UNIVERSIDAD DE CÓRDOBA

DEPARTAMENTO DE GENÉTICA

TESIS DOCTORAL

Programa de Doctorado "Biociencias y Ciencias Agroalimentarias"

"NUEVOS CRITERIOS DE SELECCIÓN EN LAS RAZAS CAPRINAS ESPAÑOLAS"

"NEW SELECTION CRITERIA IN SPANISH GOAT BREEDS"

Chiraz Ziadi

Córdoba, Julio 2022

TITULO: *Nuevos criterios de selección en las razas caprinas españolas*

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“NUEVOS CRITERIOS DE SELECCIÓN EN LAS RAZAS CAPRINAS ESPAÑOLAS”

“NEW SELECTION CRITERIA IN SPANISH GOAT BREEDS”

MEMORIA DE TESIS DOCTORAL PRESENTADA POR

Chiraz Ziadi

Para optar al Grado de Doctor por la Universidad de Córdoba

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Córdoba, a 14 de Julio de 2022

TÍTULO DE LA TESIS: NUEVOS CRITERIOS DE SELECCIÓN EN LAS RAZAS CAPRINAS ESPAÑOLAS

DOCTORANDO: Chiraz Ziadi

INFORME RAZONADO DEL DIRECTOR DE LA TESIS

La Tesis Doctoral que se presenta está integrada por tres artículos publicados en revistas ISI, de gran impacto en el campo de la Ciencia Animal, y un cuarto artículo que actualmente se encuentra enviado a otra revista indexada.

La Tesis se ha estructurado en cuatro capítulos:

Capítulo I: Genetic analysis of litter size and number of kids born alive across parities in Spanish goat breeds using a random regression.

Los resultados de este estudio se han publicado en el trabajo: **Ziadi, C.,** Muñoz-Mejías, E., Rodríguez, M.S., López, M.D., González-Casquet, O., and Molina-Alcalá, A.
Italian Journal of Animal Science. 2021. Número: 20(1). Páginas: 94-101.
ISSN: 15944077. doi: DOI: 10.1080/1828051X.2020.1869601
IF= 2.18 (Q2) en Animal Science and Zoology

Capítulo II: Selection Criteria for Improving Fertility in Spanish Goat Breeds: Estimation of Genetic Parameters and Designing Selection Indices for Optimal Genetic Responses.

Los resultados de este estudio se encuentran en el trabajo: **Ziadi, C**., Muñoz-Mejías, E., Sánchez, M., López, M., González-Casquet, O., and Molina, A.
Revista: Animals. Año: 2021. Número: 11(2). Páginas: 409.
ISSN: 2076-2615. doi: DOI: 10.3390/ani11020409
IF= 2.752 (Q1) en Veterinary Sciences

Capítulo III: Genetic analysis of reproductive efficiency in Spanish goat breeds using a random regression model as a strategy for improving female fertility.

Los resultados de este estudio se han publicado en el trabajo: **Ziadi, C**., Muñoz-Mejías, E., Sánchez, M., López, M.D., González-Casquet, O., and Molina, A.

Revista: Italian Journal of Animal Science. Año: 2021. Número: 20(1). Páginas: 1681-1688.
ISSN: 15944077. DOI: 10.1080/1828051X.2021.1979900
IF= 2.18 (Q2) en Animal Science and Zoology

Capítulo IV: Genetic analysis for productive life in Florida dairy goats using a Cox proportional hazards model.

Los resultados de este estudio se encuentran en el trabajo: **Ziadi, C**., Sánchez, J. P., Sánchez, M., Morales, R., and Molina, A. Genetic analysis for productive life in Florida dairy goats using a Cox proportional hazards model. Livestock science. 2022. Sometido. IF=1.97 (Q1) en Agriculture, Dairy and Animal Science

Por tanto, considero que el trabajo realizado por Dña. Chiraz Ziadi, bajo mi dirección y tutela, presenta unos elevados niveles de innovación y calidad y autorizo su presentación y defensa como Tesis Doctoral en el Departamento de Genética de la Universidad de Córdoba, para obtener el **grado de Doctor.**

Córdoba, a 14 de julio de 2022

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Director de la Tesis

y Responsable de la Línea de Investigación

Universidad de Córdoba, España

“El conocimiento es la conformidad del
intelecto”

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RESUMEN

RESUMEN

Esta Tesis Doctoral ha tenido como objetivo el análisis genético de nuevos criterios de selección para el caprino de leche relacionados con la reproducción y la longevidad de las reproductoras y la puesta a punto de nuevas metodologías de valoración genética para dichos criterios.

Para la realización de los trabajos incluidos en la presente Tesis Doctoral, se ha tomado como ejemplo de razas autóctonas españolas de aptitud lechera, la Florida y la Payoya, como representación de los dos sistemas productivos existentes, en el primer caso un sistema semi-intensivo a semi-extensivo y en el segundo uno semi-extensivo a extensivo. La Asociación Nacional de Criadores de Ganado Caprino de Raza Florida (ACRIFLOR) y la Asociación de Criadores de Raza Caprina Payoya (ACAPA), nos han facilitado las bases de datos y la información genealógica, a partir de las cuales se han desarrollado los distintos estudios.

El programa de mejora genética del caprino lechero español ha venido basando sus criterios de mejora en el incremento de la producción lechera y sus componentes en cantidad y calidad, y recientemente en la mejora de la morfología. La fuerte selección para el incremento de la producción lechera ha creado un estrés productivo en los animales, que, junto al antagonismo genético con las características reproductivas, ha provocado un efecto negativo sobre estos caracteres del ámbito reproductivo de gran importancia económica y un gran peso en la rentabilidad de las ganaderías. Por lo tanto, la inclusión de caracteres relacionados con la aptitud reproductiva (como son los relacionados con la fertilidad, la productividad numérica global o la longevidad productiva de las reproductoras) en los esquemas de mejora genética del ganado caprino lechero es crítico para corregir este impacto negativo.

Para la consecución de los objetivos de esta Tesis, el documento se ha estructurado en cuatro capítulos:

En el primer capítulo, se estimaron los componentes de varianza y los parámetros genéticos a lo largo de los partos de la cabra para el carácter prolificidad medido como tamaño de camada (LS) y número de nacidos vivos (NBA). Se analizaron 130.849 y

67.478 registros de partos recogidos entre el primer y séptimo parto procediendo de hembras Florida y Payoya, respectivamente. Los componentes de varianza se estimaron ajustando un modelo umbral bivariado mediante regresión aleatoria (RRM) usando polinomios de Legendre. Se consideró la varianza residual heterogénea a través el número de parto con cinco clases. El análisis se realizó con el software THRGIBBS3F90 del paquete BLUPF90 (Misztal et al., 2016), usando la metodología de inferencia Bayesiana. Las estimaciones de la heredabilidad presentaron un promedio de 0,07 y 0,17 para LS y 0,05 y 0,08 para NBA, mientras que las estimaciones de repetibilidad promedio fueron 0,15 y 0,28 para LS y 0,09 y 0,19 para NBA en Florida y Payoya, respectivamente. Las h^2 oscilaron entre cero y 0,37 para LS y entre 0,02 y 0,20 para NBA, mientras que los valores de repetibilidad oscilaron entre 0,008 y 0,60 y entre 0,03 y 0,44 para LS y NBA, respectivamente. Las correlaciones fenotípicas entre carácter a lo largo de los partos variaron ampliamente de -0,31 a 0,97, mientras que las correlaciones genéticas entre carácter a través de los partos mostraron un rango y una magnitud de valores más amplios, de -0,98 a 0,99 para LS y de -0,72 a 0,99 para NBA. Las estimaciones de correlaciones genéticas entre LS y NBA en los diferentes partos fueron positivas en los dos primeros partos y negativas en los últimos. Los resultados de este estudio demostraron que, debido a los cambios notables en la varianza a lo largo de la trayectoria de partos y las correlaciones genéticas diferentes de unidad en los diferentes partos, se recomienda el uso de un modelo de regresión aleatoria para analizar la trayectoria genética de LS y NBA para estos rasgos en razas caprinas. Las correlaciones obtenidas entre el tamaño de camada y el número de nacidos vivos indican que la selección por uno de estos caracteres genera una respuesta positiva o negativa en el otro, dependiendo del momento de selección que puede ser durante los dos primeros partos en este estudio.

En el segundo capítulo, se llevó a cabo una estimación de los componentes de varianza y los parámetros genéticos de varios criterios de selección relacionados con la fertilidad de las reproductoras: edad al primer parto (AgFiKid), intervalo entre primer y segundo parto (Int12Kid), intervalo entre el segundo y tercer parto, entre el tercer parto y el resto (Int3toKid), e intervalo entre todos los partos (IntAllKid) de las razas Florida y Payoya. Para la estimación de los parámetros genéticos, se utilizó el programa VCE v.6.0.3 con metodología de máxima verosimilitud (REML). Se empleó la teoría de los índices de selección (Gutiérrez et al., 2014) para simular las respuestas a la selección obtenidas, definiendo distintas combinaciones de criterios para los principales criterios de selección con el fin de elegir el índice de selección más adecuado para estas dos razas. Las estimaciones de heredabilidad y repetibilidad fueron bajas, como se esperaba para ese tipo de caracteres. Las correlaciones genéticas entre los criterios de fertilidad cubrieron un amplio rango de valores desde 0.07 (AgFiKid-Int12Kid) a 0.71 (Int3toKid-IntAllKid) en Florida y de -0.02 (AgFiKid-Int12Kid) a 0.82 (Int3toKid-IntAllKid) en Payoya. En general, los resultados de este estudio indicaron que IntAllKid brinda la mayor respuesta genética en ambas razas, pero se expresa tarde en la vida de la hembra. Por ello, podrían recomendarse como criterios de selección temprana para la fertilidad de la hembra en ambas razas el AgFiKid e Int12Kid.

En el tercer capítulo, se abordó un estudio genético de la eficacia reproductiva (ER) en un amplio rango de edad de hembras mediante regresión aleatoria usando polinomios de Legendre. La estimación de los componentes de la varianza se basó en la inferencia Bayesiana utilizando el GIBBS3F90 del paquete BLUPF90 (Misztal et al., 2016). La ER fue definida como desviación entre parto óptimo y real a cada edad de la cabra. Las estimaciones de heredabilidad fueron moderadas, oscilando entre 0,21 y 0,32 para Florida y entre 0,25 y 0,35 para Payoya. Las correlaciones genéticas entre las distintas edades variaron de 0,36 a 0,98 para Florida y de 0,80 a 0,99 para Payoya. Los resultados de este estudio apoyaron la validez de este parámetro como criterio de selección indirecto para la fertilidad. Según nuestros resultados, la eficacia reproductiva es un rasgo altamente hereditario que se expresa temprano en la vida de la hembra, y podría utilizarse como criterio de selección precoz para mejorar la fertilidad de las hembras en las cabras lecheras españolas. De la misma manera, las correlaciones genéticas entre la ER a diferentes edades, determina que este carácter deba ser considerado diferente (aunque fuertemente correlacionado) en los diferentes partos de la reproductora y que se recomiende el uso del modelo RRM para analizar genéticamente la eficacia reproductiva en cabras lecheras españolas a lo largo de la vida del animal.

Finalmente, en el último capítulo de esta Tesis, se realizó un análisis genético de la longevidad de la reproductora medida como la longitud de la vida productiva (LPL, tiempo desde el primer parto hasta la última fecha conocida de secado o de desecho). En total, se analizaron los datos de 25.722 hembras, de las cuales 19.495 habían terminado su ciclo productivo y 6.227 (24.2%) continuaban vivas y, por tanto, tenían su información censurada. Los factores de riesgo y los parámetros genéticos se analizaron mediante la distribución de Cox (Mészáros et al., 2013) utilizando el software Survival Kit de Ducrocq and Sölkner (1994). La LPL se vio afectada por dos tipos de factores: tiempo-independientes (edad al primer parto y rebaño-año-época de nacimiento de la cabra) y tiempo-dependientes (edad al parto, rebaño-año-época de parto, nivel productivo e interacción número de lactación-estado de lactación). La h^2 fue sorprendentemente alta (0,40) para proponer a la LPL como criterio de selección de la longevidad. En un análisis previo, en el que no se tuvo en cuenta el nivel productivo, dicha heredabilidad disminuyó a 0,17, certificando el gran peso de dicho nivel productivo de la cabra en las decisiones de descarte por parte del ganadero.

Como conclusión final resaltamos que las metodologías puestas a punto en la presente Tesis para el análisis de nuevos criterios de selección en las razas caprinas lecheras, están siendo incorporadas ya dentro de su Esquema de Selección, colaborando al progreso genético de las razas, aunque en algunos casos sea necesario ampliar los estudios realizados y efectuar un mayor control de algunos aspectos relacionados principalmente con el comportamiento reproductivo y el análisis de las causas de desvieje.

SUMMARY

The aim of this Doctoral Thesis has been the genetic analysis of new selection criteria in dairy goats related to female reproduction and longevity, and the development of new genetic evaluation methodologies for these criteria.

In order to carry out the work included in this Doctoral Thesis, the Florida and Payoya breeds have been taken as examples of Spanish autocthonous dairy breeds, as a representation of the two existing production systems, in the first case a semi-intensive to semi-extensive system and in the second one a semi-extensive to extensive system. The Asociación Nacional de Criadores de Ganado Caprino de Raza Florida (ACRIFLOR) and the Asociación de Criadores de Raza Caprina Payoya (ACAPA), have provided us with the databases and genealogical information, from which the different studies have been developed.

The genetic improvement program of the Spanish dairy goat has been basing its improvement criteria on the increase of milk production and its components in quantity and quality, and recently on the improvement of morphology. The strong selection for the increase of milk production has created a productive stress in the animals, which, together with the genetic antagonism with the reproductive characteristics, has caused a negative effect on these reproductive traits of great economic importance and a great weight in the profitability of the herds. Therefore, the inclusion of traits related to reproductive fitness (such as those related to fertility, overall numerical productivity or productive longevity of does) in genetic improvement schemes for dairy goats is critical to correct this negative impact.

In order to achieve the objectives of this Thesis, the document has been structured in four chapters:

In the first chapter, variance components and genetic parameters were estimated across parities for the prolificacy trait measured as litter size (LS) and number born alive (NBA). A total of 130,849 and 67,478 kidding records collected between the first and seventh parities of Florida and Payoya females, respectively, were analysed. Variance components were estimated by fitting a bivariate random regression threshold model

(RRM) using Legendre polynomials. Heterogeneous residual variance was considered across parity number with five classes. The analysis was performed with the THRGIBBS3F90 software of the BLUPF90 package (Misztal et al., 2016), using Bayesian inference methodology. Heritability estimates were 0.07 and 0.17 for LS and 0.05 and 0.08 for NBA, while average repeatability estimates were 0.15 and 0.28 for LS and 0.09 and 0.19 for NBA in Florida and Payoya, respectively. The h^2 ranged between zero and 0.37 for LS and between 0.02 and 0.20 for NBA, while repeatability values ranged between 0.008 and 0.60 and between 0.03 and 0.44 for LS and NBA, respectively. Phenotypic correlations between traits across parities ranged widely from - 0.31 to 0.97, while genetic correlations between traits across parities showed a wider range and magnitude of values, from -0.98 to 0.99 for LS and -0.72 to 0.99 for NBA. Estimates of genetic correlations between LS and NBA at the different parities were positive for the first two parities and negative for the last two ones. The results of this study showed that, due to the remarkable changes in variance along the parity trajectory and the genetic correlations within-trait different from unity at successive parities, the use of a random regression model to analyse the genetic trajectory of LS and NBA in goat breeds is recommended. The correlations obtained between litter size and number born alive indicate that selection for one of these traits generates a positive or negative response in the other, depending on the time of selection which may be during the first two kiddings in this study.

In the second chapter, an estimation of the variance components and genetic parameters of several selection criteria related to the female fertility was carried out: age at first kidding (AgFiKid), interval between first and second kidding (Int12Kid), interval between second and third kidding, between third kidding and the rest (Int3toKid), and interval between all kidding (IntAllKid) of the Florida and Payoya breeds. For the estimation of genetic parameters, the VCE v.6.0.3 program with maximum likelihood methodology (REML) was used. The selection index theory (Gutiérrez et al., 2014) was used to simulate the selection responses obtained, defining different combinations of criteria for the main selection criteria in order to choose the most appropriate selection index for these two breeds. Heritability and repeatability estimates were low, as expected for these traits. Genetic correlations between fertility criteria covered a wide range of values from 0.07 (AgFiKid-Int12Kid) to 0.71 (Int3toKid-IntAllKid) in Florida and from -0.02 (AgFiKidInt12Kid) to 0.82 (Int3toKid-IntAllKid) in Payoya. Overall, the results of

this study indicated that IntAllKid provides the highest genetic response in both breeds, but is expressed late in the female's life. Therefore, AgFiKid and Int12Kid could be recommended as early selection criteria for female fertility in both breeds.

In the third chapter, a genetic study of reproductive efficiency (RE) in a wide age range of females was developped by random regression model (RRM) using Legendre polynomials. Estimation of variance components was based on Bayesian inference using the software GIBBS3F90 of the BLUPF90 family programs (Misztal et al., 2016). RE was defined as the deviation between optimal and real parity at each female age. Heritability estimates were moderate, ranging from 0.21 to 0.32 for Florida and 0.25 to 0.35 for Payoya. Genetic correlations between the trait at the different ages ranged from 0.36 to 0.98 for Florida and 0.80 to 0.99 for Payoya. The results of this study supported the validity of this parameter as an indirect selection criterion for fertility. According to our results, reproductive efficiency is a highly heritable trait that is expressed early in the female's life, and could be used as an early selection criterion to improve female fertility in Spanish dairy goats. In the same way, the genetic correlations between RE at different ages, determines that this trait should be considered different (although strongly correlated) in the different ages of the female and that the use of the RRM is recommended to genetically analyse the reproductive efficiency in Spanish dairy goats throughout the life of the animal.

Finally, in the last chapter of this Thesis, a genetic analysis of the longevity trait measured as the length of productive life (LPL, time from first kidding to the last known drying or culling date) was carried out. In total, data from 25,722 females were analysed, of which 19,495 had completed their productive cycle and 6,227 (24.2%) were still alive and therefore had their information censored. Risk factors and genetic parameters were analysed by Cox distribution (Mészáros et al., 2013) using the Survival Kit software of Ducrocq and Sölkner (1994). LPL was affected by two types of factors: time-independent (age at first kidding and herd-year-season of birth of the doe) and time-dependent (age at kidding, herd-year-season of kidding, productive level and the interaction lactation number-stage of lactation). The h^2 was clearly high (0.40) indicating that LPL should be proposed as a selection criterion for longevity. In a previous analysis, in which milk production effect was not taken into account, this heritability decreased to 0.17, certifying the great weight of the goat's production in the farmer's decision of culling.

As a final conclusion, we highlight that the methodologies developed in this Thesis for the analysis of new selection criteria in dairy goat breeds are already being incorporated into their Selection Scheme, contributing to the genetic progress of the breeds, although in some cases it is necessary to extend the studies carried out and carry out a greater control of some aspects mainly related to reproductive behaviour and the analysis of the causes of culling.

INTRODUCCIÓN GENERAL
Y JUSTIFICACIÓN

INTRODUCCIÓN GENERAL

El sector del caprino lechero en España y en Andalucía

Según los datos del Ministerio de Agricultura, Pesca y Alimentación (2021), el censo total de ganado caprino lechero en el año 2020 asciende a 2,65 millones de cabezas, de las cuales 2,1 millones son hembras reproductoras. La importancia de este sector se ve reflejada en el hecho que el ganado caprino lechero español ocupa el segundo lugar en la Unión Europea en cuanto a censo y producción, precedido por Grecia en censo y Francia en producción. En los últimos años, se registró un incremento en el volumen de producción de leche caprina, cuyo valor de producción final en la economía ganadera española alcanzó en el año 2020 un valor de 358 millones de euros.

En Andalucía, el censo de ganado caprino es superior al millón de animales, repartidos en más de diez mil unidades productivas, lo que sitúa a esta comunidad autónoma como la primera región española en censo, con el 37,24% del total nacional. A nivel productivo, con sus más de 200 millones de litros de leche de cabra producidos al año, Andalucía también lidera el ranking con el 40,67% de la producción total del país. En el sector caprino andaluz coexisten multitud de sistemas de explotación con características propias, pero que pueden agruparse en tres grupos principales: explotaciones extensivas, semi-extensivas o mixtas, e intensivas.

La raza Florida como modelo de sistema con alto grado de intensificación

La Florida es una raza caprina lechera autóctona del Bajo Valle del Guadalquivir que data su origen a principios del siglo XX y que comenzó a inscribir animales en el libro genealógico en 1984. El origen de la raza Florida se sitúa en la influencia de animales de tipo nubiano sobre animales de tronco pirenaico autóctonos del Valle del Guadalquivir. Su núcleo principal se encuentra en Andalucía Occidental y el Sur de Extremadura, pero también se está asentándose en áreas limítrofes como Andalucía Oriental, Castilla la Mancha, Norte de Extremadura, Castilla-León e incluso Portugal, Cataluña, Aragón y La Rioja.

La raza cuenta con un censo de unas 125.000 cabras reproductoras, de las cuales 30.000 están registradas en el libro genealógico nacional raza Florida (ARCA, 2021).

La raza caprina Florida es una raza cuya finalidad principal es la producción de leche en una gran variedad de sistemas de explotación que abarcan desde los semi-extensivos en zonas de sierra, hasta los sistemas de estabulación libre, pasando por sistemas semi-intensivos en zonas de vega y campiña.

Modelo de raza con sistema de producción extensivo: la raza Payoya

La cabra Payoya es una raza autóctona andaluza, catalogada en peligro de extinción según el Real Decreto 45/2019, de 8 de febrero, de zootecnia. Tradicionalmente, ha sido explotada en la zona del actual Parque Natural de la Sierra de Grazalema y Sierra de Ronda, zonas de gran valor natural, constituyendo el sustento de muchas familias de las comarcas. A fecha de 31/12/2018, el número de animales reproductores inscritos en el libro genealógico de la raza Payoya ascendía a 10.378 hembras y 446 machos en 41 ganaderías, encontrándose el 99% del censo en la Comunidad Autónoma Andaluza, y el 1% restante en la Comunidad Autónoma de Cataluña. La cabra Payoya sigue manteniendo las aptitudes necesarias para convivir y producir en un medio duro y cambiante, siendo fuente de productos con los que comparte una magnífica y única personalidad.

El origen no está determinado, no obstante, se supone que la cabra Payoya fue el resultado de la conjunción de los troncos Alpino y Pirenaico que recibe la influencia del tronco convexo, influencia necesaria para su adaptación a las zonas de sierra donde habita (Herrera García and Luque Cuesta 2007).

En cuanto a su sistema de explotación, la raza caprina Payoya sigue un régimen de manejo semi-extensivo a extensivo, donde los recursos pastables aportan la parte más importante de la dieta. Las cabras aprovechan los pastos espontáneos, rastrojeras y los campos sembrados para el consumo por las cabras, sobre todo en primavera, que es cuando el medio ofrece más recursos alimenticios.

Esquema de selección y mejora genética de las razas Florida y Payoya

Un programa de mejora tiene como objetivo último incrementar la rentabilidad económica de la explotación, aumentando los rendimientos productivos o disminuyendo los costes asociados. Ambos objetivos dependen de un conjunto de caracteres que en parte están determinados por factores genéticos y en otra parte por condicionantes que podrían definirse como ambientales.

Los programas de cría que se emplean actualmente en el sector caprino de leche se encuentran estrechamente relacionados con dos principales objetivos: la mejora de la producción lechera y sus componentes (Molina et al. 2018), además de los caracteres morfológicos. Unas de las principales razas empleadas en estos objetivos son las razas Florida y Payoya, caracterizadas por su buena aptitud lechera, especialmente en el caso de la Florida, siendo unas razas autóctonas rústicas muy adaptadas a las condiciones productivas y ambientales.

Las razas Florida y Payoya disponen de un programa de mejora genética sistematizado aprobado por la Dirección General de Producciones y Mercados Ganaderos con sus diferentes fases que van desde la identificación y registro de animales y recogida de datos fenotípicos hasta la difusión del progreso genético. Con el transcurro del tiempo, ese programa ha logrado conseguir una mejora genética en características de aptitud lechera (en cantidad y calidad) que es la principal finalidad de explotación de esas razas. Sin embargo, no se ha tenido en cuenta otros aspectos de suma importancia para la rentabilidad de las explotaciones y que se han visto afectados negativamente por el estrés producido por la fuerte selección por la producción lechera, tales y como los caracteres reproductivos de la hembra y la longevidad. Este hecho, sumado a la aparición de nuevas tecnologías y metodologías genéticas (Ducrocq et al. 1988; Schaeffer 2004) hizo indispensable una profunda revisión de los criterios y parámetros en que se fundamenta este esquema con el fin de adaptarlo a las nuevas necesidades evolutivas de las razas y al uso de metodologías y técnicas actuales. Adicionalmente, hay una evolución creciente del sector caprino hacia la intensificación en muchas razas españolas (Peña et al. 2009; Castel et al. 2010) y especialmente, en la raza Florida (Sánchez-Rodríguez et al. 2018).

El presente programa de mejora de las dos razas contempla los siguientes objetivos específicos:

- Mejora genética de las características de aptitud lechera, que se concretan en kilos de leche producida en lactación natural; kilos de grasa producida en lactación natural; kilos de proteína producida en lactación natural, estas tres variables estando tipificadas a 210 y 240 días; porcentaje medio por lactación de proteína en la leche y porcentaje medio por lactación de grasa en la leche.
- Mejora genética de las características morfológicas (aptitud productiva y longevidad), que se concretan en la mejora de los rasgos primarios de la calificación morfológica lineal (CML) y en la mejora de los índices morfológicos a partir de a valoración de las diferentes áreas (ubre, estructura y capacidad, estructura lechera y patas y pies) que se desarrollen.

Además, en la raza Payoya, catalogada como raza amenazada, el programa de cría tiene como segunda finalidad su conservación a través de los siguientes objetivos:

- Conservar *in vivo* e *in situ* y de manera sostenible los efectivos de la raza en sus ecosistemas singulares, manteniendo las peculiaridades para los animales y para el medio.
- Mantener la variabilidad genética y minimizar el incremento de la consanguinidad de la población.
- Conservación *ex situ*. Preservar mediante en banco de germoplasma la raza.

JUSTIFICACIÓN

Durante los últimos años, el sector de los pequeños rumiantes en general y del caprino lechero en particular venía sufriendo una crisis de rentabilidad, debida al incremento de los costes y al descenso del precio de venta de los productos. Hoy día, la vorágine de subida de precios de la energía, las materias primas y del coste de la vida en general, está sometiendo al sector a una crisis sin precedentes. La subida del precio de la leche que está recibiendo el criador no compensa bajo ninguna circunstancia la espiral inflacionista. Por ello, la mejora de la rentabilidad de las explotaciones lecheras se ha convertido en una prioridad para el ganado caprino español. Este objetivo se puede lograr por diversas vías, como son la optimización de la alimentación, la sanidad, el manejo reproductivo, o la propia mejora genética, como se aborda en el trabajo de esta tesis.

Actualmente, los programas de mejora genética de las razas caprinas lecheras españolas están enfocados exclusivamente en los caracteres productivos, en concreto: producción de leche y del extracto quesero (producción de grasa y de proteína). Sin embargo, esa fuerte selección para el incremento de la producción lechera ha creado un estrés productivo en los animales, que, junto al antagonismo genético con las variables reproductivas, ha provocado un efecto negativo sobre la fertilidad de las hembras. Por lo tanto, la inclusión de la fertilidad en los esquemas de mejora genética del ganado caprino lechero se ha hecho imprescindible para corregir este impacto negativo.

Por otro lado, la prolificidad es un factor importante para aumentar la rentabilidad de las ganaderías, generando ingresos por la venta de animales. Las hembras que tienen gemelos o partos múltiples aportan mayores beneficios económicos que las que tienen sólo un cabrito a la vez. En razas catalogadas en peligro de extinción, como en el caso de la Payoya, aumentar el número de crías producidas por hembra es de vital importancia para el mantenimiento del tamaño efectivo de la población. En las razas Florida y Payoya, ese rasgo ya representa una importante fuente de ingresos para los criadores (especialmente en el caso de la Florida).

Además, para conseguir una mayor rentabilidad se requiere seleccionar cabras, que además de alta producción y buena fertilidad, permanezcan el mayor tiempo posible en el rebaño, con lo cual se consiguen hembras con más lactaciones y, por lo tanto, reducir el coste de amortización. Esto se ve reflejado en la longevidad que representa la capacidad para sobrevivir en el rebaño, ya sea al desecho voluntario (debido a baja producción de leche) como al involuntario (debido a problemas reproductivos o de salud).

Es por ello, que estos tres factores (aumento de la prolificidad, fertilidad y la extensión de la vida productiva de las reproductoras), son probablemente los puntos de actuación más importantes sobre los cuales se podría incidir para mejorar la eficacia de un programa de mejora que permita incrementar la rentabilidad en los sistemas de producción ganadera del caprino lechero español.

Para llevar adelante un programa de mejora genética, debemos partir del conocimiento de la magnitud de los parámetros genéticos de los diferentes criterios de selección para los caracteres (objetivos) de importancia económica. Sin embargo, hasta la fecha no se ha realizado estudios que aborden la estimación de parámetros genéticos de los caracteres relacionados con la prolificidad, fertilidad y longevidad en las razas caprinas lecheras españolas.

Valoración genética de la prolificidad a lo largo de la trayectoria de partos de las reproductoras

La prolificidad tiene un alto valor económico y es uno de los rasgos reproductivos más importantes en pequeños rumiantes, y especialmente en razas que están en peligro de extinción, tales como la raza caprina Payoya. La prolificidad es un carácter umbral que presenta una distribución fenotípica discontinua, con un reducido número de clases. No obstante, esa característica se suele ignorar al usar los modelos lineales mixtos. La forma propuesta por algunos autores (Thompson 1979; Gianola 1982; Sorensen et al. 1995) podría ser una forma de abordar este problema, ya que se obtiene parámetros y valores genéticos en la escala subyacente, mediante muestreo de Gibbs usando metodología Bayesiana. Por otra parte, la prolificidad ha sido evaluada generalmente utilizando modelos de repetibilidad, en los que se considera la prolificidad de los diferentes partos del animal como reflejo del mismo carácter. Estos modelos asumen que la (co)varianza a través la trayectoria de partos es constante y que las correlaciones genéticas entre tamaños de camada de diferentes partos son igual a unidad. Sin embargo, estudios realizados con modelos multivariados y más modernamente con modelos de regresión aleatoria han mostrado que la correlación genética entre la prolificidad de los diferentes partos es estadísticamente inferior a la unidad, por lo que han recomendado el uso de modelos de Regresión Aleatoria para el análisis genético del tamaño de camada (Alfonso et al. 1994; Fernández et al. 2008; Skorput et al. 2014). Estos modelos, de regresión aleatoria, como los empleados en el presente trabajo, son considerados en la actualidad como el enfoque estadístico más pertinente para la evaluación genética de los caracteres de medidas repetidas en la vida de los animales (Schaeffer 2004). En ese sentido, en el presente trabajo se ha llevado a cabo por primera vez en caprino de leche y en razas españolas la puesta a punto de modelos de regresión aleatoria para analizar la prolificidad de las reproductoras definida como un carácter umbral.

Estimación de los parámetros genéticos de clásicos y nuevos criterios relacionados con la fertilidad de la hembra

En ganado lechero, la eficacia reproductiva tiene un impacto importante en la rentabilidad general de las explotaciones y se considera uno de sus mayores determinantes (Leblanc 2010). Está ampliamente demostrada la correlación genética y ambiental desfavorable entre este carácter y los rasgos de producción lechera (Montaldo et al. 2010), lo que implica que un alto nivel productivo viene asociado a una baja fertilidad y, por lo tanto, el desecho del rebaño y la reducción de la vida productiva de las hembras poco fértiles. Por eso, se ha incluido la fertilidad en los objetivos de selección en especies como el ovino o el vacuno (VanRaden et al. 2004), demostrándose que seleccionar por rasgos asociados a la fertilidad como la edad al primer parto o el intervalo entre partos aumenta la vida productiva de las hembras reproductoras (Castañeda-Bustos et al. 2014 en caprino lechero). Existen muchos indicadores para evaluar la eficacia reproductiva del rebaño lechero, entre los que se pueden citar: edad al primer parto, intervalo entre partos, días abiertos calculado como el intervalo entre parto e inseminación fecundante, etc. (Ruiz, et al. 2002). En caprino, en otros países y en razas extranjeras, se han ido evaluando caracteres de fertilidad como la edad al primer parto y el intervalo entre todos los partos (Castañeda-Bustos VJ et al. 2014; Bangar et al. 2022). Estos trabajos han determinado que estos caracteres asociados a la fertilidad son poco heredables, lo que hace difícil encontrar un criterio objetivo fácil de integrar en los núcleos de control y que presente suficiente heredabilidad para asegurar una respuesta a la selección adecuada. No existe hasta la actualidad ningún estudio que determine un rasgo asociado a la fertilidad de las reproductoras caprinas, que presente suficiente heredabilidad para poder usarse en los programas de mejora con cierta probabilidad de éxito. Es por ello que el presente trabajo tiene como objetivo el estimar, por primera vez, los parámetros genéticos de los caracteres clásicos de fertilidad e investigar un nuevo criterio que presentaría una mayor heredabilidad que los criterios clásicos.

Análisis de la vida productiva usando modelos de supervivencia

La longevidad o vida productiva de un animal es un rasgo muy importante para la rentabilidad económica de las explotaciones lecheras, ya que existe una fuerte correlación positiva entre longevidad, vida productiva y productividad acumulada. En cuanto a la definición del carácter, (Ducrocq 1994) propuso diferenciar entre lo que es longevidad real (desde el punto de vista de la mejora genética) y longevidad funcional, basándose en la distinción entre eliminación voluntaria e involuntaria. La longevidad real es la capacidad del animal para evitar tanto la eliminación voluntaria como la eliminación involuntaria, mientras que la longevidad funcional es la capacidad de evitar la eliminación involuntaria. El uso de la longevidad funcional proporciona nueva información, más o menos independiente de los rasgos de producción y, en consecuencia, más útil en los programas de mejora (Kern et al. 2016). El objetivo de obtener animales con una elevada longevidad funcional, permite al criador determinar el momento óptimo del desvieje de los animales menos productivos, incrementando por lo tanto la rentabilidad de la explotación, y un progreso genético adecuado. Una elevada eliminación por razones no productivas (muerte, infertilidad, sanidad, etc…), es decir una baja longevidad funcional, imposibilita la adecuada eliminación de los animales menos productivos, comprometiendo el progreso genético.

En el análisis de longevidad, el uso de los modelos de riesgos proporcionales fue inicialmente sugerido por (Smith and Quaas 1984) en bovino de leche y ha sido ampliamente utilizado en la mayoría de las especies ganaderas, como el vacuno de leche (Terawaki et al. 2006; Meszaros et al. 2008; Imbayarwo-Chikosi et al. 2017), vacuno de carne (Rogers et al. 2004; Morales et al. 2017), equino (Solé et al. 2017), cerdo (Mészáros et al. 2010; Sobczyńska and Blicharski 2015) y conejo (Sánchez et al. 2006).

La aparición en 1998 del Survival Kit (Ducrocq and Sölkner 1998), un paquete de programas informáticos que implementan estas técnicas en producción animal, ha facilitado el estudio de los datos de longevidad del ganado vacuno lechero mediante análisis de supervivencia. Dicho paquete permite tener en cuenta los datos censurados (reproductoras que no han llegado al final de su vida productiva) a la hora de realizar la valoración genética y de analizar los efectos ambientales que inciden en la longevidad y que cambien en función del tiempo.

A diferencia de los abundantes estudios realizados en el vacuno de leche, la estimación de los parámetros genéticos de rasgos de longevidad en ganado caprino ha sido muy escasa y los trabajos realizados se han limitado a la aplicación de modelos lineales (Castañeda-Bustos VJ et al. 2014; Palhière et al. 2018; Scholtens et al. 2018). De igual manera, existe hasta la fecha sólo dos estudios que han abordado la longevidad con modelos de riesgos proporcionales, pero con el objetivo de estudiar los factores de riesgo de desecho de las hembras y ninguno de ellos ha estimado los parámetros genéticos de este rasgo (Gautam et al. 2017; Ferreira et al. 2020).

Es por ello que, el presente trabajo plantea ser el primero en analizar genéticamente la vida productiva de la hembra utilizando un modelo de riesgos proporcionales y la puesta a punto de esta metodología mediante el uso del software Survival Kit (Ducrocq and Sölkner 1998) en una raza de caprino de leche español.

OBJETIVOS E HIPÓTESIS

OBJETIVOS E HIPÓTESIS

El objetivo global de esta tesis ha sido analizar nuevos criterios de selección relacionados con la productividad y la longevidad de las hembras reproductoras. La hipótesis de partida de esta tesis consiste en que el estudio de nuevos criterios de selección para incorporarlos a los esquemas actuales de selección aplicando nuevas metodologías tal como la regresión aleatoria y el análisis de supervivencia, podrá mejorarse el nivel productivo y la rentabilidad de los rebaños, a través de la puesta a punto de criterios de selección para la prolificidad, la eficacia reproductiva y la longevidad. Para ello se pretende utilizar dos razas prototipo de los modelos productivos semi-extensivo a extensivo (cabra Payoya) y semi-extensivo a semi-intensivo (cabra Florida) de las cabras lecheras españolas.

Los objetivos específicos de la presente tesis son los siguientes:

- Estimar los componentes de varianza y los parámetros genéticos para la prolificidad, definida como tamaño de camada y número de nacidos vivos a lo largo del número de partos en las razas caprinas lecheras españolas utilizando modelos de regresión aleatoria.
- Definir los criterios de selección relacionados con la fertilidad de las reproductoras más adecuados para la especie caprina mediante la estimación de sus parámetros genéticos y la posibilidad de su obtención de forma rutinaria en los núcleos de selección.
- Investigar nuevos criterios de fertilidad (la eficacia reproductiva calculada como la desviación parto óptimo-real a cada edad de la hembra) y estimar sus parámetros genéticos a lo largo de la vida de la reproductora utilizando un modelo de regresión aleatoria.
- Análisis genético de la longevidad de la reproductora definida como longitud de la vida productiva usando un modelo Cox de riesgos proporcionales.

CAPÍTULO I

Capítulo I: Genetic analysis of litter size and number of kids born alive across parities in Spanish goat breeds using a random regression model

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Abstract

Genetic parameters of litter size (LS) and number of kids born alive (NBA) were estimated across parities in Florida and Payoya goat breeds using a threshold random regression model (RRM). We analysed the reproductive records for the Florida and Payoya breeds separately, and a total of 130.849 and 67.478 reproductive records from the first to the seventh parities from Florida and Payoya, respectively, were included in the analysis. Random regressions on Legendre polynomials of standardised parity were included for permanent environmental and additive genetic effects. We based our estimation of all the covariance components on Bayesian inference under categorical distribution and considered heterogeneous residual variances in the model. The estimates of heritabilities ranged from null to 0.37 for LS and from 0.02 to 0.20 for NBA, while the repeatability estimates were between 0.008-0.60 and 0.03-0.44 for LS and NBA, respectively. Phenotypic correlations within-trait along parities ranged widely from -0.31 to 0.97, while the genetic correlations within-trait through parities showed a wider range and magnitude of values, from -0.98 to 0.99 for LS and from -0.72 to 0.99 for NBA. The estimates of genetic correlations between LS and NBA in the different parities were positive in the first two parities and negative in the later ones. Due to the noticeable changes in variance and the incomplete genetic correlations, the use of a random regression model to analyse LS and NBA is recommended in goat breeds.

Highlights

- A bivariate threshold random regression model has been used for the first time to estimate genetic parameters of litter size and number of kids born alive across parities in Spanish goat breeds.

- The evolution of genetic parameters along parities is different between Florida and Payoya that have different production systems, being more intensive in the case of the Florida breed.
- Estimates of variance were not constant across parities for both traits and breeds.
- Genetic correlations within-trait across parities were different from unity.
- Thus, LS and NBA should be treated as different traits in successive parities.
- Given that the estimates of variance and covariances are not constant across parities for both traits and breeds, the use of RRM is highly recommended.

Introduction

Over the last years, genetic improvement in Spanish dairy goats has focused on milk production and milk composition traits (Menéndez-Buxadera et al. 2008, 2010; Molina et al. 2018). Nevertheless, there are other important economic traits in small ruminants, such as litter size and number of kids born alive, especially for breeds facing extinction like the Payoya breed. In the Florida breed, they already represent a significant source of income for breeders by producing a large average litter size. Florida and Payoya breeds are native Spanish dairy goats reared under different production systems varying from semi-extensive to semi-intensive for Florida and from semi-extensive to extensive for Payoya. Florida is spread all over the country (Andalusia, Castilla la Mancha, Extremadura, etc) and in different countries in the world (Italy, Portugal, Venezuela, etc) whereas the Payoya breed is present only in the Andalusian Spanish region. Several approaches have been used to carry out genetic evaluation of litter size in goat, the most common being repeatability and multiple-trait models. A repeatability animal model assumes that genetic correlations between litter sizes are equal to the unity and that the variance is constant in successive parities (Mrode and Thompson 2005). Nevertheless, it has been argued in several studies using multiple-trait model and random regression model (RRM) that phenotypic and additive genetic correlations between litter sizes in adjacent parities are often lower than unity (Alfonso et al. 1994; Irgang et al. 1994; Fernández et al. 2008; Skorput et al. 2014), especially between the first and the later parities (Serenius et al. 2003; Oh et al. 2005; Skorput et al. 2014). Multiple-trait model and random regression model consider subsequent measures to be different traits. Nevertheless, a random regression model has some advantages in comparison with multiple-trait model: the possibility of estimating covariance structure and breeding values at any point of the trait trajectory, and the reduction on the number of parameters to be estimated (Kirkpatrick et al. 1990; Meyer and Hill 1997). Also, RRM offers more accurate modelling of covariance structure, giving more accurate predictions of breeding values (Huisman 2002). In goat, RRM has been used for analysing growth and feed intake (Barazandeh et al. 2012 in Raini; Kheirabadi and Rashidi 2016 in Markhoz; Desire et al. 2018 in mixed-breed Saanen, Alpine, and Toggenburg dairy goats) and milk yield and composition traits (Menéndez-Buxadera et al. 2008 in Payoya; 2010 in Murciano-Granadina; Andonov et al. 2013 in Norwegian goats; Silva et al. 2013 in Alpine; Arnal et al. 2019 in Saanen); however, their application to genetic evaluation of litter size has not yet been implemented, and estimation of genetic parameters for litter size or number born alive using RRM has been reported only in pigs (Lukovic et al. 2003, 2004, 2006; Fernández et al. 2008; Chen et al. 2010; Skorput et al. 2014; Ogawa et al. 2019). Litter size is measured more than once in an animal’s lifetime and, despite being different from longitudinal traits because the parity number is a discrete variable, the application of RRM to analyse this trait is feasible (Schaeffer 2004).

Therefore, the main aim of this study was to estimate for the first time in Florida and Payoya goat breeds genetic parameters and their changes across parities for litter size (LS) and number of kids born alive (NBA) treated as threshold traits using a bivariate random regression model (RRM).

Material and methods

Data description

The reproductive and genealogical records of the Florida and Payoya goats were provided by ACRIFLOR (National Association of Florida Goat Breeders) and ACAPA (Association of Payoya Goat Breeders), respectively. The original datasets comprised 143,002 and 72,514 records, respectively. Data from herds with less than 10 records or scarce genetic connections were removed. Genetic links were due to the use of artificial insemination sires. After data editing, a total of 130,849 records from 48,984 Florida females collected between 1986 and 2019 (an average of 2.67 kiddings per female) and 67,478 records from 14,942 Payoya females recorded between 2003 and 2019 (an average of 4.51 kiddings per female) were used in this analysis. Traits considered were litter size (LS), estimated as the total number of kids born per kidding and number of kids born alive (NBA), both recorded on the day of kidding from the first to the seventh parity in both breeds. For the Florida pedigree, only animals with approved parentage tests using DNA microsatellites were considered. The pedigree was traced back for as many generations as available in the breeds herd book, being 7.3 equivalent generations for Florida and 4 generations for Payoya. The total number of animals in the pedigree was 55,748 for Florida and 26,392 for Payoya.

Statistical analysis

The analyses were performed for the Florida and Payoya breeds separately, fitting the following bivariate random regression model (RRM) for LS and NBA:

$$y=\text{fixed}+\sum_{k=0}^{p-1}\beta_k X_k+\sum_{k=0}^{p-1}\alpha_{ik} Z_k+\sum_{k=0}^{p-1}\mu_{ik} W_k+e$$

where y is a vector with n observations of LS and NBA, ‘fixed’ is the combined effect of herd-year-month of kidding (2629 levels for Florida and 803 for Payoya), $\boldsymbol{\beta_k}$ are **k** coefficients of fixed regression of the LS and NBA traits across parities with orthogonal second order Legendre polynomials. Seven parity classes were considered as the unit of time **t** for both traits and breeds corresponding to parity numbers (**t** = 1-6 and **t** ≥ 7). $\boldsymbol{\alpha_{ik}}$ and $\boldsymbol{\mu_{ik}}$ are the random regression coefficients associated with the additive genetic function of animals and the permanent environmental function of the goat with LS and NBA records, respectively, and **e** is the residual modelled with heterogeneous variance according to parity with three measurements for Florida (parity 1, 2, and ≥ 3) and five measurements for the Payoya breed (parity 1, 2, 3 and 4, 5 and ≥ 6). **X**, **Z**, and **W** are incidence matrices relating y with the new parameters in **b**, **a**, and **m**, respectively. To deal with the non-normal distribution of LS and NBA, these traits were treated as a threshold trait, divided into two categories in both breeds (one; more than one). The (co)variance components, heritabilities ($\mathbf{h^2}$), repeatabilities (***t***), and additive genetic correlations ($\mathbf{r_g}$) throughout the scale of values of parity were estimated by the expression proposed by Jamrozik and Schaeffer (1997). Estimation of all the (co)variance components was based on the Bayesian inference methodology using the Gibbs Sampling algorithm in the THRGIBBS3F90 software (Misztal et al. 2016). Flat priors were assumed for systematic effects of herd-year-month of kidding, as well as for additive genetic, permanent environmental, and residual effects. Chains of 100,000 samples were used, with a burn-in period of 20,000. One sample per 100 was saved to avoid high correlations between consecutive samples. A post-Gibbs analysis using the POSTGIBBSf90 program (Tsuruta and Misztal 2006) was performed in order to calculate posterior means and high posterior density intervals and to check convergence with the Geweke test.

Results and discussion

Up to now, there have been no studies on the estimation of genetic parameters for litter size with random regression model in goat: previous studies on the genetic analysis of litter size have normally used repeatability and multiple-trait approaches. In this work, we analysed the change in genetic parameters of LS and NBA across female parities with a threshold random regression model in Florida and Payoya goat breeds. The distribution of number of records and average female age at different parities in Florida and Payoya breeds is provided in Table 1.

Table 1. Distribution of data over parities in Florida and Payoya breeds[1].

	Florida		Payoya	
Parity	Nº records	Age	Nº records	Age
1	45.310	1.37	20.408	1.61
2	33.122	2.32	16.300	2.51
3	22.142	3.31	11.658	3.45
4	13.851	4.29	7.919	4.41
5	7.998	5.25	5.132	5.39
6	4.338	6.21	3.228	6.36
7	4.088	7.87	3.850	7.78

[1]: average female age is expressed in years.

The least-squares means for litter size (LS) and number of kids born alive (NBA) over the seven parities are summarised in Figures 1 and 2, respectively. The average values were 1.61-1.6 and 1.6-1.57 for LS and NBA, for Florida and Payoya breeds, respectively. The maximum values of LS and NBA were observed in the fourth parity in Florida and in the sixth parity in Payoya. The phenotypic trajectories of both traits (Figures 1 and 2) reflected the high reproductive performance of Florida and Payoya breeds and their high persistence. However, the initial increase and the final decline in both traits in the Florida breed were more remarkable and occurred earlier than in Payoya, possibly due to its high production level and the fact that the Payoya breed is a more rustic (less improved) breed and is, therefore, less precocious.

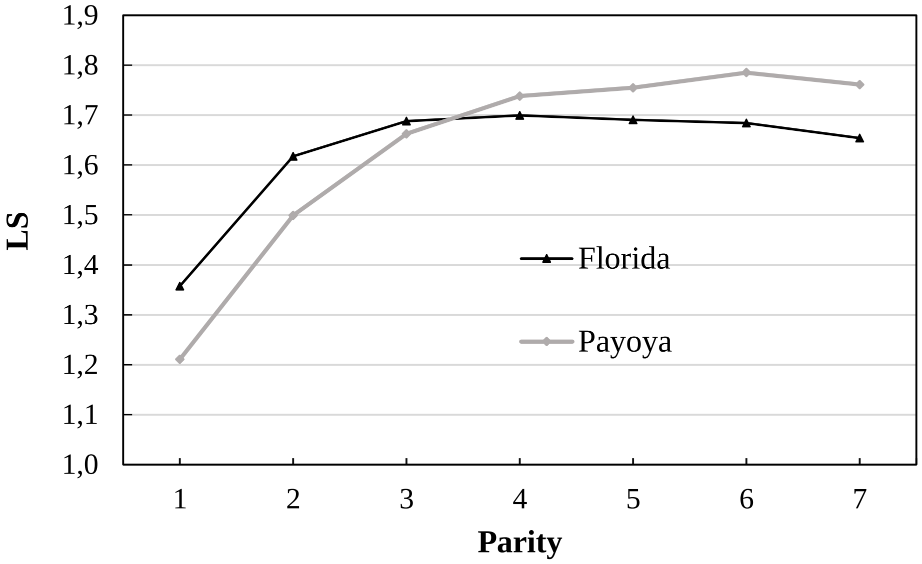

Figure 1. Least-squares means of litter size (LS) across parities in Florida and Payoya breeds.

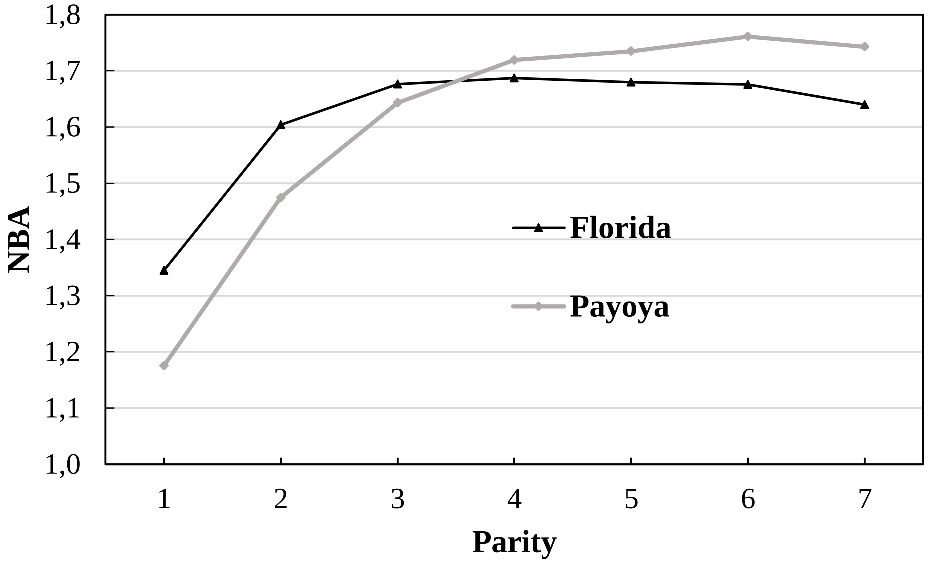

Figure 2. Least-squares means of number of kids born alive (NBA) across parities in Florida and Payoya breeds.

The results of variance components (additive genetic, permanent environmental, and residual), heritabilities (h^2), and repeatabilities (*t*) across the seven parities in Florida and

Payoya breeds for litter size and number of kids born alive are presented in Tables 2 and 3, respectively. All estimates of variance components, heritabilities, repeatabilities, and additive genetic correlations in this study for LS and NBA in both breeds were presented on a liability scale. Estimates of variance components for LS in both breeds presented the same tendency, decreasing from the first parity to the second parity which presented the lowest values, and increasing up to the latest parities, reaching the highest values in the sixth and seventh parities.

Heritability and repeatability estimates of LS in both breeds showed the same pattern as the variance components. Their estimated values oscillated between null to 0.22 and 0.008 to 0.42 in Florida and from 0.01 to 0.37 and 0.02 to 0.60 in Payoya for heritability and repeatability, respectively (Table 2). Variance components, h^2, and *t* for NBA in both breeds did not present a clear pattern from the first to the seventh parity. Nevertheless, in the Payoya breed, the first parity presented the lowest estimates. Besides, the highest values for variance components, h^2, and *t* were observed in the latest parity (h^2 was 0.19 and 0.20 and *t* was 0.30 and 0.44 in Florida and Payoya, respectively, Table 3).

The estimated variance components and h^2 for LS and NBA changed over parities and differed slightly between Florida and Payoya breeds, showing low values, as expected for reproductive traits. In general, all $HPD_{95\%}$ for heritabilities for LS and NBA in both breeds were small. To date, there are no works on the estimation of genetic parameters of reproductive traits in goat using threshold RRM. In previous studies conducted in other goat breeds, a wide range of h^2 values has been reported for LS (Kasap et al. 2013 in Saanen; Atoui et al. 2018 in local Tunisian breed; Abdoli et al. 2019 in Markhoz), but all these estimates have been obtained with linear repeatability models. For NBA, there are no available studies on estimating its genetic parameters, and this work is the first to estimate it in goat using RRM. The high estimated repeatabilities observed in the last parities could be explained by the fact that at this stage, the least reproductively efficient animals have already been discarded. The differences found between Florida, Payoya and other breeds may be attributable to estimation errors due to differences in the used methodologies, the size of the datasets, the genetic structure of the populations, or management practices.

Table 2. Estimates of variance components, heritabilities, and repeatabilities for litter size (LS) across parities in Florida and Payoya breeds using a threshold random regression model[1]. with second-order Legendre polynomials.

	Florida					Payoya				
Parity	σ^2_a	σ^2_{pe}	h^2	$HPD_{95\%}$	*t*	σ^2_a	σ^2_{pe}	h^2	$HPD_{95\%}$	*t*
1	0.087	0.081	0.07	0.06 0.09	0.14	0.270	0.260	0.18	0.13 0.21	0.34
2	0.003	0.005	0.00	0.002 0.005	0.008	0.009	0.015	0.01	0.006 0.01	0.02
3	0.012	0.010	0.01	0.009 0.01	0.02	0.042	0.026	0.04	0.03 0.05	0.06
4	0.041	0.043	0.04	0.03 0.04	0.07	0.158	0.108	0.13	0.09 0.14	0.21
5	0.075	0.091	0.06	0.05 0.08	0.14	0.282	0.185	0.19	0.15 0.22	0.32
6	0.154	0.175	0.12	0.08 0.15	0.24	0.475	0.293	0.27	0.22 0.33	0.43
7	0.374	0.353	0.22	0.15 0.27	0.42	0.933	0.582	0.37	0.25 0.47	0.60

[1]: residual variance for threshold model is equal to unity. σ^2_a: additive genetic variance; σ^2_{pe}: permanent environmental variance; h^2: heritability; $HPD_{95\%}$: high posterior density interval at 95% for h^2 estimates; *t*: repeatability.

Table 3. Estimates of variance components, heritabilities, and repeatabilities for number of kids born alive (NBA) across parities in Florida and Payoya breeds using a threshold random regression model[1]. with second-order Legendre polynomials.

	Florida					Payoya				
Parity	σ^2_a	σ^2_{pe}	h^2	$HPD_{95\%}$	*t*	σ^2_a	σ^2_{pe}	h^2	$HPD_{95\%}$	*t*
1	0.022	0.023	0.02	0.01 0.02	0.04	0.029	0.025	0.03	0.02 0.04	0.05
2	0.035	0.010	0.03	0.03 0.04	0.04	0.088	0.109	0.07	0.05 0.09	0.16
3	0.057	0.016	0.05	0.04 0.06	0.07	0.145	0.204	0.11	0.08 0.14	0.26
4	0.046	0.015	0.04	0.03 0.05	0.06	0.125	0.181	0.10	0.07 0.12	0.23
5	0.019	0.012	0.02	0.01 0.02	0.03	0.052	0.063	0.05	0.03 0.06	0.10
6	0.049	0.042	0.04	0.03 0.05	0.08	0.054	0.034	0.05	0.03 0.06	0.08
7	0.267	0.167	0.19	0.15 0.22	0.30	0.361	0.431	0.20	0.14 0.27	0.44

[1]: residual variance for threshold model is equal to unity.

σ^2_a: additive genetic variance; σ^2_{pe}: permanent environmental variance; h^2: heritability; $HPD_{95\%}$: high posterior density interval at 95% for h^2 estimates; *t*: repeatability.

Estimates of the phenotypic (r_p) and additive genetic (r_g) correlations within-trait over the seven parities in Florida and Payoya breeds are provided in Tables 4 and 5 for LS, and Tables 6 and 7 for NBA, respectively.

Table 4. Estimates of genetic correlations (above diagonal) and phenotypic correlations (below diagonal) between litter size (LS) across parities in Florida breed using a threshold random regression model. with second-order Legendre polynomials.

	Parity						
Parity	1	2	3	4	5	6	7
1	-	0.94	-0.90	-0.81	-0.52	-0.09	0.25
2	0.17	-	-0.78	-0.74	-0.50	-0.12	0.19
3	-0.09	0.55	-	0.96	0.77	0.41	0.07
4	-0.18	0.51	0.82	-	0.91	0.63	0.32
5	-0.23	0.49	0.82	0.91	-	0.89	0.67
6	-0.26	0.47	0.80	0.91	0.95	-	0.93
7	-0.24	0.45	0.78	0.89	0.94	0.96	-

Table 5. Estimates of genetic correlations (above diagonal) and phenotypic correlations (below diagonal) between litter size (LS) across parities in Payoya breed using a threshold random regression model. with second-order Legendre polynomials.

	Parity						
Parity	1	2	3	4	5	6	7
1	-	0.99	-0.96	-0.89	-0.71	-0.38	-0.02
2	0.06	-	-0.98	-0.93	-0.77	-0.47	-0.12
3	-0.13	0.61	-	0.97	0.86	0.60	0.26
4	-0.20	0.60	0.85	-	0.95	0.75	0.46
5	-0.23	0.60	0.87	0.93	-	0.92	0.71
6	-0.26	0.60	0.87	0.94	0.96	-	0.92
7	-0.31	0.59	0.86	0.93	0.96	0.97	-

Table 6. Estimates of genetic correlations (above diagonal) and phenotypic correlations (below diagonal) between number of kids born alive (NBA) across parities in Florida breed using a threshold random regression model. with second-order Legendre polynomials.

	Parity						
Parity	1	2	3	4	5	6	7
1	-	0.51	0.29	0.35	0.78	0.75	0.49
2	0.16	-	0.97	0.98	0.90	-0.13	-0.48
3	-0.08	0.55	-	0.99	0.79	-0.35	-0.66
4	-0.17	0.51	0.81	-	0.83	-0.28	-0.61
5	-0.21	0.49	0.82	0.91	-	0.28	-0.08
6	-0.24	0.47	0.80	0.90	0.95	-	0.93
7	-0.23	0.45	0.78	0.89	0.94	0.96	-

Table 7. Estimates of genetic correlations (above diagonal) and phenotypic correlations (below diagonal) between number of kids born alive (NBA) across parities in Payoya breed using a threshold random regression model. with second-order Legendre polynomials.

	Parity						
Parity	1	2	3	4	5	6	7
1	-	0.63	0.52	0.55	0.80	0.68	0.20
2	0.08	-	0.98	0.99	0.95	-0.09	-0.61
3	-0.09	0.60	-	0.99	0.91	-0.23	-0.72
4	-0.15	0.59	0.85	-	0.93	-0.18	-0.68
5	-0.20	0.60	0.86	0.93	-	0.17	-0.37
6	-0.24	0.60	0.87	0.94	0.96	-	0.84
7	-0.30	0.59	0.86	0.93	0.96	0.97	-

Phenotypic correlations within-trait along parities ranged widely from -0.26 to 0.96 for LS and -0.24 to 0.96 for NBA in Florida (Tables 4 and 6, respectively) and from -0.31 to 0.97 for LS and -0.30 to 0.97 for NBA in the Payoya breed (Tables 5 and 7, respectively). The estimated genetic correlations for LS were generally similar in both breeds and covered a very wide range of values varying from -0.90 to 0.96 in Florida (Table 4) and from -0.98 to 0.99 in Payoya (Table 5). These estimates were high between the adjacent parities (in the diagonal) and close to unity, except for r_g between the second and third parities in both breeds, and decreased as the interval between parities increased, except for r_g between the seventh parity and the first and second parities, which showed a small increase. In both breeds, the decrease in r_g from the first-second parities to the second-third parities was sudden, with clearly contrasting values. For NBA, estimates of r_g varied from -0.66 to 0.99 in Florida (Table 6) and from -0.72 to 0.99 in Payoya (Table 7). Estimated r_g among the first five parities, unlike LS, presented only positive values. In subsequent parities, the values were high, except for r_g between the fifth and sixth parities (0.28 in Florida and 0.17 in Payoya, Table 7). Unlike LS, the variation in r_g as the interval between parities increased did not present a clear pattern in both breeds. A low genetic correlation within-trait in different parities indicates that LS and NBA records from different parities should be treated as different traits (Irgang et al. 1994; Roehe and Kennedy 1995; Skorput et al. 2014). Direct additive genetic correlations were highest between adjacent parities and decreased as the interval between parities increased. This decreasing tendency of r_g with the increasing distance between parities was in agreement with the findings of Lukovic et al. (2006) and Skorput et al. (2014) in pigs. This could be explained by the smaller amount of data in later parities and the imprecise recording of parity order (Skorput et al. 2014).

Additive genetic and phenotypic correlations between LS and NBA in Florida and Payoya breeds across parities are presented in Table 8.

Table 8. Estimates of phenotypic (r_p) and genetic (r_g) correlations between litter size (LS) and number of kids born alive (NBA) across parities in Florida and Payoya breeds using a threshold random regression model. with second-order Legendre polynomials.

	Florida		Payoya	
Parity	r_p	r_g	r_p	r_g
1	0.96	0.81	0.89	0.93
2	0.96	0.56	0.94	0.66
3	0.96	-0.35	0.95	-0.45
4	0.97	-0.21	0.95	-0.30
5	0.97	-0.09	0.95	-0.25
6	0.97	-0.11	0.95	-0.53
7	0.96	-0.18	0.96	-0.62

r_p: phenotypic correlation; r_g: genetic correlation.

The estimated r_g between both traits covered a wide range and magnitude of values, being positive in the first two parities with the highest values in the first parity for Florida (0.81, Table 8) and the first and second ones in Payoya (0.93 and 0.66 for first and second parity, respectively, Table 8), and negative in the later parities.

Therefore, a selection made at any parity will have a positive or negative impact on the other trait throughout the rest of the productive life of the goat, particularly after the third parity. On the other hand, the phenotypic correlations were much smoother compared to the genetic ones. The wide range and magnitude of r_g estimates between LS and NBA at different parities implies that selection for increasing one of these traits will produce a genetic response (limited given the low magnitude of heritabilities) whose magnitude will depend on the moment it is selected. The maximum direct and correlated responses can be obtained by selecting during the first two parities in Payoya and the first parity in Florida. It is also important to recognise litter size as a complex trait (Pérez-Enciso et al. 1994, Rauw et al. 1999; Menéndez-Buxadera et al. 2004). LS is the best natural index as it combines ovulation rate and survival rate of the embryos (directly dependent on the maternal uterine environment). Litter size is therefore considered as a trait genetically related only to the mother of the litter, although some authors (Menéndez- Buxadera et al. 2004) have shown that there may be a small paternal component (probably due to the fact that there is an additive component of the embryo or embryos that make them more or less robust), consistent with Falconer’s (1960) hypothesis.

Random regression model has become commonly used to analyse longitudinal data or repeated records of individuals over time. RRM is a suitable way of dealing with repeated traits since it describes performance over time for each animal to allow for individual variation in the course of the trajectory (Meyer 1998). To estimate the genetic parameters for LS and NBA in Florida and Payoya goat breeds, the use of RRM is justified since both traits show a very wide variation in variances and genetic correlations throughout parities. Even for lower values of h^2, as in the case of reproductive traits, and for negative genetic correlations, the possibility of optimally selecting for increasing female prolificacy is suggested.

The wide range of estimates of genetic correlations for LS and NBA between the different parities confirms that these traits are partially controlled by different genes at the first two parities and at the later parities. Genetic selection of animals for reproductive traits could be implemented involving LS and NBA in the first and second parities in Florida and in the first parity in Payoya.

Finally, this study provides estimates of genetic parameters for LS and NBA across the female parities, using a random regression model that can be used in the future to support decisions about selection aims within the current selection programs of Florida and Payoya breeds. It also suggests that future research should evaluate the traits of litter size and number of kids born alive in conjunction with the current selection criteria (milk production and milk composition traits).

Conclusions

Using a threshold model in which a continuous variable underlying LS and NBA traits across parities by a bivariate RRM in Florida and Payoya goats, our results indicate that litter size and the number of kids born alive in subsequent parities are genetically not the same traits because estimated variances and covariances were not constant over parities and genetic correlations between repeated measures of the traits differed from unity. Hence, the use of a random regression model to genetically analyse litter size or the number of kids born alive over parities is recommended in both breeds. Although low heritability estimates were obtained, improvement of litter size and number of kids born alive by selection is feasible. Given the genetic correlations between both traits across parities, an early genetic response can be achieved if selection occurs in the two first parities for Payoya and the first one for Florida breed.

Ethical approval

This study did not require manipulation or modification of the usual handling of the animals, since we have worked directly with the routine records provided by the breeders' associations of the Florida and Payoya breeds.

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Disclosure statement

The authors declare that there is no conflict of interest associated with the paper.

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CAPÍTULO II

Capítulo II: Selection Criteria for Improving Fertility in Spanish Goat Breeds: Estimation of Genetic Parameters and Designing Selection Indices for Optimal Genetic Responses

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Simple Summary

Up to now, the genetic evaluation of Spanish dairy goats has been based only on milk production traits. However, fertility is also an important economic trait for goats and is vital for maintaining the profitability of dairy farms, and the estimation of its genetic parameters and selection responses is, therefore, crucial for the genetic improvement of dairy goats. In this study, we estimated the genetic parameters of various fertility traits in the Florida and Payoya goat breeds, which are prototype breeds exploited under different production systems in Spain. Next, we assessed selection indices to determine the most suitable one to produce the highest number of expected selection responses. The overall interval between kiddings gives the highest genetic response but cannot be recommended as early selection criteria because it is expressed late in the female's life, especially in the Florida breed, in which a high early culling is carried out in females with low fertility. Nevertheless, an index including the age at first kidding and the interval between the first and second kiddings can be used as a precocious selection criterion in both breeds. The results from this study can be used as a basis for the future genetic improvement of fertility traits.

Abstract

The aim of this study was to estimate genetic parameters for several female fertility criteria and to choose the most suitable selection index in Spanish Florida and Payoya goat breeds. In this study, we analysed as fertility traits, the age at first kidding (AgFiKid), and the interval between the first and second kiddings (Int12Kid), between the second, third, and remaining kiddings (Int3toKid), and between all kiddings (IntAllKid) in 51,123 and 22,049 Florida and Payoya females, respectively. Genetic parameters were estimated by fitting animal models using restricted maximum likelihood (REML) methodology. We proposed six selection indices to compare the genetic responses for all traits included, based on a new selection index theory. The heritability and repeatability estimates of the traits were low, as expected. The genetic correlations among fertility traits covered a wide range of values from 0.07 (AgFiKid-Int12Kid) to 0.71 (Int3toKid-IntAllKid) in Florida and from -0.02 (AgFiKid-Int12Kid) to 0.82 (Int3toKid-IntAllKid) in Payoya. Overall, the results of this study indicate that IntAllKid gives the highest genetic responses in both breeds but is expressed late in a female’s life. However, AgFiKid and Int12Kid could be recommended as early selection criteria for female fertility in both breeds.

Keywords: female fertility, genetic parameters, selection index, dairy goat.

Introduction

Spanish dairy goat breeds are farmed under different production systems varying from extensive, semi-extensive, and semi-intensive to intensive systems, depending on their productive aptitude and performance. The Florida and Payoya breeds are among the autochthonous dairy goats with the widest range of geographic distribution and production systems. The Florida goat can be found in different countries in the world and several regions of Spain (Extremadura, Castilla-la-Mancha, etc.), but especially in Andalusia, where it is raised under semi-extensive to semi-intensive production systems, while the Payoya breed is present only in Spain in the region of Andalusia, under semi-extensive to extensive production systems.

Nowadays, the genetic evaluation of Spanish dairy goats is based mainly on milk production traits (milk, protein, and fat yields, and protein and fat percentages), and studies have focused on estimating the genetic parameters of these traits [1,2,3]. However, other economically important traits, such as fertility, have not been studied and are not taken into consideration in the current genetic program: In fact, up to now, no estimations of genetic parameters have been made available for traits related to fertility in Spanish dairy goats.

Most studies of the genetic and environmental association between milk production and reproductive traits in various species showed an unfavorable relationship between them not only in dairy cattle [4,5] and in dairy sheep [6] but also in dairy goats [7]. Ignoring the genetic and phenotypic correlations between traits in selection programs could lead to undesirable outcomes in the correlated response of certain traits. To overcome this problem, selection indices have been developed to improve several traits related to global economic profitability simultaneously. The economic selection index implemented by Hazel (1943) [8] has been commonly used in a wide range of livestock species: meat goat [9], dairy goat [10,11], dairy cattle [12], beef cattle [13], and meat sheep [14]. Recently, this classic methodology of selection indices has been modified to overcome its limitations, to allow direct work with genetic values [15,16]. In addition to genetic values, their reliabilities, and all genetic relationships, the knowledge of traits' economic weights is necessary. Economic weight is the value of one unit superiority of a trait when all other traits in the aggregate genotype remain constant [8]. Economic weights in goat have been derived for many traits in dairy goat: dairy, functional, and fattening traits ([17,18]).

Thus, the main objectives of the present study were to estimate the genetic parameters of fertility traits for the first time in Spanish dairy goats, using Florida and Payoya breeds as models, and to find the best selection index for the desired expected genetic response.

Materials and methods

Phenotypic data and pedigree

In this study, we used reproductive records and pedigree information from ACRIFLOR (National Association of Florida Goat Breeders) and ACAPA (Association of Payoya Goat Breeders), which contained information on age at first kidding and the different intervals between the kiddings of Florida and Payoya females, respectively. To estimate the genetic parameters, herds with few records or scarce genetic connections were discarded. The genetic links were due to artificial insemination sires. Artificial insemination (AI) has been implemented in the Florida and Payoya breeds since 2005 within the selection scheme carried out by ACRIFLOR and ACAPA, respectively. In the last years, approximately 1808 AI with 5 bucks (from a set of 25 semen donors) and 600 AI with 3-4 bucks (from a set of 8 semen donors) were realized in Florida and Payoya, respectively.

Connectedness was estimated by calculating the coefficient of similarity between herds (SG), which is the number of daughters of a connector male shared between two herds in relation to the total number of animals that have been evaluated in those two herds, establishing an SG equal to 5% as a limit for a herd to enter in the genetic evaluation process. Animals from the Payoya breed are reared under semi-extensive to extensive production systems, whereas the Florida breed presents a higher level of intensification. The following traits were considered in this study as measures of a goat's fertility: the age at first kidding (AgFiKid), the interval between first and second kiddings (Int12Kid), the interval between second, third, and remaining kiddings (Int3toKid), and the interval between all kiddings (IntAllKid). All traits were expressed in months. After data editing, the final data set contained information on 130,849 and 67,478 reproductive records from 51,123 and 22,049 Florida and Payoya females, respectively. In total, the pedigree included 56,305 animals for Florida and 26,392 for Payoya.

Statistical analysis

Genetic parameters of fertility traits

The following model was fitted to estimate the genetic parameters for all the fertility traits for Florida and Payoya breeds:

$$\mathrm{y} = \mu + \mathrm{age} + \mathrm{Xb} + \mathrm{Zu} + \mathrm{Wpe} + \mathrm{e}$$

where **y** is the vector of observations of each trait, **μ** is the overall mean, **age** is a covariate representing the age at first kidding used in the model for Int12Kid or the age at kidding for the model for Int3toKid and IntAllKid; **b** is the vector of fixed effects including the interaction herd-year-season of kidding, in which the season of kidding was coded as 1 if a goat gave birth in the period June through September and was otherwise coded as 2, lactation length (4 levels: short, medium, long, and very long) and herd productive level (3 levels: low, medium, and high); **u** is the random additive genetic effect, **pe** is the random permanent environmental effect of the female, and **e** is the random residual effect. **X**, **Z**, and **W** are incidence matrices relating observations to fixed, random additive genetic and random female permanent environmental, respectively. The non-genetic effects in the model varied depending on the individual trait: neither the age at first kidding nor the interval between first and second kiddings had the lactation length, the herd production level, or the permanent environmental effects. The Florida and Payoya breeds were analysed independently. Covariance components for all the traits were estimated with an animal model, using AIREMLF90 software from the BLUPF90 family of programs [19], applying a restricted maximum likelihood (REML) approach.

Expected genetic responses

The genetic responses using different selection objectives/criteria were computed and compared in the Florida and Payoya breeds according to the classic selection index theory [20] reformulated by Gutiérrez et al. (2014) [15] for the use of genetic parameters rather than performances. Two selection objectives were designed (the IntAllKid, and the IntAllKid combined with the AgFiKid), and six groups of indices were constructed to combine the different fertility traits as selection criteria. In the selection indices with the second selection objective, the desired economic weight in the vector $\mathbf{p}'$ for IntAllKid was five times greater than that of AgFiKid. Weights in vector $\mathbf{f}'$ to be used for weighting the expected breeding values (EBVs) on $\mathbf{v}$ were calculated by $\mathbf{f}' = \mathbf{p}'\mathbf{C}'\mathbf{G}^{-1}$, where $\mathbf{C}'$ is the covariance matrix between the objectives in vector $\mathbf{u}$ and the EBV used as criteria in vector $\mathbf{v}$, and $\mathbf{G}^{-1}$ is the inverse of the (co)variance matrix for the selection criteria $\mathbf{v}$. Matrices $\mathbf{C}'$ and $\mathbf{G}$ were obtained from the genetic parameters by assuming all the additive genetic variances to be standardized ($\sigma^2_{\mathrm{u1}} = \sigma^2_{\mathrm{u2}} = \sigma^2_{\mathrm{u3}} \cdots = \sigma^2_{\mathrm{uk}} = 1$), where σ^2_{uk} is the additive genetic variance of trait *k*: as a result, all of them were on the same genetic scale. When considering the different objectives and/or criteria, the coefficients in $\mathbf{f}'$ varied, and matrices $\mathbf{C}$ and $\mathbf{G}$ also changed. When objective and criteria are the same traits, the (co)variance matrix between the objectives and the criteria $\mathbf{C}$ becomes a genetic additive (co)variance matrix, in which the diagonals are equal to one [15]. Off-diagonal elements are the additive genetic correlations between objectives and criteria, given that $\mathrm{r_{ukul}} = \frac{\sigma_{\mathrm{ukul}}}{\sqrt{\sigma^2_{\mathrm{uk}}\sigma^2_{\mathrm{ul}}}}$, where $\mathrm{r_{ukul}}$ is the additive genetic correlation between traits *k* and *l* and $\sigma^2_{\mathrm{uk}} = 1$ for any trait, thus becoming $\sigma_{\mathrm{ukul}} = \mathrm{r_{ukul}}$ and $\mathbf{C}'$:

$$\mathrm{C}' = \mathrm{Var}(\mathrm{u}) = \begin{bmatrix} \sigma^2_{\mathrm{u1}} & \sigma_{\mathrm{u1u2}} & \sigma_{\mathrm{u1u3}} & \cdots & \sigma_{\mathrm{u1um}} \\ \sigma_{\mathrm{u2u1}} & \sigma^2_{\mathrm{u2}} & \sigma_{\mathrm{u2u3}} & \cdots & \sigma_{\mathrm{u2um}} \\ \ldots & \ldots & \ldots & \ldots & \ldots \\ \ldots & \ldots & \ldots & \ldots & \ldots \\ \sigma_{\mathrm{umu1}} & \sigma_{\mathrm{umu2}} & \sigma_{\mathrm{umu3}} & \cdots & \sigma^2_{\mathrm{um}} \end{bmatrix}$$

$$= \begin{bmatrix} 1 & \mathrm{ru1u2} & \mathrm{ru1u3} & \ldots & \mathrm{ru1um} \\ \mathrm{ru2u1} & 1 & \mathrm{ru2u3} & \ldots & \mathrm{ru2um} \\ \ldots & \ldots & \ldots & \ldots & \ldots \\ \ldots & \ldots & \ldots & \ldots & \ldots \\ \mathrm{rumu1} & \mathrm{rumu2} & \mathrm{rumu3} & \ldots & 1 \end{bmatrix}$$

As **G** and **C′** are directly dependent on the genetic parameters, these matrices can be derived directly from Tables 3 and 4 to build the desired index. Next, the genetic responses were obtained by weighting, for each of the traits, all those responses obtained in the correlated selected traits, including the direct genetic response to itself. Thus, assuming the EBVs are known and applying the assumption given above about all the additive genetic variances being one, the direct genetic response would be the selection intensity (*i*) reduced by the accuracy of the EBV. The correlated response would be the additive genetic correlation times the selection intensity reduced by the accuracy of the EBV. Gathering this information into a matrix expression, the cumulated genetic responses will be obtained by:

$$t = b'Ti = b'\begin{bmatrix} h_1 & h_1 r_{u_1u_2} & h_1 r_{u_1u_3} & \dots & h_1 r_{u_1u_k} \\ h_2 r_{u_2u_1} & h_2 & h_2 r_{u_2u_3} & \dots & h_2 r_{u_2u_k} \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ h_k r_{u_ku_1} & h_k r_{u_ku_2} & h_k r_{u_ku_3} & \dots & h_k \end{bmatrix} i,$$

where each $\mathbf{t_k}$ in **t** is the cumulated genetic response in trait *k* and h_k the squared root of the heritability of trait *k*. For the comparison of the expected responses, a constant selection intensity of one was assumed, leading to comparable relative results.

Results and discussion

This study estimated for the first time the genetic parameters related to female fertility traits in Florida and Payoya dairy goat breeds (AgFiKid, Int12Kid, Int3toKid, and IntAllKid), and expected to find the genetic responses by combining these traits in selection indices as a step towards their incorporation into the routine genetic evaluation.

Phenotypic parameters of fertility traits

The basic descriptive statistics for Florida and Payoya female fertility traits are presented in Table 1. The AgFiKid ranged between 12 and 24.6 months in Florida and 12 and 33 months in Payoya, with an average of 15.98 months ± 2.85 and 18.93 months ± 4.83 for Florida and Payoya, respectively, and was within the range of the values reported by other authors in US dairy goats [19,20] and Mexican Saanen goat [23], higher than those observed in Polish and Norwegian [24] and Brazilian dairy goat [25], and lower than that for the Toggenburg breed [26]. The more intensive production system (Florida) reduced

AgFiKid by 88.5 days in comparison with the extensive system (Payoya). The same finding was reported between intensive (283.83 days ± 31.16) and semi-intensive (370.26 days ± 25.48) Black Bengal goats [27].

The values for Int12Kid, Int3toKid, and IntAllKid were similar in both breeds and ranged between 5.7and 17.1 months in Florida and 6.3 and 16.7 months in Payoya. Their averages varied from 10.78 months ± 1.74 (for Int12Kid in Payoya) to 11.46 months ± 1.72 (for Int3toKid in Payoya) and were lower than the ones mentioned in US dairy goats [7,19,20], but higher than the values obtained in Toggenburg [26] and Brazilian goats [25]. The coefficients of variation oscillated between 16.8% and 18.2% (for Int3toKid and Int12Kid, respectively) in Florida and 15.0 and 25.5% (for Int3toKid and AgFiKid, respectively) in Payoya. The values were, in general, similar between both breeds, except for AgFiKid, which was 30% higher in Payoya than in Florida, and lower than the 30% and 22% values reported by García-Peniche et al.(2012) [21] for AgFiKid and IntAllKid, respectively.

Table 1. Basic descriptive statistics for fertility traits in Florida and Payoya breeds.

Item	Nº of Records		Mean ± SD		Min		Max		CV (%)	
Traits[1]	**Florida**	**Payoya**	**Florida**	**Payoya**	**Florida**	**Payoya**	**Florida**	**Payoya**	**Florida**	**Payoya**
AgFiKid	40.652	13.909	15.98 ± 2.85	18.93 ± 4.83	12	12	24.6	33.0	17.83	25.52
Int12Kid	24.106	9.108	10.87 ± 1.98	10.78 ± 1.74	5.7	6.3	17.1	16.5	18.23	16.15
Int3toKid	42.858	23.623	11.41 ± 1.91	11.46 ± 1.72	5.7	6.3	17.1	16.7	16.77	15.00
IntAllKid	75.315	34.006	11.22 ± 2.01	11.28 ± 1.77	5.7	6.3	17.1	16.7	17.88	15.67

[1]: all traits are expressed in months; AgFiKid: age at first kidding; Int12Kid: interval between first and second kiddings; Int3toKid: interval between second, third, and remaining kiddings; IntAllKid: interval between all kiddings; SD: standard deviation; Min: minimum; Max: maximum; CV: coefficient of variation.

Genetic parameters

The range of solutions for the fixed effects: herd–year–season of kidding, lactation length, and herd production level affecting fertility traits are shown in Table 2. It should be noted that all these effects, with their different levels, had a significant effect on fertility parameters, to greater or lesser degrees. This illustrated how increasing herd fertility can be achieved through environmental improvement (reproduction management, health care, feeding, etc.). The herd–year–season of kiddings' effect had the highest levels, the widest range of values, and the most significant effect.

Table 2. Solutions for fixed effects for fertility traits in Florida and Payoya breeds[1].

Effects	Levels	AgFiKid		Int12Kid		Int3toKid		IntAllKid	
		Florida	**Payoya**	**Florida**	**Payoya**	**Florida**	**Payoya**	**Florida**	**Payoya**
Herd-year-season[2]	1 to *n*	12.36 to 24.38 (876)	12.15 to 28.09 (328)	8.29 to 15.57 (620)	7.91 to 13.75 (278)	9.63 to 16.27 (774)	9.32 to 15.39 (338)	9.39 to 16.51 (1072)	8.02 to 16.70 (389)
Lactation length[3]	1	-	-	−1.32 (0.021)	−0.92 (0.05)	−2.97 (0.025)	−2.75 (0.027)	−2.84 (0.017)	−2.61 (0.021)
	2	-	-	0.0 -	0.0 -	−1.28 (0.016)	−1.65 (0.016)	−1.28 (0.012)	−1.61 (0.014)
	3	-	-	1.13 (0.023)	1.39 (0.07)	0.0 -	0.0 -	0.0 -	0.0 -
	4	-	-	2.86 (0.029)	2.81 (0.10)	1.69 (0.020)	1.35 (0.019)	1.73 (0.016)	1.36 (0.017)
Herd production level[3]	1	-	-	−0.16 (0.019)	0.0 -	−0.28 (0.024)	−0.04 (0.019)	−0.13 (0.014)	−0.12 (0.014)
	2	-	-	0.0 -	0.25 (0.027)	−0.13 (0.015)	0.0 -	0.0 -	0.0 -
	3	-	-	0.18 (0.020)	0.66 (0.067)	0.0 -	0.11 (0.017)	0.13 (0.011)	0.14 (0.016)

[1]: solutions of the different levels of the fixed effects are significantly different at 99%; [2]: number of levels for herd–year–season effect is presented between parenthesis; [3]: standard errors of estimates are presented between parenthesis; AgFiKid: age at first kidding in months; Int12Kid: interval between first and second kiddings in months; Int3toKid: interval between second, third, and remaining kiddings in months; IntAllKid: interval between all kiddings in months.

Estimates of the components of variance (additive genetic, permanent environmental, and residual), heritabilities (h^2), and repeatabilities (t) for the evaluated traits are shown in Table 3. The estimates of the additive genetic and residual variances for AgFiKid in Payoya were about four times greater than those observed in Florida, which indicates a wider genetic and environmental variability in this breed. For the kidding interval traits, the variance estimates were quite similar for the Florida and Payoya breeds, with only a slight difference in the additive genetic variance for Int12Kid and the residual variance for Int3toKid and IntAllKid. As expected for reproductive traits, the estimates of heritabilities presented a low magnitude and varied from 0.01 ± 0.004 for Int3toKid to 0.098 ± 0.01 for AgFiKid in the Florida breed and from 0.021 ± 0.004 for IntAllKid to 0.112 ± 0.02 for AgFiKid in Payoya. The estimated h^2 values for AgFiKid were lower than the estimates in other dairy goat breeds (0.31 ± 0.09; [23]; 0.16 ± 0.04 to 0.61 ± 0.14; [21]; 0.16 ± 0.01; [22]; 0.21; [25]). The h^2 estimates for kidding intervals in both breeds were within the range of values reported in other studies (0.015 ± 0.036 and 0.03 ± 0.007; [24]; 0.00 to 0.15 ± 0.06; [7]; 0.02 ± 0.01 to 0.08 ± 0.02; [21]; 0.09 ± 0.02; [22]; 0.06; [25]). Other authors [28] in a meta-analysis of several studies on dairy goats have reported h^2 values of 0.17 ± 0.012 for AgFiKid, 0.002 ± 0.018 for the first kidding interval, and 0.09 ± 0.01 for IntAllKid.

The repeatability for Int3toKid and IntAllKid showed very low estimated values, of the same magnitude as their corresponding heritabilities in both breeds (0.033−0.03 for Int3toKid and 0.023−0.022 for IntAllKid in Florida and Payoya, respectively), and similar to the values obtained by García-Peniche et al. (2012) [21], dos Santos et al. (2015) [25], and the weighted average estimated by Jembere et al. (2017) [28] from six studies. Due to their low heritability and repeatability, kidding interval traits depend mostly on environmental conditions and could be improved by management practices in addition to genetic selection. Moreover, the decision on culling females should be taken based on more than one record.

Table 3. Estimates of genetic parameters of fertility traits in Florida and Payoya breeds[1].

Traits	**AgFiKid**		**Int12Kid**		**Int3toKid**		**IntAllKid**	
Parameters	**Florida**	**Payoya**	**Florida**	**Payoya**	**Florida**	**Payoya**	**Florida**	**Payoya**
σ_a^2	0.463 (0.05)	1.86 (0.3)	0.088 (0.014)	0.025 (0.013)	0.013 (0.005)	0.022 (0.004)	0.024 (0.005)	0.018 (0.004)
σ_{pe}^2	-	-	-	-	0.03 (0.008)	0.0015 (0.002)	0.007 (0.006)	0.0013 (0.002)
σ_e^2	4.249 (0.05)	14.71 (0.32)	0.93 (0.015)	0.81 (0.018)	1.23 (0.01)	0.76 (0.008)	1.29 (0.008)	0.83 (0.007)
h^2	0.098 (0.01)	0.112 (0.02)	0.086 (0.013)	0.03 (0.016)	0.01 (0.004)	0.028 (0.005)	0.018 (0.004)	0.021 (0.004)
t	-	-	-	-	0.033	0.03	0.023	0.022

[1]: standard errors of estimates are presented between parenthesis; AgFiKid: age at first kidding in months; Int12Kid: interval between first and second kiddings in months; Int3toKid: interval between second, third, and remaining kiddings in months; IntAllKid: interval between all kiddings in months; σ_a^2: additive genetic variance; σ_{pe}^2: permanent environmental variance; σ_e^2: residual variance; h^2: heritability; t: repeatability.

The estimates of genetic correlations among fertility traits are shown in Table 4. They were positive in all cases, except the value observed for the r_g between AgFiKid and Int12Kid in Payoya, and covered a wide range of values. The genetic correlations between

AgFiKid and kidding interval traits ranged from 0.07 (AgFiKid-Int12Kid) to 0.19 (AgFiKid-Int3toKid) in Florida and from −0.02 (AgFiKid-Int12Kid) to 0.07 (AgFiKid-Int3toKid) in Payoya. Estimated r_g among kidding intervals oscillated between 0.24 (Int12Kid-Int3toKid) and 0.71 (Int3toKid-IntAllKid) in Florida, and between 0.12 (Int12Kid-Int3toKid) and 0.82 (Int3toKid-IntAllKid) in the Payoya breed.

Table 4. Estimates of genetic correlations among fertility traits in Florida and Payoya breeds^1.

Item	**Int12Kid**		**Int3toKid**		**IntAllKid**	
	Florida	**Payoya**	**Florida**	**Payoya**	**Florida**	**Payoya**
AgFiKid	0.07	−0.02	0.19	0.07	0.11	0.05
Int12Kid	-	-	0.24	0.12	0.58	0.58
Int3toKid	-	-	-	-	0.71	0.82

^{1}: all estimates of genetic correlations are significantly different from 0 at the 0.05 level; AgFiKid: age at first kidding in months; Int12Kid: interval between first and second kiddings in months; Int3toKid: interval between second, third, and remaining kiddings in months; IntAllKid: interval between all kiddings in months.

Correlations between age at first kidding and kidding intervals in other studies were reported to be negative (-0.71 ± 0.27 in Anglo-Nubian goats [29]; -0.43 ± 0.11 in Arsi-Bale goats [30]) or positive (0.64 ± 0.01 in Saanen goats [29]. These values indicate that the magnitude and the sign of direct and indirect responses for selection for these traits will depend heavily on the choice of the selection criteria. The use of AgFiKid as a selection criterion was demonstrated to increase female productive life at 72 months by 2.77 days per generation, while selecting for IntAllKid decreased female productive life at 72 months by 8.28 days per generation [22].

In general, however, there are few estimates available in the literature of the genetic correlations among fertility traits in dairy goats.

Expected genetic responses

The selection indices in this study were computed based on genetic parameters rather than phenotypic performances according to the methodology developed by other authors [15]. This approach has the advantage of using accurate values adjusted for the environmental effects. In addition, it allows a natural connection between the net merit of an animal’s genotype and its relationship to profitability [16]. Many authors working with selection indices (in dairy cattle [31], in beef cattle [13], in meat sheep [32], and dairy goats [11]) have demonstrated that the selection index is extremely accurate for animal selection because it takes into account the genetic relationship between traits and their economic weights.

Table 5. Expected genetic responses for the fertility indices in Florida and Payoya breeds[1].

Indices	**Selection Criteria**	**Selection Objectives**			
		IntAllKid		**IntAllKid, AgFiKid**	
		Florida	**Payoya**	**Florida**	**Payoya**
1	AgFiKid	−0.0001	−0.0000	−0.0447	−0.0277
2	Int12Kid	−0.0035	−0.0029	−0.0150	−0.0061
3	IntAllKid	−0.0106	−0.0088	−0.0431	−0.0279
4	AgFiKid, Int12Kid	−0.0036	−0.0030	−0.0535	−0.0352
5	AgFiKid, IntAllKid	−0.0106	−0.0088	−0.0710	−0.0498
6	All traits	−0.0106	−0.0088	−0.0710	−0.0498

[1]: expected genetic responses for fertility traits are expressed in months per generation; AgFiKid: age at first kidding; Int12Kid: interval between first and second kiddings; IntAllKid: interval between all kiddings.

The expected genetic responses for the different fertility indices in Florida and Payoya breeds are presented in Table 5. The negative responses obtained indicated a lower age at the first kidding, shorter time intervals, and then higher fertility, and the highest values were observed in the Florida breed under all selection indices. This was due to the fact that estimated genetic parameters (h^2 and r_g) of fertility traits were higher in most cases in this breed. In general, the selection indices with combined criteria give greater selection responses than when a single criterion was used, and index 5 and the full index (index 6) presented the highest genetic responses. Moreover, it should be noted that the responses were higher when IntAllKid was included in the selection objective/criteria. In the selection indices with IntAllKid as a selection objective, the maximum expected genetic response was achieved in indices 3, 5, and 6 in Florida (−0.0106 months per generation) and Payoya (−0.0088 months per generation). In the case of a combined selection objective (IntAllKid and AgFiKid), the maximum response was obtained in indices 5 and 6 in Florida (−0.0710 months per generation) and Payoya (−0.0498 months per generation).

The expected responses varied in magnitude depending on the defined selection objectives, the traits included as criteria in the selection indices, and their genetic parameters (heritability and genetic correlations). The best global responses were achieved when both IntAllKid and AgFiKid were combined in the selection objective and when the indices included IntAllKid as a selection criterion. This can be explained by the fact that IntAllKid provides the maximum amount of information on fertility traits, which increases selection accuracy and optimizes genetic response. However, in practice, this trait is expressed later in the female's life, and direct selection for this trait will reduce this gain in accuracy by delaying the generation interval. Poor fertility is one of the most common reasons for culling females (only 52.7% of Florida females have more than six parities, compared with 78.6% in the Payoya breed), even at an early age, especially in the Florida breed, where 24.7% of females are eliminated between the first and second parities (14.8% in Payoya). Using precocious selection criteria, such as AgFiKid and Int12Kid, separately (indices 1 and 2), will generate a very slow genetic response, especially for the Payoya breed. Nevertheless, in both breeds, it could be possible to select females based on these two criteria together under a combined selection goal (AgFiKid and Int12Kid: index 4, Table 5). Moreover, further work is required in this area, especially on exploring new selection criteria that are positively correlated with IntAllKid, and which are expressed early in the animal's life and produce the desired genetic response.

4. Conclusions

Fertility traits are very important for any breeding farm, regardless of the productive objectives. Herd–year–season, lactation length, and herd production level are the key non-genetic factors affecting fertility traits, which suggest that increasing goat fertility can be achieved by improving these factors. As expected for these types of traits, the heritability estimates were of a low magnitude, which implies that direct selection for most fertility traits would lead to slow direct and indirect genetic responses. In the case of the Payoya breed, the heritability estimates were lower than those in the Florida breed, which is most likely due to its more extensive production system. The interval between all kiddings could be the best selection criteria for improving fertility, but this trait is expressed late in female's life. The use of the age at first kidding and the interval between first and second kiddings as selection criteria is recommended as a precocious criterion in both breeds.

Finally, despite the limited heritability estimates obtained for fertility traits in this study, their magnitude is high enough to ensure the genetic improvement of these traits. Modifying fertility aspects in these two breeds could be achieved by selection for one of these traits, but given the low genetic response obtained with current precocious selection criteria (AgFiKid and Int12Kid), further research is needed into other fertility criteria that are expressed early in the animal’s life.

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CAPÍTULO III

Capítulo III: Genetic analysis of reproductive efficiency in Spanish goat breeds using a random regression model as a strategy for improving female fertility

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Abstract

This study aimed to estimate genetic parameters of reproductive efficiency over a wide age range of females using a random regression model (RRM) in Spanish goat breeds. A total of 138,139 and 64,638 reproductive records from the first to the sixth parities from Florida and Payoya, respectively, were included in the analysis. Random regressions on Legendre polynomials of standardised age were included for permanent environmental and additive genetic effects. Estimation of the covariance components was based on the Bayesian inference using the GIBBS3F90 software. Differences among genetic variance components for reproductive efficiency were observed over the animal's lifetime. The estimates of heritabilities were moderate, ranging from 0.21 to 0.32 for Florida and from 0.25 to 0.35 for Payoya, while the fractions of phenotypic variance explained by the permanent environmental effect were high, varying between 0.45–0.68 and 0.58–0.71 for Florida and Payoya, respectively. The correlations for permanent environmental effect over age ranged from 0.37 to 0.99, while the genetic correlations between the different ages varied from 0.36 to 0.98 for Florida and from 0.80 to 0.99 for Payoya. The results from this study support the validity of using an RRM to genetically analyse reproductive efficiency in Spanish dairy goats following the changes in variances and the genetic correlations different from unity over the animal's lifetime. Moreover, reproductive efficiency is a highly heritable trait that is expressed early in a female's life, and it could be used as a precocious selection criterion to improve female fertility in Spanish dairy goats.

Keywords: dairy goat, reproductive efficiency, genetic parameters, random regression model.

Highlights:

- Reproductive efficiency (RE) has been proposed as a trait to improve female fertility in dairy goats.
- RE was genetically analysed using an RRM over a range of ages in females from the Florida and Payoya breeds raised under different production systems.
- Variance components for RE were not constant over age, while the genetic correlations between RE in the different ages were different from unity.
- The use of RRM for RE is therefore justified in both goat breeds.

Introduction:

Female reproductive efficiency is an economically important trait for the dairy goat industry and is considered the most important factor to ensure high productivity for certain environmental conditions (Hossain 2004). Until recently, improving the production of milk, fat, and protein per doe, together with morphology, were the main target breeding traits in genetic improvement programs of Spanish dairy goats (Menendez-Buxadera et al. 2008; Menéndez-Buxadera et al. 2010; Molina et al. 2018). Placing too much emphasis on production traits, while ignoring other traits, may lead to undesirable consequences in the animals' health and fertility, which decreases longevity (Oltenacu and Broom 2010). The classic antagonistic genetic-environmental relationship between milk production traits and female fertility has been reviewed in various studies and species (Andersen-Ranberg et al. 2005 in cattle; David et al. 2008 in sheep; Montaldo et al. 2010 in goat). The importance of including fertility traits in dairy goats breeding programs has therefore increased, as a way of correcting negative effects in this parameter due to the selection of highly productive females.

Fertility in does is a complex trait which can be defined as the doe's ability to resume its ovarian function after kidding, show a detectable estrus, become pregnant, maintain gestation and succeed at kidding; this results in a variety of measures being used in genetic evaluations across the world (Diskin and Morris 2008). To date, despite the economic importance of reproductive traits in dairy goats, there are very few studies to estimate their genetic parameters and none have carried out a longitudinal analysis with a random regression model. The most commonly used traits in the international genetic evaluation of female fertility are (1) age at first kidding (García-Peniche et al. 2012; Castañeda-

Bustos et al. 2014; Ziadi et al. 2021) and (2) different kidding intervals (Bagnicka et al. 2007; García-Peniche et al. 2012; Castañeda-Bustos et al. 2014); Atoui et al. (2018); (Ziadi et al. 2021). Nevertheless, their very low heritability estimates make it difficult to determine which traits must be used as a selection criterion to improve female fertility. A reason for the low heritability of reproductive measures considered as fitness-related traits is natural selection. The fundamental theorem of natural selection states: "The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time" (Fisher 1930). It has been construed that characters with the lowest heritabilities are those most closely connected with fitness, while characters with the highest heritabilities are those that might be judged on biological grounds to be the least important as determinants of natural selection (Falconer 1982).

Genetic parameters of fertility in Spanish dairy goats were estimated only in one study for the age at first kidding and the different intervals between kidding in the Florida and Payoya populations (Ziadi, Muñoz-Mejías, Sánchez, et al. 2021) and, as expected for this kind of traits, the magnitude of estimates was relatively low. However, this study used a repeatability model and did not deal with fertility over a time trajectory.

In Spanish dairy goat, random regression models have primarily been used to analyse milk production traits (Menéndez-Buxadera et al. 2010) and, more recently, prolificacy traits (Ziadi et al. 2021). The basic idea underlying all of these models consists of modelling the additive genetic values (or other random effects in the model) as a function of an observed dependent variable (i.e. time or weight) through a set of random coefficients.

The purpose of this study was to analyse genetically for the first time reproductive efficiency as a new fertility trait in Florida and Payoya goat populations using a random regression model over a range of ages in females. These breeds are prototypes of the Spanish breeds exploited in different production systems varying from semi-extensive to semi-intensive for Florida and from semi-extensive to extensive for Payoya.

Material and methods:

Phenotypic data and pedigree:

The data consisted of reproductive records of Florida and Payoya females and genealogical information provided by the National Association of Florida Goat Breeders and the Association of Payoya Goat Breeders, respectively. The original datasets comprised 143,002 and 72,514 reproductive records, collected between 1986-2019 and 2000-2019, respectively. Animals from the Payoya breed are reared under semi-extensive to extensive production systems, whereas the Florida breed presents a higher level of intensification. The data editing consisted of keeping herd-year contemporary groups with at least 10 records and removing herds with scarce genetic connections. Genetic links between herds were ensured by the use of artificial insemination and the sale of bucks. After data editing, the final datasets consisted of 138,139 records from 50,992 Florida females (average 2.7 records per female) and 64,638 records from 21,715 Payoya females (average 2.97 records per female). Female fertility was defined as the reproductive efficiency (RE), calculated as the deviation between optimal and real parity number of females at each age. Only records of females with up to six parities were considered in this analysis. The pedigree was traced back for as many generations as available in the breed herd book, which was 7.3 equivalent generations for Florida and 4 generations for Payoya. For the Florida pedigree, only animals with approved parentage tests using DNA microsatellites were considered. Finally, the total number of animals in the additive genetic relationship matrix was 55,748 for Florida and 26,392 for Payoya.

Statistical analysis:

The significance of the non-genetic effects for herd, year of parity and month of parity and their inclusion in the model were determined using the 'GLM2' R package. All of them had a significant effect on reproductive efficiency at a 0.05 significance level. Two models with second and third order Legendre Polynomials were tested and compared, and for both breeds, the Deviance Information Criterion (DIC) indicated that both models were equivalent.

We analysed the RE records to fit the following second-order Legendre polynomials random regression model separately for both breeds:

$$y=\text{fixed}+\sum_{k=0}^{p-1}\beta_k X_k+\sum_{k=0}^{p-1}\alpha_{ik} Z_k+\sum_{k=0}^{p-1}\mu_{ik} W_k+e$$

where y is a vector with n observations of RE, fixed is the contemporary group effect of herd-year-season of kidding (1260 and 584 levels for Florida and Payoya, respectively), in which the season of kidding was coded as 1 if a goat gave birth in the period June - September and as 2 if a goat gave birth in the period October - May, β_k are k coefficients of fixed regression of the RE trajectory in females over age with orthogonal Legendre polynomials of second order. Six age ranges were considered as the unit of time *t* (*t* = 1-5 and t ≥ 6) and their effects were considered as a continuous variable expressed in a standardized form between -1 and +1 according to the expression from (Kirkpatrick et al. 1990). The terms α_{ik} and μ_{ik} are sets of random regression coefficients of second-order associated with the animals' additive genetic function and the permanent environmental function, respectively, and e is the residual. X, Z and W are incidence matrices relating observations with the new parameters in β, α and μ, respectively. In this RRM model, the expected (co)variance components are assumed as:

$$\mathrm{var}\begin{bmatrix} G \\ P \\ R \end{bmatrix} = \begin{bmatrix} A \otimes G & 0 & 0 \\ 0 & I_p \otimes P & 0 \\ 0 & 0 & I_n \otimes R \end{bmatrix}$$

in which G is an additive genetic (co)variance matrix among all animals; P and R are respective (co) variance matrices among permanent environments and residuals, A is the relationship matrix between all animals in the pedigree; I_p and I_n are identity matrices of respective order number of animals with own record (p) and number of records (n), and ⊗ is the Kronecker product.

The Bayesian inference approach was applied to estimate variance components and genetic parameters using GIBBS3F90 software of the BLUPF90 family programs (Misztal et al. 2016). Flat priors were used for non-genetic effects and variance components. Chains of 100,000 samples were used, with a burn-in period of 20,000. One sample in 100 was saved to avoid high correlations between consecutive samples. The saved samples were used to obtain the posterior mean and posterior standard deviation of estimates and to check convergence with the Geweke test, using the POSTGIBBSF90 program (Tsuruta and Misztal 2006).

The (co)variance components, heritabilities (h^2), the fraction of phenotypic variance explained by permanent environmental variance (c^2), permanent environmental (r_{pe}), and additive genetic (r_g) correlations throughout the range of ages in females were estimated using the expression proposed by (Jamrozik and Schaeffer 1997).

Results and discussion:

In this work, we analysed reproductive efficiency in females as a fertility trait in the Florida and Payoya dairy goat breeds, estimating its genetic parameters across a range of ages using a RRM.

Phenotypic parameters of reproductive efficiency:

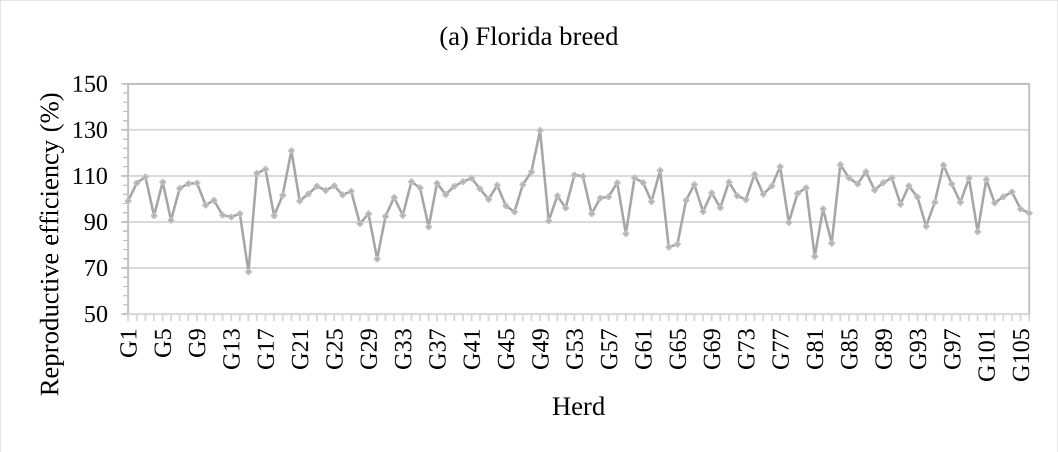
A summary of the basic statistics of reproductive efficiency in the different ages in the Florida and Payoya populations studied is shown in Table 1. A RE value less than 100% indicates that the female has registered a delay in having her real parity compared to the optimal parity of her age. In the first age group, the average RE value was lower in Payoya than in Florida, indicating that most Payoya females start their reproductive life late since they are reared in a more extensive production system. Afterwards, the average RE value increases with age in both breeds, reaching a maximum reproductive efficiency in the fourth and fifth age groups due to the fact that the less fertile females are removed from the herds at each stage. The decrease in RE in the last age group can be explained by the growing number of females with reproductive problems at these final stages. In general, the Florida breed showed a higher RE than the Payoya due to its intensive production system.

Table 1. Basic descriptive statistics for reproductive efficiency in Florida and Payoya breeds.

	Nº of records		Mean±SD		Min		Max	
Age (mo)	Florida	Payoya	Florida	Payoya	Florida	Payoya	Florida	Payoya
24	61,044	21,968	99.49±19.52	92.25±21.36	58.34	58.34	190.93	127.29
36	33,110	17,205	102.73±20.12	95.14±22.91	38.89	50.01	186.70	140.02
48	21,015	11,176	106.03±16.97	100.70±18.14	31.82	58.34	179.53	140.03
60	12,677	7,387	107.57±15.55	103.77±15.35	46.68	56.01	164.75	142.89
72	7,090	4,220	107.89±13.99	103.68±12.09	41.18	60.01	137.74	120.03
84	3,203	2,682	100.63±11.06	100.51±10.13	50.01	64.24	115.10	115.10

SD: standard deviation; Min: minimum; Max: maximum.

The preliminary GLM analysis showed that all the effects included in the model were statistically significant to greater or lesser degrees. The least-squares means for reproductive efficiency for the herd, parity year and parity month effects in both breeds are illustrated in Figures 1, 2 and 3, respectively. Figures 1a and 1b showed a wide variation in the reproductive efficiency of the different herds of these breeds, with the average RE ranging from 68.42 to 129.75% and from 60 to 118.74% in Florida and Payoya, respectively. This illustrated how increased herd fertility can be achieved through environmental improvement. Also, RE registered a decline at the end of the last century and the first decade of this century, followed by a notable improvement over the last few years when it exceeded 100% (Figure 2a). RE has also improved over recent years for the Payoya breed, although its magnitude is still below 100% (Figure 2b). Furthermore, Figure 3 indicates that there is a seasonal pattern marking the RE. The minimum RE values were recorded in the hot seasons, from June to September.


(a) Florida breed

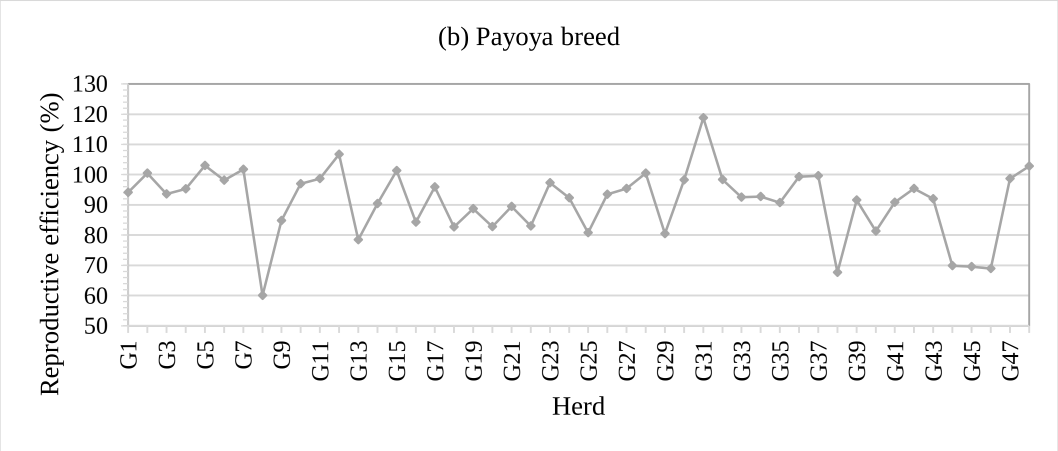

(b) Payoya breed

Figure 1: Least-squares means of herd reproductive efficiency in Florida (a) and Payoya (b) breeds ($p< .0001$).

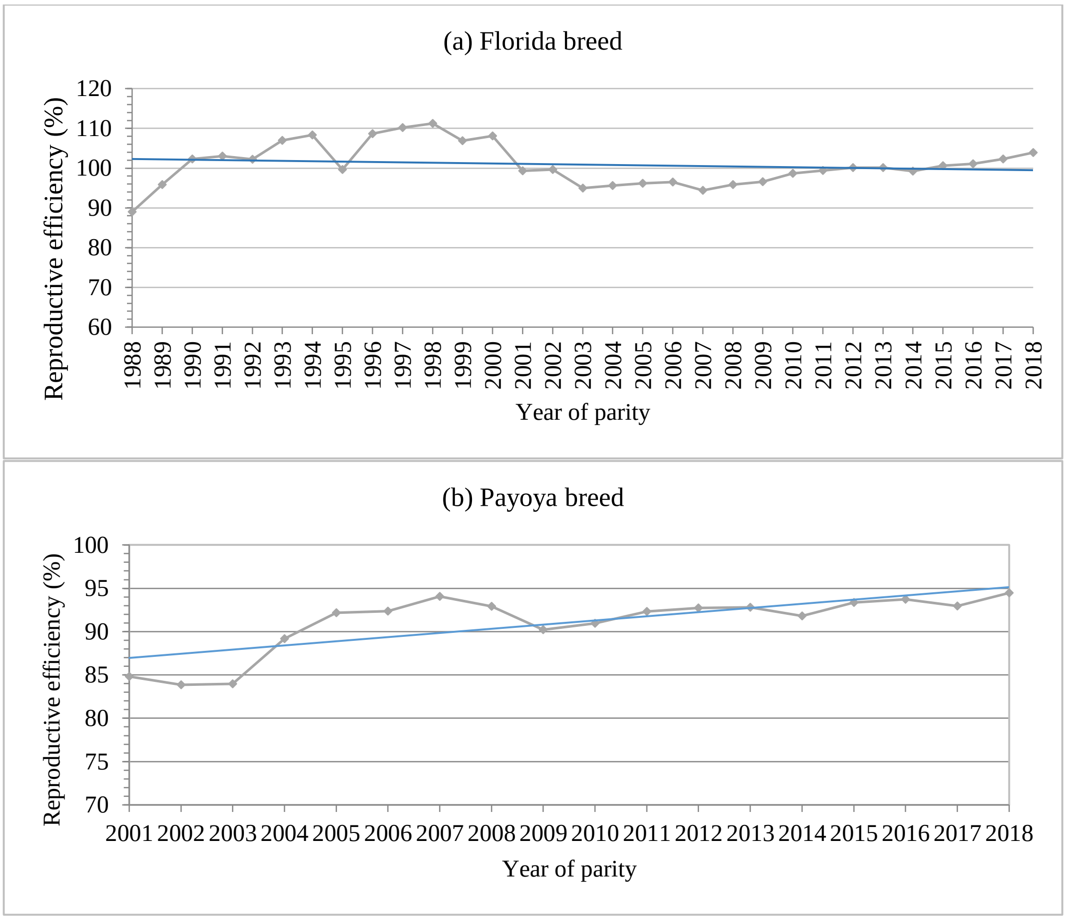


Figure 2: Least-squares means of reproductive efficiency across parity year in Florida (a) and Payoya (b) breeds (p< .0001).

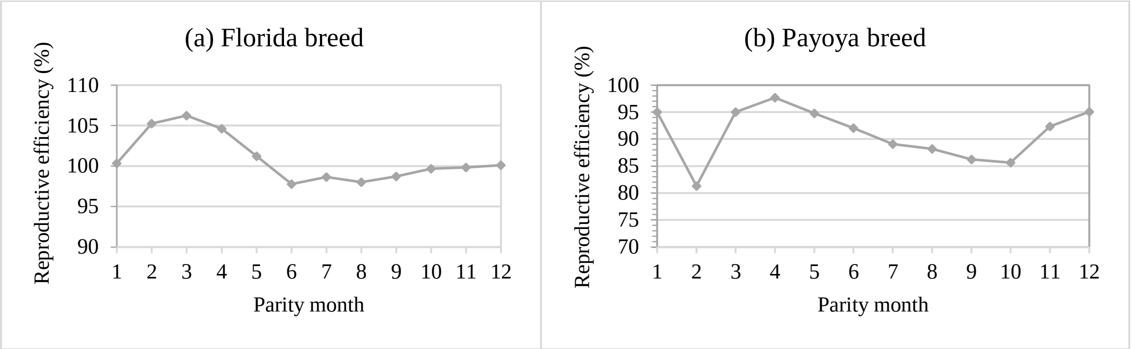


Figure 3: Least-squares means of reproductive efficiency across parity month in Florida (a) and Payoya (b) breeds (p< .0001).

Tables 2 and 3 show a summary of the changes in the posterior distributions of variance components (additive genetic, permanent environmental and residual), heritabilities (h^2) and the fraction of phenotypic variance (c^2) explained by permanent environmental effect variance for RE over the lifetime of females for Florida and Payoya, respectively. The RRM allows us to study the change in (co)variance with age. Estimates of additive genetic and permanent environmental variances tended to increase continuously with age at parity in both breeds and their magnitudes were clearly more important in the case of Florida. The permanent environmental variances were larger than the additive genetic variances for all ages, indicating that the permanent environmental effects had a higher influence on the variation of reproductive efficiency among does of both breeds than the additive genetic effects. Permanent environmental effects contribute permanently to all phenotypes, are constant across repeated measures on the same individual (Kruuk and Hadfield 2007) and are cumulative over time (Schaeffer 2011). This result implies that improvements in reproductive management (especially in the organization of the first service) and health care should lead to a greater increase in fertility in both breeds than by making a genetic selection alone.

Table 2. Estimates of variance components, heritabilities and fraction of phenotypic variance explained by permanent environmental effect for reproductive efficiency across a range of ages in females in Florida breed using a random regression model

Age (mo)	σ_a^2	σ_{pe}^2	σ_e^2	h^2	$HPD_{95\%}$		c^2
24	0.015	0.029	0.021	0.23	0.20	0.24	0.45
36	0.031	0.097	0.021	0.21	0.18	0.23	0.65
48	0.057	0.164	0.021	0.23	0.21	0.26	0.68
60	0.086	0.213	0.021	0.27	0.24	0.29	0.67
72	0.120	0.256	0.021	0.30	0.26	0.34	0.64
84	0.168	0.332	0.021	0.32	0.28	0.37	0.64

σ_a^2: additive genetic variance; σ_{pe}^2: permanent environmental variance; σ_e^2: residual variance; h^2: heritability; $HPD_{95\%}$: high posterior density interval at 95% for h^2 estimates; c^2: fraction of phenotypic variance explained by the permanent environmental effect.

The heritability estimates were moderate for both breeds: for the Florida breed, h^2 decreased slightly from 0.23 in the first age group to 0.21 in the second age group and then increased steadily until the last age group with 0.32, making an overall average of 0.26 (Table 2). In the case of Payoya, the estimates of h^2 showed a decrease from 0.35 in the first age group to 0.25 at the third and fourth intermediate ages, followed by a slight increase until the last age group, making an overall average of 0.28 (Table 3). In all cases, $HPD_{95\%}$ values for heritabilities for RE in both breeds were small. The variance components for additive genetic and permanent environmental were not constant across the range of ages in females, indicating that from a genetic point of view, RE should not be considered as the same trait throughout the life of the animal.

Table 3. Estimates of variance components, heritabilities and fraction of phenotypic variance explained by permanent environmental effect for reproductive efficiency across a range of ages in females in Payoya breed using a random regression model

Age (mo)	σ_a^2	σ_{pe}^2	σ_e^2	h^2	$HPD_{95\%}$		c^2
24	0.057	0.097	0.012	0.35	0.31	0.37	0.58
36	0.061	0.149	0.012	0.28	0.24	0.30	0.67
48	0.070	0.198	0.012	0.25	0.21	0.28	0.71
60	0.082	0.231	0.012	0.25	0.21	0.28	0.71
72	0.096	0.248	0.012	0.27	0.22	0.31	0.70
84	0.113	0.262	0.012	0.29	0.23	0.33	0.68

σ_a^2: additive genetic variance; σ_{pe}^2: permanent environmental variance; σ_e^2: residual variance; h^2: heritability; $HPD_{95\%}$: high posterior density interval at 95% for h^2 estimates; c^2: fraction of phenotypic variance explained by the permanent environmental effect.

The fraction of phenotypic variance (c^2) explained by permanent environmental variance varied from 0.45 to 0.68 in Florida (an average of 0.62) and from 0.58 to 0.71 in Payoya (an average of 0.67). Estimates of c^2 were not constant across the trajectory of age at parity in both breeds, implying that non-additive genetic effects or permanent environmental effects may not affect RE similarly at all ages.

The reasons for the apparent observed discrepancy between the Florida and Payoya breeds may be attributable to the differences in management practices and production systems, with the Florida being raised under more intensive management, in addition to the genetic structure of the populations. For instance, for the process of culling females, 24.7% of Florida females are removed between the first and second parities compared with 14.8% in the Payoya breed, and then 52.7% of Florida females have more than six parities (78.6% in Payoya) (Ziadi, Muñoz-Mejías, Sánchez, et al. 2021).

The posterior means of the additive genetic (r_g) as well as the permanent environmental (r_{pe}) correlations over a range of ages in females in the Florida and Payoya breeds are shown in Tables 4 and 5, respectively.

Table 4. Estimates of genetic[1] (above diagonal) and permanent environmental (below diagonal) correlations for reproductive efficiency across a range of ages in females in Florida breed using a random regression model

	Age (mo)					
Age (mo)	24	36	48	60	72	84
24	-	0.83	0.67	0.56	0.46	0.36
36	0.98	-	0.97	0.90	0.80	0.66
48	0.93	0.99	-	0.98	0.91	0.80
60	0.84	0.93	0.98	-	0.98	0.90
72	0.66	0.79	0.88	0.96	-	0.97
84	0.37	0.54	0.68	0.82	0.94	-

[1]: all genetic correlations were significant at 95%.

Table 5. Estimates of genetic[1] (above diagonal) and permanent environmental (below diagonal) correlations for reproductive efficiency across a range of ages in females in Payoya breed using a random regression model

	Age (mo)					
Age (mo)	24	36	48	60	72	84
24	-	0.98	0.93	0.88	0.84	0.80
36	0.97	-	0.99	0.96	0.93	0.89
48	0.92	0.99	-	0.99	0.97	0.94
60	0.87	0.96	0.99	-	0.99	0.97
72	0.80	0.90	0.95	0.98	-	0.99
84	0.69	0.79	0.85	0.92	0.97	-

[1]: all genetic correlations were significant at 95%.

The estimates of genetic correlations between RE for the different ages were all positive, varying from moderate (0.36 between the first and sixth age groups, Table 4) to high (0.98 between the fourth age group and the third and fifth, Table 4) for Florida. In the Payoya breed, they were high, ranging between 0.80 for the first and sixth age groups and 0.99 for the different r_g of the diagonal, except for the r_g between the first and second age groups (Table 5). In all cases, r_g between any two age groups decreased, with the greater distance between RE in young does and RE in older does being more noticeable in the Florida breed. This result suggests that, if a doe fails to produce a kid, her chance of having a consecutive kidding decreases with an increase in the interval between successive parities. In addition, the permanent environmental correlations were not constant over age groups in both breeds, and varied from 0.37 for the first-sixth age groups to 0.99 for the second-third age groups in Florida, with a similar pattern in the case of Payoya. These differences in r_{pe} between different ages would indicate that environmental effects and or non-additive genetic effects (dominance and epistatic effects) are not constant with age at kidding. (Hohenboken 1985) reported that some environmental effects affecting the repeated measures of the trait in the same animal seem to be semi-permanent rather than permanent. Until now, the estimation of non-additive genetic effects for fertility traits has not been reported in dairy goats.

Random regression models (RRM) are often more appropriate for the genetic analysis of traits of repeated records on the same animal since they describe the changes in the additive genetic effects and permanent environmental effects over the time scale adjusting for covariance between the different points of the trajectory (Meyer 1998).

To our knowledge, in the literature, there are no estimates of genetic parameters for reproductive efficiency, as defined in this study, or for the application of RRM for fertility traits, and this work is the first work to present them.

Comparisons with other studies are difficult because of differences in the definition of fertility, in addition to the notable absence of studies of reproductive parameters related to fertility using a random regression model. The h^2 estimates for RE in both breeds were clearly higher than those for the classical traits used worldwide for the genetic evaluation of female fertility, such as the age at first kidding and the different intervals between kidding. For example, (Jembere et al. 2017) in their meta-analysis of several studies on dairy goat breeds reported h^2 values of 0.17±0.012 for the age at first kidding, 0.002±0.018 for the first kidding interval, and 0.09±0.01 for the interval between all kidding. Similarly, in our previous study on estimating genetic parameters for the classical fertility traits in the Florida and Payoya breeds, we obtained very low h^2 estimates, varying from 0.01 for the interval between second, third, and remaining kiddings in Florida to 0.11 for the age at first kidding in Payoya (Ziadi, Muñoz-Mejías, Sánchez, et al. 2021). Besides, the higher expected genetic responses calculated using selection indices occurred when the interval between all kiddings was combined with the age at first kidding. However, the interval between all kiddings is expressed later in a female's life and direct selection for this trait will widen the generation interval, and then reduce the annual genetic response. Nevertheless, reproductive efficiency is measured from the first kidding and could be applied as a precocious fertility selection criterion. Given its high h^2 and genetic correlations with next parities, a faster genetic improvement of fertility would be achieved in both breeds.

Conclusions:

According to the results obtained from this study, the trait of RE is highly heritable and should be included in the breeding goal to improve dairy goat female fertility in Spanish breeds. However, reproductive efficiency in subsequent ages should not be considered genetically as the same trait, because estimated variances and covariances were not constant in the different ages and the genetic correlations between repeated measures of the trait differed from unity. In genetic evaluations for the fertility trait, RE should therefore be treated as a different trait in females of different ages. In the same way, the use of a random regression model to genetically analyse this trait in different age groups is recommended in both breeds. Moreover, the magnitude of h^2 in early age groups and the genetic correlations between RE in subsequent age groups are high enough to apply a precocious selection for RE to improve dairy goat female fertility, which can be used to overcome the limitations of selection using classical fertility traits.

Ethical approval:

All information used in this study was obtained from existing datasets provided by the National Association of Florida Goat Breeders and the Association of Payoya Goat Breeders. Therefore, no Animal Care and Use Committee approval was necessary.

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CAPÍTULO IV

Capítulo IV: Genetic analysis for productive life in Florida dairy goats using a Cox proportional hazard model

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Abstract

Longevity is an economically important trait since extending the functional life of a doe in order to keep the most productive females as long as possible in the herd can results in an increasing of the profitability of dairy farms. Thus, the objectives of this study were to determine the most important factors that influence the length of productive life (LPL) of Florida goat females and to estimate its genetic parameters using a Cox proportional hazards model. Data consisted of 70,695 productive life records of 25,722 Florida females kidding between 2006 and 2020. A total of 19,495 does had completed their productive life while 6227 (24.2%) does had censored information. The pedigree contained information on 56,901 animals. Average censoring age and average failure age after first kidding for LPL were 36 and 47 months, respectively. The model included as time-independent effects, the age at first kidding and the herd*year*season of birth of the doe, and as time-dependent effects the age at kidding, the herd*year*season of kidding, the within-herd class of milk production deviation, and the interaction lactation number*stage of lactation. All fixed effects had a significant effect on LPL ($P<0.05$). Does with older ages at first kidding and earlier age at kidding were at higher risk of being culled. A large difference among herds was observed in terms of culling risk which highlighted the importance of the management practices. Also, high-producing does were less likely to be culled. The estimate of the additive genetic variance was 0.8961 giving a heritability estimate of 0.40. The results of this study are expected to contribute to the development of a genetic model for genetic evaluation of length of productive life of Spanish dairy goats.

Key words: dairy goat, genetic parameters, productive life, Cox model.

Introduction

Nowadays, the breeding programs for Spanish dairy goats are generally focused on improving milk production and milk composition traits (Menéndez-Buxadera et al. 2010; Molina et al. 2018), as well as morphological and more recently, reproductive traits (Ziadi et al. 2021a,b), or somatic cell score (Jimenez-Granado et al. 2022). However, it has widely been studied the undesirable consequences on the health and fertility of animals, which decreases longevity (Oltenacu and Broom 2010). Longevity is an indirect global trait to quantify productive lifespan of livestock, and for increasing the profitability of dairy farming (Pritchard et al. 2013; Palhière et al. 2018), as it combines many traits related to the permanence of an animal in the herd (Tsuruta et al. 2005). A longer productive life of females such as dairy goats allows an older age structure and consequently greater herd milk production, and it also reduces replacement costs (Serradilla et al. 1997; Castañeda-Bustos et al. 2017).

In dairy ruminants, two different definitions of longevity were proposed by Ducrocq et al. (1988): i) true longevity defined as the ability to avoid all culling reasons, including culling due to milk production; and ii) functional longevity defined as the ability to delay involuntary culling (all culling reasons, except milk production). Genetic parameters for longevity, or similar traits, such as stayability or survivability have been reported in various studies in dairy goats (Castañeda-Bustos et al. 2014, 2017; Geddes et al., 2018; Palhière et al. 2018; Scholtens et al. 2018), but estimations were made using a linear model. Regarding the genetic evaluation of longevity, several approaches have been used, namely linear, threshold, random regression and proportional hazards model (PH). It is generally assumed that the use of linear models in the genetic analysis of longevity traits is inadequate due to a violation of assumptions of normality (Lagakos 1979). In the same way, random regression linear models, which are frequently used to analyse the length of productive life (LPL), cannot be fully considered since censored data and the non-linearity of the factors cannot be treated appropriately (Caraviello et al. 2004). Survival analysis is considered as the relevant statistical approach for the genetic evaluation of cow longevity (Olechnowicz et al. 2016). PH procedures model the hazard function of a goat at time t derived from survival from first kidding to culling, death or censoring. One of the main advantages of PH over other methods of studying longevity is that they more properly accommodate censored records and time-dependent covariates and they handle with the skewed distribution of longevity characteristics (Imbayarwo-Chikosi et al. 2017). The Cox proportional hazards model is a semi-parametric method which has been used to estimate the longevity traits of dairy cows (Zhao, 2013). This model is used to analyse the factors that affect the survival time without a clear benchmark risk rate function, which shows high statistical efficiency (Stokes 2019).

Up to now, no estimations of genetic parameters have been made available for traits related to female longevity in Spanish dairy goats.

Therefore, the current study aimed to identify the possible risk factors and to estimate genetic parameters for the length of productive life in the Florida dairy goat breed, as an example of Spanish breed with high level of intensification, using a survival analysis based on the Cox proportional hazards model.

Material and methods

Data

Milk production records and genealogical information were available from the National Association of Florida Goat Breeders (ACRIFLOR). The Florida breed is raised under semi-extensive to intensive production systems. The description of the breed is available in the study of Rodríguez et al. (2022). Records on Florida females born between 2004 and 2018 with at least a first kidding occurring between 2006 and 2020 were included in the analysis. Female longevity was evaluated using the length of productive life (LPL), estimated as the number of days between first kidding and the last known lactation end date or culling. Contemporary groups that had less than ten records were removed from the analysis. Does younger than 12 or older than 24.6 months at first kidding and does whose kidding interval fell outside the range 5.7-17.1 months were pruned. Also, females with an incomplete (age at the first kidding unknown or some intermediate kidding not controlled) were excluded from the data. After data editing, the final dataset consisted of 70,695 lactation records from 25,722 females belonging to 83 genetically connected herds. Genetic links between herds were ensured by the use of artificial insemination and the sale of bucks. Censorship was considered when does were not successful and were culled from the herd. The does were classified as presenting uncensored (dead) or censored (alive) records. Does sold to other producers were considered uncensored. Right-censored data (24.2%) included animals alive at the time of the analysis. The data did not include left-censored records because only females born in or after 2004 with kidding started after 2006 were included.

The pedigree was traced back for as many generations as available in the breed herd book to include 56,901 animals.

Estimation of genetic parameters

A preliminary analysis by fitting a Weibull hazard survival model to determine the statistical significance of each of the fixed effects was performed using Likelihood ratio tests. All of them had a significant effect on LPL at least a 0.05 significance level. The estimates of these fixed effects were expressed as relative culling risks, determined as the ratio between the risk of culling under a particular class of non-genetic factor and a specific reference class. The effects evaluated were the age at first kidding, herd-year-season of birth of the doe as time-independent effects, and they were assumed to influence the whole female productive life. Time-dependent effects were the age at kidding, herd-year-season of kidding, the within-herd class of milk production deviation, and the combination of lactation number and stage of lactation.

Length of productive life of does was evaluated by survival analysis, using a Cox's proportional hazards model (Cox 1972). A piecewise distribution of the baseline hazard function was assumed to allow an accurate description of the cyclic pattern of the hazard over successive lactations. The Cox model can be described as follows:

$$\lambda(t) = \lambda_0(t)\exp\{\text{agefirst}_i + \text{doe*herdyear*season}_j + \text{herd*year*season}_k + \text{age}_l + \text{levelprod}_m + \text{lactation number*stage of lactation}_n + g_o f\}$$

where $\lambda(t)$ is the hazard function of the doe t days after its first kidding, $\lambda_0(t)$ is the baseline hazard function t days after he most recent kidding, agefirst_i is the time-independent effect of the age at first kidding (monthly intervals from 12 to 15; >15 to 19; >19 to 24); $\text{doe*herd*year*season}_j$ is the time-independent effect of the herd combined with the year and season of birth of the doe (667 classes); $\text{herd*year*season}_k$ is the time-dependent effect of the herd combined with the year and season of kidding (726 classes); age_l is the time-dependent effect of the age at kidding (monthly intervals from 15 to 19; > 19 to 24; > 24 to 36; > 36 to 48; > 48 to 60; > 60 mo); levelprod_m is the time-dependent effect of within-herd class of milk production deviation (4 classes); this effect was calculated as the annual deviation of milk production for each doe with respect to the average production of its herd; lactation number*stage of lactation$_n$ is the time-dependent effect of lactation number (1-6) combined with lactation stage (1-4), resulting in 20 baseline hazard functions. Classes of lactation stage are defined empirically: 210d, 240d, and 300d and, a piecewise baseline hazard function to model survival for each lactation number*stage of lactation group to have a better fit of the data; and g_o is the random animal additive genetic value.

The analysis of length of productive life was carried out with a Cox proportional hazards model using the Survival Kit version 6 software (Mészáros et al. 2013). Given the non-linear nature of the models used in the survival analysis, there is no heritability definition equivalent to that from linear models. The estimate of heritability was calculated following Yazdi et al. (2002):

$$h^2 = \frac{\sigma_a^2}{\frac{1}{P} + \sigma_a^2}$$

where σ_a^2 = additive genetic variance and P = proportion of uncensored records.

The reliability R^2 for each estimated breeding value (EBV) was estimated as:

$$R^2 = \frac{pev}{\sigma_a^2}$$

where pev is the prediction error variance calculated as the square of the standard error for each EBV.

Results and discussion

In the current study, we genetically analysed for the first time the length of productive life in the Florida goat, as a model of a Spanish breed with high level of intensification. Survival analysis was carried out using a Cox proportional hazards model.

Comparisons with other studies are difficult because the scarcity of studies of longevity using a proportional hazards model in dairy goats and of differences in the definition of longevity. Nevertheless, few studies on longevity using a Cox model has been carried out until now in dairy goats (Gautam et al., 2017 in New Zealand breeds; Ferreira et al. 2020 in tropical Saanen breed). However, this authors only evaluated the influence of environment effects, together with morphometric and type traits (Ferreira et al., 2020) or milk solids (Gautam et al., 2017) on females culling, and nor genetic parameters were estimated. Up to now, there have been no studies on the estimation of genetic parameters for productive life in Spanish dairy goats and even less with proportional hazard models, so the current study is the first one to fit this kind of models.

Table 1 showed the distribution of censored and uncensored records for the length of productive life in the Florida breed. The proportion of right-censored records was quite low (24.2%), being smaller than that reported in New Zealand dairy goat (32.85%; Gautam et al., 2017) and greater than the value observed in the Saanen breed (19.52%; Ferreira et al., 2020). LPL ranged from 214 to 4761 days (7 to 156 months). Average censoring age and average failure age after first kidding for LPL were 1096.93 and 1445.55 days (36 and 47 months), respectively. Previous studies with different definitions of longevity in dairy goat estimated an average of 625 d for productive life at 72 months in US breeds (Castañeda-Bustos et al., 2017), 1726 d for length of true life in UK dairy goats (Geddes et al., 2018), 967 d for functional longevity in Saanen and 1007 d in Alpine (Palhière et al., 2018).

Table 1. Descriptive statistics of censoring and failure time (d) in the Florida breed.

Right censored records	6227 (24.21%)
Minimum censoring time	214
Maximum censoring time	4263
Average consoring time	1096.93
Uncensored records	19,495
Minimum failure time	240
Maximum failure time	4761
Average failure time	1445.55

The female longevity is a highly significant trait in Florida due to its high level of intensification in comparison with other Spanish breeds (e.g: Payoya). This breed is known by its high milk production with an average milk yield of 611.4 ± 7.8 kg (ARCA, 2022). Then, extending the doe productive life is crucial for farm profit by producing a large number of lactations. A previous study determined that only 52.7% of Florida females have more than six parities, compared with 78.6% in the Payoya breed (Ziadi et al., 2021a). In this regard, the inclusion of longevity traits in the selection program of this breed is necessary.

Fixed effects and relative risks

Table 2 presented the results of the Likelihood ratio test used to check the importance of the factors that have an effect on a doe´s hazard risk. All covariates in the fixed model significantly contributed to the relative risk of culling at $p < 0.0001$, except for the effect of age at kidding that was significant at $p < 0.02$. The same environment factors were founded to remarkably influence longevity in dairy cattle (M'hamdi et al., 2010 in Tunisian Holstein breed; Imbayarwo-Chikosi et al., 2016 in South African Holsteins; Kern et al., 2016 in Brazilian Holstein).

Table 2. Likelihood ratio last test statement for LPL in the Florida survival analysis.

	CHI^2	Prob > CHI^2	R^2 Maddala
Age at first kidding	19.229	0.0001	0.4623
Herd-year-season of birth of the doe	1792.1	0.0000	0.4240
Age at kidding	14.861	0.0214	0.4624
Herd-year-season of lactation	3506.4	0.0000	0.3843
Within-herd class of milk production deviation	413.64	0.0000	0.4540
Lactation number*stage of lactation	245.17	0.0000	0.4576

LPL: length of productive life.

In dairy goats, studies were carried out to identify risk factors for females' removal (Malher et al., 2001 in Alpine and Saanen; Pérez-Razo et al., 2004 in Mexican breeds; Gautam et al., 2017 in New Zealand breed; Ferreira et al., 2020 in Saanen), but they remain scarce in comparison with the abundant information in dairy cattle.

The estimates of the time-independent and time-dependent fixed effects expressed as relative culling risks were provided in Figures 1 and 2, respectively. Age at first kidding significantly influenced LPL (Figure 1a). Higher hazard ratios for the end of productive life were observed in females which were older at first kidding. Indeed, the highest risk (1.14) was for does whose first kidding age was above 19 months, while the lowest risk (1.00) was for does starting to kid at early ages (> 12–15). Greater culling risk for older ages at first kidding may be related to reproductive problems (Vukasinovic et al. 2001). Consequently, it affects production due to fewer kiddings and lactations (Sewalem et al.

2005). On the contrary, some authors reported that age at first parity in dairy females had no effect on functional longevity (Ducrocq et al. 1988; Vukasinovic et al. 2001). Conversely, Essl (1998) indicated that there is some evidence of antagonism between early maturity and longevity.

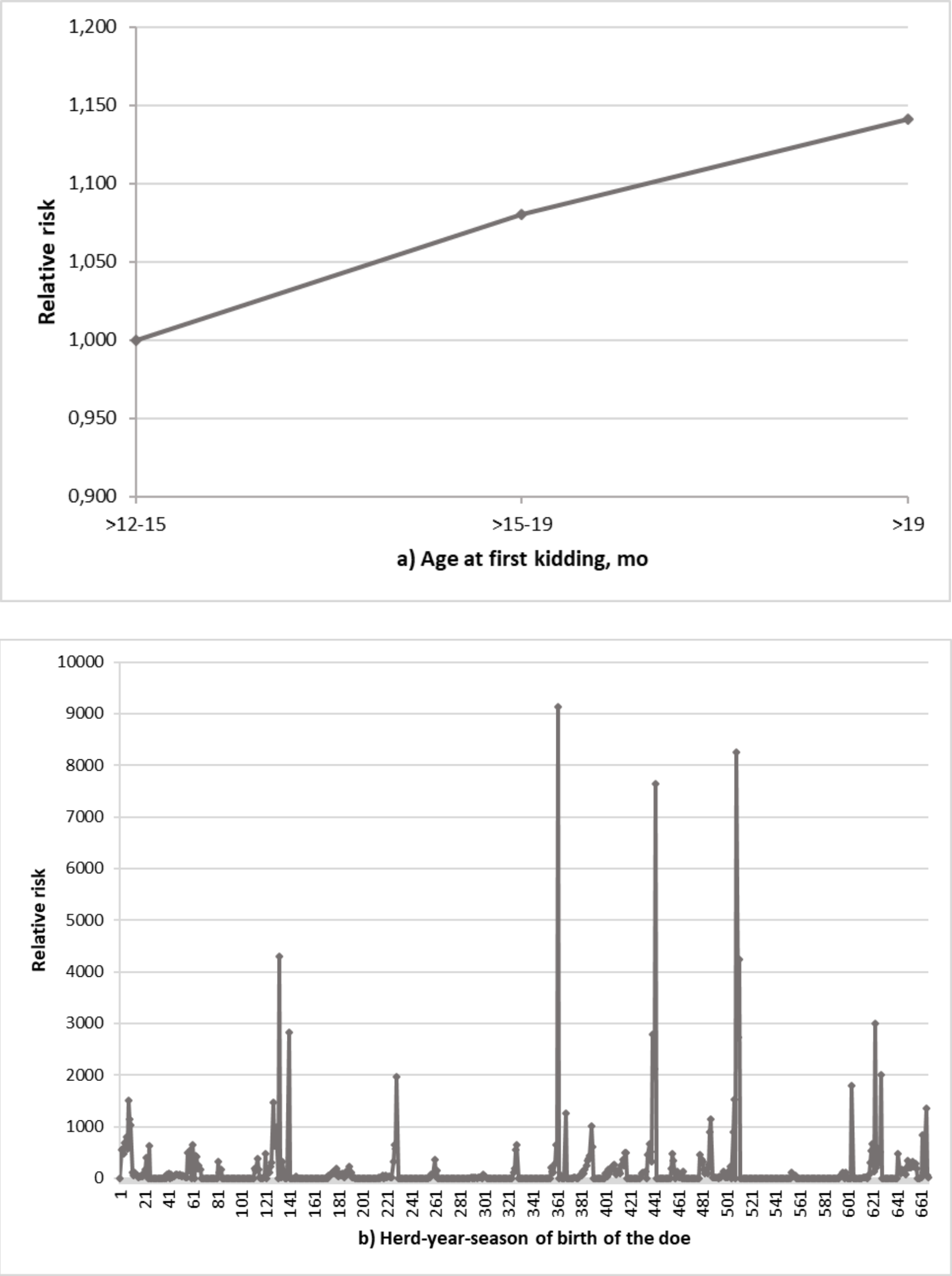

Figure 1. Time-independent effects expressed as hazard ratios for the length of productive life in Florida survival analysis.

It was noticeable that the highest risk (15.88) for age at kidding was for young females (>12-15 months) and then, it decreased suddenly until last ages (Figure 2a). There was also a wide variation in the relative risks from one to another birth of the doe herd*year*season, oscillating from 0.00 to 9139.3 (Figure 1b). In the same way, relative risks based on herd*year*season of kidding covered a wide range of values from 0.00 to 9178.15 (Figure 2d). This large discrepancy among herds could be explained by the differences in management practices, including nutrition, health, reproduction and replacement female strategy.

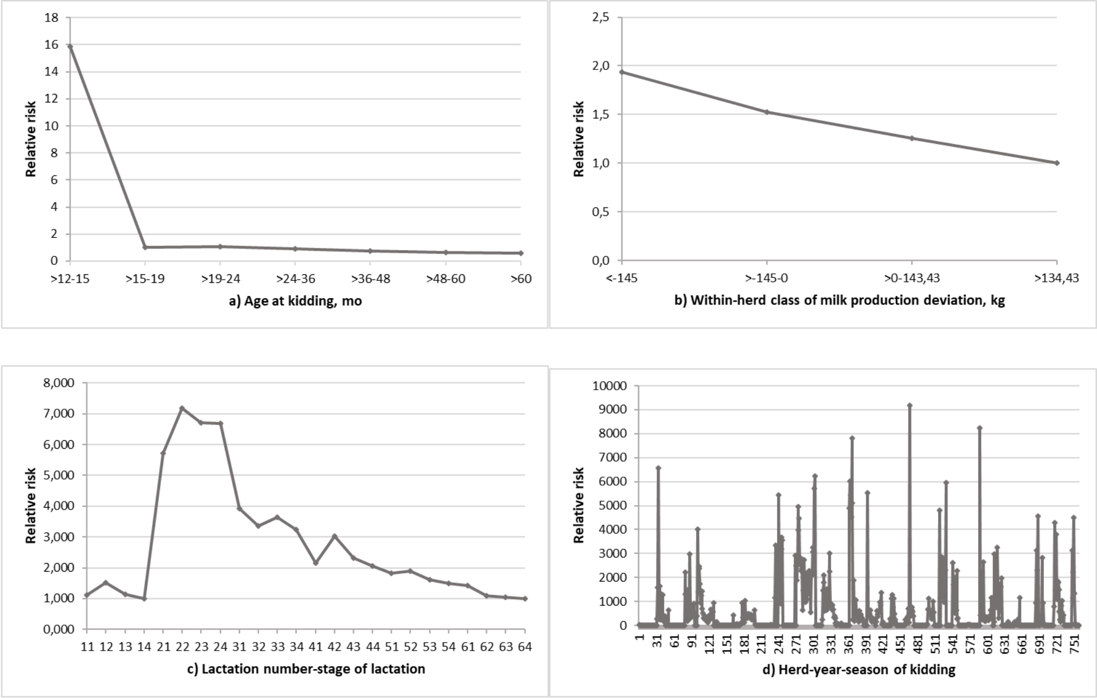

Figure 2. Time-dependent effects expressed as hazard ratios for the length of productive life in Florida survival analysis.

The estimates of the relative risk of the within-herd class of milk production deviation revealed that does that produce low milk yields were at a higher risk of culling (1.94), while high-producing does were at lower risk of being culled (1.00) (Figure 2b).

Milk production has been identified as one of the main factors that affect the productive life of females, because of its relationship to profitability in the dairy industry. Many genetic evaluations for longevity include milk production as a covariate because voluntary culling is based upon phenotypic production (Sewalem et al. 2005; M'hamdi et al. 2010; Kern et al. 2016).

The effect of the lactation number*stage of lactation interaction together with the baseline hazard is shown in Figure 2c. It can be observed that the hazard rate increased sharply from the first to the second lactation, then decreased clearly and stayed low until last lactations. Also, the relative risk of being culled varied throughout the lactation. In general, the greatest risk was in the beginning and the middle of the lactation except for females of second lactation and at their first stage of lactation (<210d).

According to Terawaki et al. (2006), culling during the early stage of the lactation corresponds to extreme cases, such as very low milk production or severe functional problems. On the contrary, the risk of culling is more intense at the end of the lactation, when production is lower, when it is known whether the female is pregnant or not and when her body condition score is better (Ducrocq 1999). Hence, the choice of a piecewise model within lactation number and stage of lactation accounts for these changes in risk of culling during productive life and ensure a better fit compared to the use of a single baseline hazard function (Ducrocq 2005; Terawaki et al. 2006).

Heritability, EBVs and reliability

The estimates of parameters from Cox survival analysis for LPL and the derived parameters (heritability, EBV averages, reliability, and relative risk averages) were presented in Table 3. The marginal posterior mean estimate of the additive genetic variance in this study was 0.896 giving a heritability estimate of 0.40. This indicated a large variability for longevity of goat does, and thereby it may be possible to improve the length of productive life in the Florida population by direct genetic selection for this trait. In a preliminary analysis in this same breed with a Cox model, not including the effects related to milk production, we obtained a h^2 of 0.17 (Ziadi et al., 2022). This finding highlighted the importance of milk production level in the productive life of dairy females, and ignoring this effect in the survival model leads to an underestimation of heritability of this trait.

Previous studies conducted in dairy goats estimated lower heritability for longevity (0.19 in US breeds; Castañeda-Bustos et al. 2017; 0.14 in UK breeds; Geddes et al., 2018; 0.07 and 0.08 in Saanen and Alpine breeds, respectively; Palhière et al. 2018). However, all these estimates have been obtained with linear models and the definition of the longevity trait was different from that of the present study, in addition to the proper genetic structure of the breeds. Indeed, it has been studied that linear, threshold, and random regression models generally produce lower estimation of longevity heritability than survival analysis models on the original scale (Ducrocq 1997; Kern et al. 2014).

Table 3. Estimates of parameters from Cox analysis for LPL in the Florida breed.

Proportion uncensored/total	0.758
Estimated additive variance	0.896
Heritability	0.40
Reliability average	0.137
Reliability average uncensored does	0.368
Reliability average censored does	0.137
EBV average	-0.546
EBV average uncensored does	0.435
EBV average censored does	-0.546
Risk average	0.667
Risk average uncensored does	1.589
Risk average censored does	0.667

LPL: length of productive life.

The reliability of genetic evaluation by survival analysis depends on the proportion of censored and uncensored records available, being increased as the ratio of censored records decreased. In our study, 24,21% of the data employed was censored, being much lower than the maximum limit established by Vukasinovic et al. (1997), who recommended not much more than 40% of censored records to obtain accurate results.

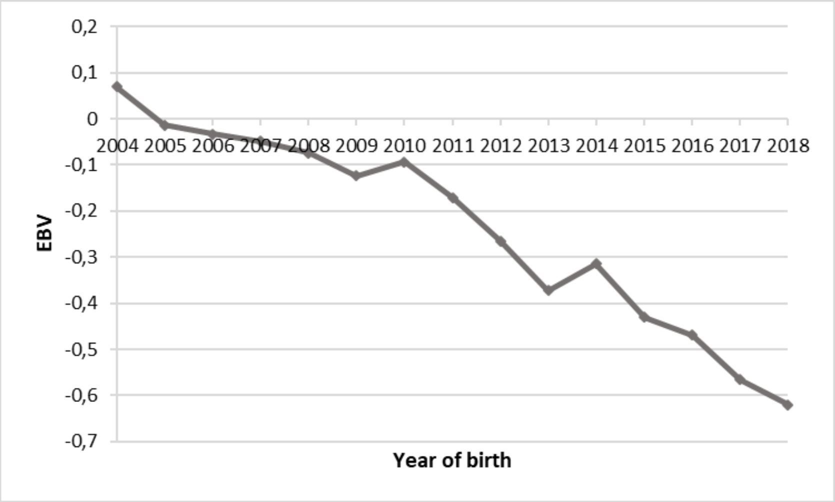

Figure 3. Average standardized female EBVs trend over time for the length of productive life in Florida survival analysis.

Finally, the standardized average female EBVs trend over time is shown in Figure 3. The standardization of genetic values was carried out using the average genetic value of the year 1980 (year of birth of the older animals) and dividing by the standard deviation of the global EBVs. A negative genetic trend in LPL was found over time and EBV decreased continuously until last years. The decline in EBVs was quite modest: about -0.69 genetic standard deviation in 18 years (0.05 genetic standard deviation per year). That means that young does had a lower probability of staying longer in the herd and, as a consequence, a lower probability of getting an increased number of kiddings and lactations. This negative genetic trend could have been due to the decline on functional traits (e.g. fertility and udder health traits) resulting from intense selection on milk production (Imbayarwo-Chikosi et al., 2016). Indeed, in this breed, a 24% of females are eliminated between the first and second parities (Ziadi et al., 2021a) and an increased incidence of somatic cell count was observed (Jiménez-Granado et al., 2022). Similarly, Kern et al. (2016) observed an unfavorable genetic trend in Brazilian Holstein cattle.

Results from this study suggested that the length of productive life is an adequate selection criterion for extending female lifespan in the Florida breed. This work should be expanded to other Spanish dairy goat breeds with different production system like Payoya breed.

Conclusions

This study was the first attempt to genetically analyse the length of productive life in a Spanish dairy goat breed, and the first one goat analysis with a proportional hazard model. According to our results, the age at first kidding, herd-year-season of birth of the doe, age at kidding, herd-year-season of kidding, the within-herd class of milk production deviation and the lactation number*stage of lactation interaction were important factors affecting longevity in the Florida goat breed. Does with older ages at first kidding and earlier age at kidding presented the highest culling risk. Since differences among herds were very large, it is very important to take care of management practices. In our study, high-producing does were less likely to be culled. The high heritability suggested that genetic variation existed for LPL to allow for genetic improvement through direct selection for this trait.

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DISCUSIÓN GENERAL

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Los programas de mejora actuales de las razas caprinas lecheras españolas vienen basando sus objetivos en aumentar la producción de leche y sus componentes, además de la mejora de los caracteres morfológicos, principalmente relacionados con la ubre. Sin embargo, la alta producción lechera es muy costosa para la fisiología y el metabolismo de los animales, manteniéndolos al límite la disponibilidad de recursos para la reproducción o la respuesta inmune frente a infecciones como la mastitis. Por tanto, hay una correlación negativa clara entre altas producciones lechera y la funcionalidad, que está ligada a la longevidad. Para minimizar esta correlación negativa hay que trabajar en incluir las valoraciones de estos criterios (reproductivos, longevidad, resistencia a enfermedades, etc) en los programas de selección, junto con el mejoramiento del ambiente a través del manejo (reproducción, sanidad, nutrición, etc).

Con el objetivo de actualizar los programas de cría de las razas españolas, incorporando nuevos criterios de selección para los caracteres reproductivos, se ha llevado a cabo esta tesis Doctoral. En la misma se ha utilizado como modelo productivo a las razas Florida y Payoya que representan sistemas de producción diferentes, siendo la Florida con un alto grado de intensificación y la Payoya con un sistema de producción semi-extensivo a extensivo.

Dentro de los posibles caracteres del ámbito de la reproducción en la especie caprina, encontramos la fertilidad, que, junto a la prolificidad, determinará el número de crías nacidas, la supervivencia de estas, y la duración de la vida productiva de la reproductora (longevidad). Así, el número total de crías paridas por hembra al año es de gran importancia para la rentabilidad de los rebaños en pequeños rumiantes tanto para la venta de animales como reposición de reproductores. En razas catalogadas en peligro de extinción como la raza caprina Payoya, esta característica es de especial importancia para mantener el tamaño efectivo de su población.

El primer capítulo de esta tesis se ha centrado en la investigación de la base genética de la prolificidad a lo largo de los partos de las reproductoras usando la metodología de Regresión Aleatoria con vistas a la mejora genética de este carácter en las razas caprinas lecheras españolas. La prolificidad de la hembra se difinió con dos criterios: tamaño de camada (LS) y número de nacidos vivos (NBA). Cabe destacar que la prolificidad es una variable discreta y presenta una distribución categórica. Por ello, se ajustó un modelo umbral asumiendo la existencia de una variable subyacente normal y unos umbrales que determinan las distintas categorías de tamaño de camada y número de nacidos vivos.

Según nuestros resultados, la máxima expresión del carácter se alcanzó en el cuarto parto en la raza Florida y en el sexto en el caso de la Payoya y en ambas razas, mostró una alta persistencia hasta los últimos partos de la hembra (capítulo 1, figuras 1 y 2).

El análisis de la evolución de los componentes de la varianza permitió detectar una tendencia claramente inconstante en los diferentes partos. Las estimaciones de h^2 para LS oscilaron entre cero a 0,22 y 0,01 a 0,37 y la h^2 para NBA variaron entre 0,02-0,19 y 0,03-0,20 en Florida y en Payoya, respectivamente (capítulo 1, tablas 2 y 3). De la misma manera, las r_g intra-carácter para los diferentes partos presentaron un mayor rango y magnitud de valores diferentes a la unidad, de -0,98 a 0,99 para LS y de -0,72 a 0,99 para NBA (capítulo 1, tablas 4 a 7). Este resultado indica que desde el punto de vista genético, tanto LS como NBA no representan exactamente el mismo caracter y por tanto hay que asumir que no están controlados por los mismos genes en los sucesivos partos de la hembra (no es homogenea la expresión génica a lo largo de los partos de la reproductora).

En estudios realizados en otras razas caprinas, se han reportado unos valores bajos para h^2 de LS (0,043; Kasap et al. 2013; 0,08; Atoui et al. 2018; 0,002; Abdoli et al. 2019; 0,08; Bangar et al. 2022), pero estas estimaciones se han obtenido con modelo de repetibilidad. Sin embargo, el NBA no ha sido estudiado y no existen hasta la fecha estimas de sus parámetros genéticos diferentes a los presentados en esta Tesis.

Las correlaciones genéticas entre LS y NBA fueron positivas en los dos primeros partos y negativas en los últimos, en ambas razas. El valor más alto de r_g se observó en el primer parto (0,81) en el caso de la florida y en el primero y segundo (0,93 y 0,66, respectivamente) en el caso de la Payoya (capítulo 1, tabla 8). Eso indica que se puede lograr una respuesta genética temprana si se aplica una selección en los dos primeros partos en Payoya y el primer parto en Florida.

Por otra parte, los resultados obtenidos en este trabajo sustentan el empleo de modelos RRM para la evaluación genética de la prolificidad en las razas Florida y Payoya. Los modelos de regresión aleatoria (RRM) permiten estimar los parámetros genéticos y los valores genéticos aditivos de los animales en cualquier punto de la trayectoria de vida del animal. En conjunto, los resultados obtenidos con el modelo de regresión aleatoria aportan matizaciones a la posible utilización de modelos alternativos al clásico de repetibilidad para el análisis genético de la prolificidad. Además, contemplan que a lo largo de la vida reproductiva puedan estar involucrados en el control de la prolificidad genes o combinaciones de genes parcialmente distintos (o expresarse de forma diferencial) (Roehe and Kennedy 1995; Noguera et al. 2002). Aunque se ha propuesto su empleo en la evaluación del tamaño de camada (Schaeffer 2004), son pocos los trabajos con este enfoque publicados hasta la fecha y limitados al porcino (Lukovic et al. 2004; Fernández et al. 2008).

Existen otros aspectos asociados a la productividad que, por su importancia, deben ser analizados y considerados para su posible introducción en el esquema de selección de las razas caprinas lecheras. Entre ellos, la fertilidad ya que es bien sabido la existencia de un antagonismo genético y ambiental entre fertilidad de la reproductora y producción lechera (Montaldo et al. 2010). Eso implica que la selección por alto nivel productivo viene asociada a una baja fertilidad y, por lo tanto, el desecho del rebaño y la reducción de la vida productiva de las hembras poco fértiles, que en muchos casos cuando aún podrían mantener niveles productivos elevados. Por eso, se ha incluido la fertilidad en los objetivos de selección (VanRaden et al. 2004) en vacuno lechero y se ha mostrado que seleccionar por rasgos de fertilidad como la edad al primer parto o el intervalo entre partos aumenta la vida productiva de las hembras reproductoras (Castañeda-Bustos et al. 2014 en caprino lechero).

En el caso de las razas caprinas lecheras españolas, por ejemplo, en la Florida que presenta un mayor nivel de intensificación, el 24,7% (14,8% en Payoya) de las hembras se eliminan entre el primer y segundo parto y sólo el 52,7% (78,6% en Payoya) llegan a tener más de seis partos por causa de la baja fertilidad.

En el segundo capítulo de esta tesis se han estimado los parámetros genéticos y los valores genéticos de los animales de cuatro caracteres, clasicamente asociados a la fertilidad de la hembra: a) AgFiKid: edad al primer parto, b) Int12Kid: intervalo entre primer y segundo parto, c) Int3toKid: intervalo entre segundo y tercer parto y el resto, d) IntAllKid: intervalo entre todos los partos.

Los rasgos de fertilidad estudiados se vieron afectados por rebaño-año-época de parto, nivel productivo del rebaño y duración de la lactación (capítulo 2, tabla 2). Eso implica que la mejora de la fertilidad de la hembra depende en mayor parte en la mejora de las condiciones ambientales.

Nuestros resultados de estimación de parámetros genéticos de las cuatro variables de fertilidad han dado unos valores bajos de h^2 entre 0,01 para Int3toKid en Florida y 0,11 para AgFiKid en Payoya, que limitarán conseguir una respuesta a la selección rápida (capítulo 2, tabla 3). La h^2 para AgFikid es más baja que las encontradas por Castañeda-Bustos et al. (2014) y dos Santos et al. (2015) (0,16 y 0,21, respectivamente), pero más elevada que el valor 0,06 estimado por Bangar et al. (2022). En cuanto a la h^2 para los diferentes intervalos, nuestras estimas están dentro del rango encontrado en otros estudios en caprino (Bagnicka et al. 2007; Montaldo et al. 2010).

Las correlaciones genéticas entre las cuatro variables cubrieron un amplio rango de valores de 0,07 (AgFiKid-Int12Kid) a 0,71 (Int3toKid-IntAllKid) en Florida y de 0,02 (AgFiKid-Int12Kid) a 0,82 (Int3toKid-IntAllKid) en Payoya (capítulo 2, tabla 4). Eso implica que las respuestas directa y indirecta a la selección van a depender y sus magnitudes variarán en función de que si eligimos un criterio u otro por separado o mediante un índice de selección.

Basado en una nueva teoría de los índices de selección (usando parámetros y valores genéticos en vez de fenotipos), se propusieron y se evaluaron distintos índices de selección para determinar el más adecuado para producir las respuestas de selección deseadas. Estos índices de selección evaluados, en general, los que incluyen el IntAllKid dan mayores respuestas a la selección que cuando se utiliza un sólo criterio. Sin embargo, la principal limitante del uso de IntAllKid como criterio de selección es que este carácter se expresa tardíamente en la vida de la reproductora, lo cual produce un mayor intervalo intergeneracional y un menor progreso genético. En la Florida, por ejemplo, donde se aplica una importante intensidad de selección entre los dos primeros partos, la aplicación de este criterio no es aconsejable. No obstante, el uso de la edad al primer parto y el intervalo entre primer y segundo parto se podría recomendar en ambas razas como caracteres de selección precoces, pero no es de esperar una respuesta rápida a la selección debido a su baja heredabilidad.

Dado que la heredabilidad de estos criterios clásicos de fertilidad ha sido baja (en consonancia también con otros múltiples trabajos en otras especies y razas caprinas), nos propusimos la utilización de otros criterios indirectos para evaluar la fertilidad de las reproductoras que previamente no habían sido puestos a punto en la especie caprina. La escasez de datos de cubriciones dirigidas o de inseminaciones artificiales ha hecho complicado el estudio de otros parámetros de fertilidad como los días abiertos. Por ello nos planteamos en el tercer capítulo de esta Tesis, la propuesta de un nuevo criterio de selección para la fertilidad y su análisis genético en función de la edad de la hembra, utilizando también modelos de Regresión Aleatoria.

Así, en este capítulo se abordó por primera vez en caprino un nuevo parámetro de fertilidad definido como eficacia reproductiva y calculado como desviación parto óptimo-real a cada edad de la hembra (expresado en escala continua). Los componentes de la varianza y los parámetros genéticos se estimaron en función de la edad de la reproductora utilizando un modelo de Regresión Aleatoria.

En las dos razas, los componentes de la varianza (genética aditiva y del ambiente permanente) no fueron constantes y aumentaron de forma continua conforme mayor era la edad de la hembra, siendo su magnitud más alta en el caso de la Florida (capítulo 3, tablas 2 y 3). Las varianzas ambientales permanentes fueron mayores que las genéticas aditivas para todas las edades, lo cual indica que la mejora en el manejo reproductivo (especialmente en la organización de la primera cubrición) y la atención sanitaria deben llevar a un mayor aumento de la fertilidad en ambas razas que cuando se aplica sólo una selección genética.

La evolución de la h^2 mostró resultados moderados (0,21 a 0,32 en Florida y 0,25 a 0,35 en Payoya; capítulo 3, tablas 2 y 3, respectivamente), lo que asegura un importante progreso genético si se comienza a utilizar como criterio de selección en estas razas, siendo además un parámetro fácilmente comprensible por el ganadero. Estas heredabilidades son claramente más elevadas que las de los criterios clásicos de fertilidad (capítulo 2 de esta tesis). Las altas h^2 observadas en las últimas edades pueden ser debidas a la eliminación de reproductoras menos fértiles en edades tempranas.

Las estimaciones de las r_g entre RE para las diferentes edades fueron todas positivas, variando entre 0,36 y 0,98 en Florida y entre 0,80 y 0,99 en Payoya (capítulo 3, tablas 4 y 5, respectivamente). Estos valores inferiores a la unidad, sugieren de manera clara que se trata también de un rasgo que debe ser analizado como carácter diferente a lo largo de la vida de la reproductora.

En base a nuestros resultados, la propuesta de la eficacia reproductiva como nuevo criterio de selección de la fertilidad se considera factible y muy recomendable en ambas razas, ya que ese criterio es mucho más heredable que los criterios clásicos y, por lo tanto, su utilización permitiría acelerar la respuesta a la selección. Además, este parámetro tiene la ventaja de tener en cuenta la edad óptima al primer parto y el intervalo óptimo entre partos, lo que permitiría seleccionar hembras precoces y con intervalos entre partos cortos. Por este hecho, el presente trabajo ha concluido que la eficacia reproductiva debería ser la variable a utilizar en las valoraciones genéticas de la fertilidad en las razas Florida y Payoya.

Es importante señalar que en los estudios detallados anteriormente (capítulos 1, 2 y 3), se observaron diferencias entre las dos razas. Éstas pueden ser atribuibles a las diferencias en los sistemas de producción (más intensivo en el caso de la Florida que la Payoya), además de a la estructura genética propia de estas dos poblaciones.

Por último, se empleó la metodología de análisis de supervivencia con el objetivo de analizar genéticamente la longevidad de las reproductoras y estudiar la posible introducción de este parámetro en los programas de mejora de ambas razas. Se analizó la longitud de la vida productiva (LPL: tiempo desde el primer parto hasta la última fecha conocida de secado o de desecho) usando un modelo Cox de riesgos proporcionales implementado en el software Survival Kit (Mészáros et al. 2013).

En primer lugar, se realizó un análisis preliminar con un modelo Weibull con el fin de identificar los factores permanentes (independientes del tiempo) y tiempo-dependientes de eliminación de las reproductoras y los resultados correspondientes están presentados en las figuras 1 y 2 (capítulo 4), respectivamente. Dentro del primer grupo, se encontró la edad al primer parto donde el riesgo a ser desechada del rebaño es más bajo entre las cabras que paren por primera vez entre los 12 y 15 meses de edad y más alto en aquellas cabras que empiezan tarde su vida reproductiva (a partir de los 19 meses de edad al primer parto). Probablemente, este retraso estaría ligado a una menor eficacia reproductiva. Además, la longitud de la vida reproductiva está influenciada por el efecto rebaño-año-época de nacimiento de la cabra con una amplia variación en los riesgos relativos de los distintos niveles de este efecto. Este resultado estaría relacionado con las condiciones de manejo reproductivo, nivel de intensificación y sanidad de cada explotación (y su evolución en el tiempo).

Dentro del grupo de las variables dependientes del tiempo, se encuentran la mayor parte de los factores que fueron significativos. Entre éstos, se encuentra la variable rebaño-año-época de parto, que afecta de manera clara a la longevidad, debido a que nuestros datos corresponden a rebaños con diferentes sistemas de gestión. También se observaron diferencias en la edad al parto, manifestando las hembras más jóvenes (de 12 a 15 meses) el riesgo más alto de ser eliminadas en comparación con las últimas edades (capítulo 4, figura 2a). Este resultado podría estar en consonancia con el relativamente elevado número de reproductoras que se eliminan del rebaño precozmente. Una vez se ha superado ese primer descarte, la probabilidad de ser eliminada desciende claramente.

Además, la interacción número de lactación-estado de lactación tiene una incidencia clara e importante en la longevidad (figura 2c, capítulo 4). Esto podría ser explicado por el hecho de que, durante la primera fase de la lactación, se eliminan hembras debido a casos extremos, como la muy baja producción de leche o problemas funcionales severos. Además, las hembras más viejas y con baja producción lechera corren más riesgo de ser eliminadas del rebaño que las hembras jóvenes y altamente productivas. Estos hallazgos concuerdan con estudios previos realizados en vacuno de leche (Kern et al. 2016; Imbayarwo-Chikosi et al. 2017).

Por otra parte, cabe destacar que la baja producción en razas lecheras constituye la principal causa de eliminación voluntaria de las productoras. En efecto, en el presente estudio, se reveló la significación del nivel productivo (desviación anual de la producción de leche de cada hembra con respecto a la producción media de su rebaño) como factor muy importante de riesgo de desecho (capítulo 4, figura 2b). De hecho, en un análisis previo en el que no se incluyó dicho efecto, la heredabilidad sufrió una disminución muy significativa, pasando de 0,40 (capítulo 4, tabla 3), a 0,17 (Ziadi et al. 2022).

Esta heredabilidad estimada para la longitud de la vida productiva es de una magnitud muy alta, lo que permitiría obtener un progreso genético rápido si se empieza a seleccionar por LPL para mejorar la longevidad en esta raza. Esta h^2 es más elevada que las encontradas en otros estudios en caprino de leche llevados a cabo con modelos de repetibilidad y con diferentes definiciones de la longevidad (Castañeda-Bustos et al. 2017; Geddes et al. 2018; Palhière et al. 2018).

Al analizar la tendencia genética de esta variable a lo largo de los últimos 14 años para las hembras, se encontró una tendencia negativa (un descenso de LPL, capítulo 4, figura 3). Esto coincide con la percepción del criador, el número de hembras que llegan a tener 6 partos y estaría relacionado con la creciente intensificación del sistema productivo, la disminución de rasgos funcionales como la fertilidad o el incremento de problemas de salud de la ubre como resultado de la fuerte selección por la producción lechera.

Con el presente trabajo se puede concluir que la LPL debería ser incorporado al programa de cría de esta raza. Actualmente, dentro de este programa se incluye la calificación morfológica lineal (aunque aún a una proporción de la población baja) con el objetivo de mejorar la morfología de la ubre e indirectamente, con la mejora de otros rasgos lineales, la longevidad de las reproductoras. La incorporación de los valores genéticos para la LPL aceleraría la mejora de la longevidad en esta población.

CONCLUSIONES

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Durante el desarrollo de la presente tesis doctoral se ha podido llegar a las siguientes conclusiones:

Capítulo I

1. El análisis de la prolificidad mediante metodología de regresión aleatoria reveló diferentes patrones de evolución de los parámetros genéticos a lo largo de la vida productiva de las reproductoras (varianzas y covarianzas no constantes en los diferentes partos), con correlaciones genéticas entre medidas repetidas del carácter diferentes de la unidad, por lo que concluimos que, desde el punto de vista genético, la prolificidad no debe ser considerado el mismo carácter en los sucesivos partos de la hembra en las valoraciones genéticas.
2. A pesar de que las heredabilidades fueron bajas, es de esperar una buena respuesta a la selecciónca temprana si se aplica una selección por prolificidad en los dos primeros partos en Payoya y el primer parto en Florida.

Capítulo II

3. Como era de esperar para los caracteres clásicos de fertilidad, las heredabilidades obtenidas fueron de muy baja magnitud, determinando que la respuesta a la selección esperada sea baja.
4. La selección por la edad al primer parto y el intervalo entre primer y segundo parto se podría recomendar en ambas razas como caracteres de selección precoces, pero no es de esperar una respuesta rápida a la selección debido a su baja heredabilidad.
5. Los índices de selección evaluados indicaron que, en general, los que incluyen el intervalo global entre partos dan mayores respuestas a la selección, pero al expresarse tardíamente en la vida de la reproductora, también produce un limitado progreso genético.

Capítulo III

6. El estudio de la eficacia reproductiva identificó una importante variabilidad genética y dada la alta magnitud de su heredabilidad, se esperará un progreso

genético rápido si se hace la selección por este caracter para la mejora de la fertilidad en las razas Florida y Payoya.

7. La ER debe tratarse como carácter diferente a lo largo de la vida de la reproductora, debido al hecho de que las estimaciones de los componentes de la varianza no fueron constantes a lo largo de la trayectoria de la edad y las correlaciones genéticas fueron diferentes de la unidad.

Capítulo IV

8. El análisis de la longitud de la vida productiva de la reproductora demostró un efecto significativo de diferentes factores relacionados con el manejo reproductivo de la explotación, pero también con el nivel productivo de la hembra, presentando una heredabilidad suficientemente alta para recomendar su incorporación al programa de cría para la mejora de la longevidad de las reproductoras.

Conclusión Global

9. Finalmente, en base a los resultados obtenidos en la presente tesis, se puede recomendar la incorporación al programa de cría de la eficacia reproductiva para la mejora de la fertilidad, el número de nacidos para la mejora de la productividad numérica, y la longitud de la vida productiva para el incremento de la longevidad funcional en las razas caprinas Florida y Payoya.

CONCLUSIONS

During the development of this doctoral thesis it has been possible to reach the following conclusions:

Chapter I

1. The analysis of prolificacy using random regression methodology revealed different patterns of evolution of the genetic parameters throughout the productive life of the females (non-constant variances and covariances in the different parities), with genetic correlations between repeated measurements of the trait different from unity, so we conclude that, from a genetic point of view, prolificacy should not be considered the same trait in the successive parities of the female in the genetic evaluations.
2. Although heritabilities were low, a good response to early selection can be expected if selection for prolificacy will be applied in the first two kiddings in Payoya and the first kidding in Florida.

Chapter II

3. As expected for the classical fertility traits, the heritabilities obtained were of very low magnitude, determining that the expected response to selection is low.
4. Selection for age at first kidding and interval between first and second kidding could be recommended in both breeds as early selection traits, but a rapid response to selection is not expected due to their low heritability.
5. The selection indices evaluated indicated that, in general, those that include the overall kidding interval give higher responses to selection, but because they are expressed late in the lifetime of the female, they also produce limited genetic progress.

Chapter III

6. The reproductive efficiency study identified an important genetic variability and given the high magnitude of its heritability, rapid genetic progress will be expected if selection is made for this trait to improve fertility in the Florida and Payoya breeds.

7. ER should be treated as a different trait throughout the life of the goat, due to the fact that the estimates of the variance components were not constant along the age trajectory and the genetic correlations were different from the unity.

Chapter IV

8. The analysis of the length of the productive life of the female showed a significant effect of different factors related to the reproductive management of the farm, but also with the productive level of the female, presenting a sufficiently high heritability to recommend its incorporation into the breeding program for the improvement of the longevity of females.

Overall Conclusion

9. Finally, based on the results obtained in this thesis, it can be recommended the incorporation into the breeding program of reproductive efficiency to improve fertility, prolificacy to improve numerical productivity, and the length of productive life to increase functional longevity in the Florida and Payoya goat breeds.

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Ziadi, C., Sánchez, J.P., Morales, R., Muñoz-Mejías, E., Sánchez, M., López, M. D., and Molina, A. 2022. Genetic analysis of productive life in the Florida goat breed using a Cox proportional hazards model. 73rd Annual Meeting of European Federation of Animal Science.

PRODUCCIÓN CIENTÍFICA

PRODUCCIÓN CIENTÍFICA

En esta sección se presenta un listado en el que se recogen todas las publicaciones a las que ha dado lugar esta Tesis Doctoral, a nivel nacional e internacional.

Publicaciones en revistas indexadas en el Journal of Citation Reports (JCR) de la Web of Science:

AUTORES: **Ziadi, C**., Muñoz-Mejías, E., Rodríguez, M.S., López, M.D., González-Casquet, O., and Molina-Alcalá, A.
TÍTULO: **Genetic analysis of litter size and number of kids born alive across parities in Spanish goat breeds using a random regression model.**
Revista: Italian Journal of Animal Science. Año: 2021. Número: 20(1). Páginas: 94-101.
ISSN: 15944077. doi: DOI: 10.1080/1828051X.2020.1869601
IF= 2.18 (2º cuartil) en Animal Science and Zoology

AUTORES: **Ziadi, C**., Muñoz-Mejías, E., Sánchez, M., López, M., González-Casquet, O., and Molina, A.
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Revista: Animals. Año: 2021. Número: 11(2). Páginas: 409.
ISSN: 2076-2615. doi: DOI: 10.3390/ani11020409
IF= 2.752 (1er cuartil) en Veterinary Sciences

AUTORES: **Ziadi, C**., Muñoz-Mejías, E., Sánchez, M., López, M.D., González-Casquet, O., and Molina, A.
TÍTULO: **Genetic analysis of reproductive efficiency in Spanish goat breeds using a random regression model as a strategy for improving female fertility.**
Revista: Italian Journal of Animal Science. Año: 2021. Número: 20(1). Páginas: 1681-1688.
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TÍTULO: **Genetic analysis for productive life in Florida dairy goats using a Cox proportional hazard model**
Revista: Livestock Science. Año: 2022. Sometido.
IF= 1.97 (Q1) Agriculture, Dairy and Animal Science

Congresos Nacionales

AUTORES: **Ziadi, C**., Muñoz, E., González-Casquet, O., Sánchez, M., López, M.D., y Molina, A.
TÍTULO DE LA COMUNICACIÓN: **Parámetros genéticos del tamaño de camada y el número de nacidos vivos en las razas Florida y Payoya.**
CONGRESO: X Foro Nacional del Caprino
ENTIDAD ORGANIZADORA: La Federación Andaluza de Asociaciones de Caprino de Raza Pura "CABRANDALUCÍA)
TIPO DE PARTICIPACIÓN: Póster.
PUBLICACIÓN: Libro de actas
LUGAR DE CELEBRACIÓN: Antequera, España.
AÑO: 30 y 31 de mayo de 2019.

AUTORES: Muñoz-Mejías, E., **Ziadi, C**., González-Casquet, O., Sánchez, M., López, M.D., y Molina, A.
TÍTULO DE LA COMUNICACIÓN: **Mejora genética de los caracteres reproductivos en el caprino lechero: estimación de los parámetros genéticos de la fertilidad.**
CONGRESO: X Foro Nacional del Caprino
ENTIDAD ORGANIZADORA: La Federación Andaluza de Asociaciones de Caprino de Raza Pura "CABRANDALUCÍA)
TIPO DE PARTICIPACIÓN: Póster.
PUBLICACIÓN: Libro de actas
LUGAR DE CELEBRACIÓN: Antequera, España
AÑO: 30 y 31 de mayo de 2019.

AUTORES: **Ziadi, C**., y Molina, A.
TÍTULO DE LA COMUNICACIÓN: **Estimación de los parámetros genéticos de la eficacia reproductiva en la raza caprina Payoya usando un modelo de regresión aleatoria.**
CONGRESO: IX Congreso Científico de Investigadores en Formación de la Universidad de Córdoba
ENTIDAD ORGANIZADORA: Escuela Internacional de Doctorado en Agroalimentación ceidA3
TIPO DE PARTICIPACIÓN: Póster
PUBLICACIÓN: Libro de actas
LUGAR DE CELEBRACIÓN: Córdoba, España.
AÑO: 3 al 6 de mayo de 2021

AUTORES: **Ziadi, C.**, Muñoz-Mejías, E., Sánchez, M., López, M.D., González-Casquet, O., y Molina, A.
TÍTULO DE LA COMUNICACIÓN: **Nuevos criterios de selección para los programas de cría del caprino lechero Andaluz.**
CONGRESO: XI Foro Nacional del Caprino
ENTIDAD ORGANIZADORA: La Federación Andaluza de Asociaciones de Caprino de Raza Pura "CABRANDALUCÍA)
TIPO DE PARTICIPACIÓN: Póster
PUBLICACIÓN: Libro de actas
LUGAR DE CELEBRACIÓN: Almería, España

AÑO: 23 y 24 de septiembre de 2021.

AUTORES: **Ziadi, C**., Muñoz-Mejías, E., Sánchez, M., López[4] M.D y Molina, A.
TÍTULO DE LA COMUNICACIÓN: **Nuevos criterios de selección para la mejora de la fertilidad en la raza caprina Florida.**
CONGRESO: XX Reunión de Mejora Genética Animal
ENTIDAD ORGANIZADORA: Comité organizador de XX Reunión de Mejora Genética Animal
TIPO DE PARTICIPACIÓN: Comunicación
PUBLICACIÓN: Libro de actas
LUGAR DE CELEBRACIÓN: Madrid, España
AÑO: 1 al 3 de junio de 2022.

AUTORES: **Ziadi, C**., Muñoz-Mejías, E., González-Casquet, O., Benítez, F., Ramírez, V., y Molina A.
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CONGRESO: XII Foro Nacional del Caprino
ENTIDAD ORGANIZADORA: La Federación Andaluza de Asociaciones de Caprino de Raza Pura “CABRANDALUCÍA)
TIPO DE PARTICIPACIÓN: Póster
PUBLICACIÓN: Libro de actas
LUGAR DE CELEBRACIÓN: Aracena (Huelva), España
AÑO: 30 de junio y 1 de julio de 2022.

Congresos Internacionales

AUTORES: **Ziadi, C., Muñoz, E., González, O., Molina, A.**
TÍTULO DE LA COMUNICACIÓN: **Parámetros genéticos del tamaño de camada y el número de nacidos vivos usando modelos de regresión aleatoria en la raza caprina Payoya.**
CONGRESO: XLIV Congreso Nacional y XX Congreso Internacional de la SEOC
ENTIDAD ORGANIZADORA: Universidad de Córdoba
TIPO DE PARTICIPACIÓN: Comunicación
PUBLICACIÓN: Libro de actas
LUGAR DE CELEBRACIÓN: Córdoba, España
AÑO: 18 al 20 de septiembre del 2019.

AUTORES: Muñoz-Mejías, E., González-Casquet, O., Benitez, F., Medina, C., **Ziadi, C**., y Molina, A.
TÍTULO DE LA COMUNICACIÓN: **Criterios para la mejora de la fertilidad en caprino lechero de raza Payoya.**
CONGRESO: XLIV Congreso Nacional y XX Congreso Internacional de la SEOC
ENTIDAD ORGANIZADORA: Universidad de Córdoba
TIPO DE PARTICIPACIÓN: Comunicación
PUBLICACIÓN: Libro de actas
LUGAR DE CELEBRACIÓN: Córdoba, España
AÑO: 18 al 20 de septiembre del 2019.

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TÍTULO DE LA COMUNICACIÓN: **Genetic analysis of productive life in the Florida goat breed using a Cox proportional hazards model.**
CONGRESO: 73rd Annual Meeting of European Federation of Animal Science
ENTIDAD ORGANIZADORA: EAAP
TIPO DE PARTICIPACIÓN: Póster
PUBLICACIÓN: Book of abstracts of the 73rd Annual Meeting of European Federation of Animal Science
LUGAR DE CELEBRACIÓN: Porto, Portugal
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