gaouar, M. Piro, K.S. Kim, H. Dadi, C. Iglesias Pastrana, H. Al-Haddad, M. Al-Abri and C. Persichilli. Whole-genome diversity of dromedary camels from the entire geographic distribution range. *The 39th International Society for Animal Genetics Conference (ISAG)*. Cape Town (South Africa), 2nd-7th July 2023.

xviii. M. Di Civita, G. Senczuk, S. Bruno, V. Landi, S. Brooks, F. Almathen, B. Faye, S. B. S. Gaouar, M. Piro, K. S. Kim, H. Dadi, C. Iglesias Pastrana, H. Al-Haddad, M. Al-Abri and F. Pilla. ISAG Bursary Award: The development of a 61K Illumina? SNP chip for dromedaries under the frame of the 2019 Agricultural Greater Good (AGG) initiative. *The 39th International Society for Animal Genetics Conference (ISAG)*. Cape Town (South Africa), 2nd-7th July 2023.

xix. Carlos Iglesias Pastrana, Francisco Javier Navas González, Elena Ciani and Juan Vicente Delgado Bermejo. Rangos termográficos para la monitorización de salud física/bienestar animal y selección fenotípica en camellos. *XXIV Simposio Iberoamericano sobre conservación y utilización de Recursos Zoogenéticos*. Veracruz (Mexico), 2nd-6th October 2023. *Accepted for presentation*.

xx. Carlos Iglesias Pastrana, Francisco Javier Navas González, Elena Ciani, Antonio González Ariza and Juan Vicente Delgado Bermejo. Criterios de selección basados en comportamiento para camellos dedicados a ocio turístico. *XXIV Simposio Iberoamericano sobre conservación y utilización de Recursos Zoogenéticos*. Veracruz (Mexico), 2nd-6th October 2023. *Accepted for presentation*.

xxi. Carlos Iglesias Pastrana, Francisco Javier Navas González, Martina Macrì, Amparo Martínez Martínez, Elena Ciani and Juan Vicente Delgado Bermejo. Análisis genómico de diversidad en la raza camello canario. *XXIV Simposio Iberoamericano sobre conservación y utilización de Recursos Zoogenéticos*. Veracruz (Mexico), 2nd-6th October 2023. *Accepted for presentation*.

c. ***Poster*.**

i. C. Iglesias Pastrana, F.J. Navas González, J.V. Delgado Bermejo, R. Araujo, D. Duarte, A.M. Gil, D.C.G.A. Pinto, I.F. Duarte and E. Ciani. Caracterización metabolómica preliminar de orina de camello: potencialidad de uso en investigación biomédica. *III Congreso Andaluz de Salud Pública Veterinaria*. Cordoba (Spain), 23th-24th September 2021.

ii. C. Iglesias Pastrana, F.J. Navas González, E. Ciani, A. Arando Arbulu and J.V. Delgado Bermejo. Influencia de variables sociodemográficas, morfo-fanerópticas y fisiológicas en el comportamiento de liderazgo en dromedarios. *II Congreso Anual Internacional de Estudiantes de Doctorado (CAIED)*. Online, 3rd-4th February 2022.

iii. Rivas López, C., García Martínez, A., Fresno Baquero, M., Martín Martel, S., Iglesias Pastrana, C., Navas González, A. and Barba Capote, C. Caracterización preliminar de los sistemas de producción del dromedario en España. *XXIII Simposio Iberoamericano sobre conservación y utilización de Recursos Zoogenéticos/XIII Congreso Ibérico SERGA-SPREGA sobre Recursos Genéticos Animales*. Cordoba (Spain), 21th-23th October 2022.

iv. C. Iglesias Pastrana, F.J. Navas González, T. Kamal Sayed Osman, E. Ciani and J.V. Delgado Bermejo. Individual curve estimation regression analysis to identify the model that best fits camel biomechanics: applications for selective breeding. *The Sixth Conference of ISOCARD (The International Society of Camelid Research and Development)*. Al-Hofuf (Saudi Arabia), 12th-16th March 2023.

v. Carlos Iglesias Pastrana, Francisco Javier Navas González, Elena Ciani and Juan Vicente Delgado Bermejo. Fase lunar y climatología como variables condicionantes del inicio del trabajo de parto según el sexo de la descendencia en dromedarios. *I Congreso Internacional Multidisciplinar de Estudiantes de Doctorado (CIMED)*. La Laguna (Santa Cruz de Tenerife, España), 22th-24th March 2023.

D. Technology transfer activities

a. Active Member of the 'Sheep, Goats and Camelids Working Group'. *The International Committee for Animal Recording (ICAR)*.

b. Coordination of the international discussion online platform CAMEL-PWHM (Production-Welfare-Health Management): initiative contextualized within the framework of *RedIRIS*, the academic and research network that provides advanced communication services to the scientific and university community and which is financed by the Spanish Ministry of Science and Innovation.

c. Presentation of the mathematical model for the reliable extraction of linear and tridimensional measurements from 2D-images in dromedary camels. *2nd Salon International du Dromadaire et des Camélidés*. Janvry (Francia), 17th-18th September 2022.

E. Divulgation activities/articles

a. Aplicaciones terapéuticas de los productos derivados de la ganadería camellar. *TV programme 'Salud al día', Canal Sur*. Matalascañas (Huelva, España), 24th June 2020.

b. Valorización de fibras naturales de origen animal. *Comercial Ovino EA Group*. Villanueva de la Serena (Badajoz, España), 13th August 2020.

c. Proyecto Europeo CARAVAN: Selección y mejora genética para la transnacionalización de la cadena de valor de la producción ganadera camellar en el Mediterráneo. *Boletín* *de difusión de la Transferencia del Conocimiento de la Universidad de Córdoba (TRUCO)*, Nº 39. October 2020.

d. Paseos en camello, una alternativa sostenible para evitar la extinción de razas autóctonas. *Unidad de cultura científica y de la innovación, University of Cordoba (Spain)*. 19th October 2020.

e. Biodiversidad, genética y conservación: Caracterización zoométrica, cinemática y etológica del camello canario. *XX Semana de la Ciencia en Andalucía*. Córdoba (España), 3th-15th November 2020.

f. Un modelo matemático permite, por primera vez, obtener medidas tridimensionales de animales a partir de fotografías 2D. *Unidad de cultura científica y de la innovación, University of Cordoba (Spain)*. Córdoba (España), 31st October 2022.

g. Modelo matemático para la extracción de medidas lineales y tridimensionales a partir de imágenes 2D en dromedarios. *Radio-TV programme 'En red', Canal Sur*. Matalascañas (Huelva, España), 19th January 2023.