UNIVERSIDAD DE CÓRDOBA

DEPARTAMENTO DE GENÉTICA

TESIS DOCTORAL

"NUEVOS OBJETIVOS DE SELECCIÓN DE LA RAZA BOVINA RETINTA: MEJORA GENÉTICA DE LA PRODUCTIVIDAD, Y DE LA RESISTENCIA AL ESTRÉS TÉRMICO. ESTIMACIÓN DE PARÁMETROS MEDIANTE TÉCNICAS DE REGRESIÓN ALEATORIA Y DE NORMA DE REACCIÓN."

"NEW BREEDING OBJECTIVES OF RETINTA CATTLE BREED: GENETIC IMPROVEMENT OF PRODUCTIVITY AND HEAT STRESS RESISTANCE TRAITS BY RANDOM REGRESSION AND NORM-REACTION METHODOLOGIES"

Rosa Mª Morales Cid

Córdoba, Junio 2017

TITULO: *Nuevos objetivos de selección de la Raza Bovina Retinta: mejora genética de la productividad y de la resistencia al estrés térmico. Estimación de parámetros mediante técnicas de regresión aleatoria y de norma de reacción*

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“NEW BREEDING OBJECTIVES OF RETINTA CATTLE BREED: GENETIC IMPROVEMENT OF PRODUCTIVITY AND HEAT STRESS RESISTANCE TRAITS BY RANDOM REGRESSION AND NORM-REACTION METHODOLOGIES”

MEMORIA DE TESIS DOCTORAL PRESENTADA POR

Rosa Mª Morales Cid

Para optar al Grado de Doctor con Mención Internacional
por la Universidad de Córdoba

Prof. Dr. Antonio Molina Alcalá **Prof. Dr. Alberto Menéndez-Buxadera**

Prof. Dr. Sebastián Demyda Peyrás

Córdoba, a 26 de Junio de 2017

TÍTULO DE LA TESIS: **NUEVOS OBJETIVOS DE SELECCIÓN DE LA RAZA BOVINA RETINTA: MEJORA GENÉTICA DE LA PRODUCTIVIDAD, Y DE LA RESISTENCIA AL ESTRÉS TÉRMICO. ESTIMACIÓN DE PARÁMETROS MEDIANTE TÉCNICAS DE REGRESIÓN ALEATORIA Y DE NORMA DE REACCIÓN.”**

DOCTORANDO: **Rosa Mª Morales Cid**

INFORME RAZONADO DE LOS DIRECTORES DE LA TESIS Y EL TUTOR

La Tesis Doctoral que se presenta está integrada por dos artículos publicados en revistas ISI, de gran impacto en el campo de la Ciencia Animal, dos artículos que actualmente se encuentran en fase de revisión en otras revistas indexadas y un quinto artículo que será enviado a otra revista indexada próximamente.

La Tesis se ha estructurado en cinco capítulos:

Capítulo I: Direct and maternal genetic effects for preweaning growth in Retinta cattle estimated by a longitudinal approach throughout the calving trajectory of the cow.

> Los resultados de este estudio se han publicado en el trabajo: **Morales, R.**, Menéndez-Buxadera, A., Avilés C. y Molina A. Direct and maternal genetic effects for preweaning growth in Retinta cattle estimated by a longitudinal approach throughout the calving trajectory of the cow. J. Anim. Breed. Genet. 2013. 141 (4): 277-283. ISSN: 0931-2668. DOI: ISSN. doi:10.1111/jbg.12038. IF= 1.877 (1er cuartil) en Agriculture, Dairy and Animal Science

Capítulo II: Genetic analysis of accumulated productivity of Retinta breeding cows.

> Los resultados de este estudio se encuentran en el trabajo: **Morales, R.**, Menéndez-Buxadera, A., Demyda Peyrás S. y Molina, A. Genetic analysis of accumulated productivity of Retinta breeding cows.

Capítulo III: Breeding beef cattle for an extended productive life: Evaluation of selection criteria in the Retinta breed.

> Los resultados de este estudio se encuentran en el trabajo: **Morales, R.**, Phocas, F., Demyda-Peyrás, S., Menendez-Buxadera, A. y Molina, A. Breeding beef cattle for an extended productive life: Evaluation of selection criteria in the Retinta breed as example. Livestock Science. 2017. Sometido IF= 1.377 (2º cuartil) en Agriculture, Dairy and Animal Science

Capítulo IV: Effect of inbreeding depression on bull sperm quality and field fertility.

Los resultados de este estudio se han publicado en el trabajo: Dorado, J., **Morales, R.**, Molina, A., Hidalgo, M., Ariza, J., Moreno-Millán, M. y Demyda-Peyrás, S. Effect of inbreeding depression on bull sperm quality and field fertility. Reprod Fertil Dev. 2015 ISSN: DOI: 10.1071/RD15324.

IF= 2.656 (2º cuartil) en Reproductive Biology.

Capítulo V: Genetic effects of climatic seasons on preweaning growth of beef cattle: a first approach to Retinta calves.

Los resultados de este estudio se encuentran en el trabajo: **Morales, R.**, Menéndez-Buxadera, A., Demyda Peyrás S. y Molina, A. Genetic effects of climatic seasons on preweaning growth of beef cattle: a first approach to Retinta calves. Livestock Science. 2017. Sometido IF= 1.377 (2º cuartil) en Agriculture, Dairy and Animal Science

Por tanto, consideramos que el trabajo realizado por Dña. Rosa Mª Morales Cid, bajo nuestra dirección y tutela, presenta unos elevados niveles de innovación y calidad y autorizamos su presentación y defensa como Tesis Doctoral en el Departamento de Genética de la Universidad de Córdoba, para obtener el **grado de Doctor Internacional.**

Córdoba, a 26 de junio de 2017

Firma de los directores

Fdo.: D. Antonio Molina Alcalá
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TÍTULO DE LA TESIS: **NUEVOS OBJETIVOS DE SELECCIÓN DE LA RAZA BOVINA RETINTA: MEJORA GENÉTICA DE LA PRODUCTIVIDAD, Y DE LA RESISTENCIA AL ESTRÉS TÉRMICO. ESTIMACIÓN DE PARÁMETROS MEDIANTE TÉCNICAS DE REGRESIÓN ALEATORIA Y DE NORMA DE REACCIÓN.**

DOCTORANDA: **ROSA MARÍA MORALES CID**

MENCIÓN DE DOCTORADO INTERNACIONAL

Esta Tesis reúne los requisitos establecidos en el artículo 35 de Normativa de Doctorado de la Universidad de Córdoba para la obtención del título de Doctor con Mención Internacional:

Estancia internacional predoctoral de 3 meses (02/09/2013 AL 02/12/2013) en el Instituto Nacional de investigación Agronómica (INRA), dentro de la unidad GABI, AgroParisTech, en la Universidad de Paris-Saclay, (Jouy-en-Josas) bajo la supervisión de la Dra. Florence Phocas.

La Tesis cuenta con el informe previo de dos doctores expertos y con experiencia investigadora acreditada perteneciente a alguna institución de educación superior o instituto de investigación de fuera de España:

- Dr. Pablo Juan Ross. Associate Professor of Animal Science Department. University of California, Davis. California
- Dra. Mª Elena Fernández. Assistan Researcher Institute of Animal Genetics “Ing. Fernando Noel Dulout”. National Research Council (CONICET). Argentina.

Parte de la Tesis se ha redactado en español e inglés y será presentada en estos dos idiomas.

“Para empezar un gran proyecto, hace falta valentía.

Para terminar un gran proyecto, hace falta perseverancia.”

-Anónimo-

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ÍNDICE

RESUMEN

RESUMEN

Esta Tesis Doctoral ha tenido como objetivo el análisis de nuevos criterios de selección para el vacuno de carne relacionados con la productividad global de los reproductores y su grado de resistencia al estrés térmico.

Para la realización de los trabajos incluidos en la presente Tesis Doctoral, se ha tomado como ejemplo de raza autóctona de aptitud cárnica, la raza Retinta, que se caracteriza por su rusticidad y su marcado carácter maternal. *La Asociación Nacional de Criadores de Ganado Vacuno Selecto de Raza Retinta*, nos ha facilitado la base de datos, con más de 25 años de información, y un número total de 294.977 registros, a partir de la cual se han desarrollado los distintos estudios.

El sistema extensivo de producción de carne ha venido basando sus criterios de mejora en el crecimiento de los terneros. Pero ante la situación del mercado actual y su previsible evolución, hacen necesaria la mejora de otros caracteres con gran peso en la rentabilidad de las ganaderías, como son los relacionados con la longevidad productiva, la productividad global de las reproductoras, el control de la endogamia o la resistencia al estrés térmico.

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

En el primer capítulo se llevó a cabo una estimación de los componentes de la varianza para los efectos genéticos directos y maternos a lo largo de los partos de la vaca, para el carácter peso al destete y el peso a los 4 meses de edad del ternero. Se analizaron mediante tres modelos lineales: univariado (UVM), multicaracteres (MTM) y de regresión aleatoria (RRM) con el software ASREML de Gilmour et al. (2009a), los resultados del peso al destete (PD) de 5.972 terneros de la raza Retinta hijos de 1.680 vacas y 129 sementales nacidos en 14 ganaderías de referencia del Núcleo de Selección de la raza. Las heredabilidades para efectos directos ($\mathbf{h_d^2}$) fueron muy similares para UVM y MTM ($\mathbf{h_d^2} \approx 0{,}30$ para peso a 120 días (P120 y$\mathbf{h_d^2} \approx 0{,}52$ para peso a 180 días-P180) y ligeramente inferior a los estimados de RRM ($\mathbf{h_d^2}$ promedio $\approx 0{,}37$ para P120 y $\mathbf{h_d^2} \approx 0{,}57$ para P180). Las heredabilidades para efectos maternos fueron muy similares en los tres modelos ($\mathbf{h_m^2} \approx 0{,}160$ y 0,230 para p120 y p180 respectivamente). Los resultados del modelo RRM mostraron una importante variabilidad genética detectándose la existencia de una importante variación en la forma de respuesta del VG en función del número de parto, por lo que los pesos predeteste deberían considerarse como variables diferentes a lo largo de la trayectoria de partos de las reproductoras a la hora de la valoración genética para el crecimiento (Morales et al., 2013).

En el segundo capítulo, se realizó un análisis de tres variables relacionadas con la longevidad de la reproductora: duración de la vida real (LTL, tiempo desde el nacimiento hasta el último parto conocido), duración de la vida productiva (LPL, tiempo desde el primer parto hasta el último parto conocido) y número de partos (NC, número de partos entre el primero y el último conocido). Se analizaron los datos de 3.187 vacas, de las cuales 1.802 habían terminado su ciclo productivo y 1.385 continuaban vivas y por tanto tenían su información censurada. Utilizando el software Survival Kit de Ducrocq and Sölkner (1994) mediante la distribución de Weibull (Mészáros et al., 2013). Los resultados indicaron que, de diferentes factores relacionados con el manejo productivo de la explotación, tenían un efecto significativo sobre estas variables. También se encontraron diferencias significativas en el tipo de raza paternal utilizada para la producción de terneros, mostrando aquellas vacas dedicadas a la cría en pureza un menor riesgo de ser eliminadas del rebaño. Las heredabilidades obtenidas fueron moderadas para LTL y LPL (0,14 ± 0,01 y 0,14 ± 0,01 respectivamente) y más elevadas para NC (0,30 ± 0,01). Estos resultados unidos a la existencia de una correlación del 96% entre las tres variables, sugieren que se puede esperar una buena respuesta a la selección en el incremento de la vida productiva de esta raza autóctona utilizando cualquiera de ellas, aunque será mayor con la variable NC debido a su alta heredabilidad.

En el tercer capítulo, se abordó un estudio genético de la productividad acumulada (ACP, kilos de carne destetados a una edad determinada por cada reproductora aportado por Grossi et al. (2008)) mediante RRM. Los resultados mostraron la existencia de un importante componente genético, con unas heredabilidades a lo largo de las distintas edades de mediana a elevada magnitud (0,25 a 0,41). Por lo tanto, la utilización de esta variable relacionada directamente con la rentabilidad de las reproductoras como criterio de selección, permitiría una mejora más efectiva en parámetros reproductivos relacionados con la fertilidad, que presentan generalmente una heredabilidad muy baja, así como de los de crecimiento del ternero, para los cuales su utilización como criterios independientes no tiene ningún tipo de problema. La utilización de la metodología de RRM permitió observar dos tipos de patrones de evolución del valor genético de las reproductoras, unas que van disminuyéndolo o aumentándolo con respecto a la media de la población al incrementar su edad (animales plásticos) y otras que se muestran más estables a lo largo de su vida productiva (animales estables o robustos). Por lo tanto, la utilización de esta herramienta aportaría una gran flexibilidad para que el ganadero pudiese elegir el tipo de animal a seleccionar según la pauta de reposición deseada. Por último, se encontraron grandes diferencias en la evolución de las curvas de productividad media de las diferentes explotaciones analizadas sugiriendo una profunda revisión del sistema productivo de algunas de ellas.

En el cuarto capítulo, se ha analizado por primera vez de manera objetiva el efecto de la endogamia en la fertilidad de los toros de la raza Retinta. Utilizando de manera innovadora, metodologías de análisis espermático automatizado (CASA (Computer-Assisted Sperm Analysis)) en toros altamente endogámicos, se demostró que los espermatozoides provenientes de estos animales tienen fallos en su motilidad, presentando un patrón de movimiento coincidente con los observados en espermatozoides hiperactivados, pero de forma anticipada. Esto puede producir una depleción de sus reservas energéticas de manera temprana, lo que podría conllevar a un descenso en su fertilidad, hecho que explicaría los resultados obtenidos al analizar los intervalos de parto de 5.230 vacas apareadas con 743 toros (159 donantes de semen), que muestran un incremento medio del interparto de 19 días cuando intervenían toros cuyo nivel de endogamia superaba el 13% (Dorado et al., 2013).

Finalmente, en el último capítulo de esta Tesis se ha basado en la detección de un componente genético en el grado de resistencia al estrés térmico. Para ello se analizaron 7.753 registros de peso vivo a lo largo de 9 años, de un total de 3.162 terneros hijos de 1.249 vacas y 85 toros explotados en diferentes zonas de Andalucía. Mediante un estudio del índice de confort THI de Finocchiaro et al. (2005), que combina temperatura y humedad y la radiación solar, se diferenciaron dos épocas climáticas correspondientes a los meses fríos y a los cálidos, en las que se estimaron los componentes de la (co)varianza del peso al destete mediante un modelo de "norma-reacción", resueltos mediante técnicas de regresión aleatoria. A nivel global los resultados no fueron significativos, sin embargo, la interacción genotipo-ambiente hallada por Santana et al. (2016), se pudo observar en los primeros meses de vida del ternero con diferencias genéticas entre los dos periodos climáticos, encontrándose heredabilidades más altas cuando los animales se explotaban en condiciones frías en relación a cuando lo hacían en condiciones cálidas. Estos resultados abren una línea de investigación muy importante ya que debido los efectos cada vez más acusados del calentamiento global, se hace cada vez más necesaria la inclusión de variables que permitan la selección de animales más resistentes al estrés climático, sobretodo para aquellos que se explotan en extensivo en zonas muy castigadas por la climatología, como es el caso de Andalucía.

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

SUMMARY

This PhD work has aimed at the analysis of new selection criteria for beef cattle related to the overall productivity of the breeding animals and their degree of resistance to thermal stress.

To carry out the studies included in this PhD work, Retinta breed has been taken as an example of an autochthonous beef breed, which is characterized by its rusticity and a marked maternal character. The National Retinta Breeders Association has provided us with a database of more than 25 years of information and 294,977 records, from which the different studies have been carried out.

The extensive system of meat production has been based its improvement criteria on the calf's growth. However, considering the current market situation and its predictable evolution, it is necessary to improve other characteristics with great significance in the profitability of livestock, such as those related to productive longevity, the overall productivity of the cow, the inbreeding control or the resistance to thermal stress.

To achieve the objectives of this PhD study, the document has been structured into five chapters:

In the first chapter, an estimation of the direct and maternal genetic effects was considered for the pre-weaning growth of Retinta calves across parities. The results of 120 (P120) and 180 days (P180) weights of 5,972 Retinta calves with 1680 dams and 129 sires from 14 reference herds of breed selection core, were analyzed by three linear models: univariate (UVM), multi-character (MTM) and random regression (RRM) by ASREML software (Gilmour et al., 2009a). The heritability of direct effect ($\mathbf{h_d^2}$) was very similar for UVM and MTM $\mathbf{h_d^2}$ ≈ 0.30 for P120 and $\mathbf{h_d^2}$≈0.52 for P180 and slightly lower than the estimates by RRM ($\mathbf{h_d^2}$ average ≈0.37 for P120 y $\mathbf{h_d^2}$≈0.57 for P180). The heritability for maternal effects was quite similar for the three models (0.16 for P120 and 0.22 for P180). The results of the RRM model showed an important genetic variability, detecting the existence of an important variation in the response form of the EBV according to the number of calving, so that the pre-weaning weights should be considered as different traits throughout the calving trajectory of the cows to carry out a growth genetic evaluation (Morales et al., 2013).

In the second chapter, an analysis of three variables related to cow longevity was performed. Length of true life (LTL, estimated as the number of months between the birth of the cow and the birth of the last calf on record or censoring), length of productive life (LPL, number of months between the birth of the first and the birth of the last calf on record or censoring) and number of calvings (NC, estimated as the number of calvings for each cow until its last calving or censoring time). Data from 3,187 cows: 1,802 cows had complete carriers while 1,385 cows had censored information, were analyzed by Ducrocq and Sölkner (1994)

software Survival Kit, using proportional hazard model Weibull (Mészáros et al., 2013). Results indicated that different factors related to productive management herd were significant for all traits. There were also significant differences in the kind of paternal breed used for calf production, showing that cows used to purebred had a lower risk of being eliminated. The heritabilities obtained were very moderate for LTL and LPL (0.14 ± 0.01 and 0.14 ± 0.01 respectively) and more significant for NC (0.30 ± 0.01). These results together with the existence of a 96% of correlation among the three traits, suggest that an elevated response to selection to increase the productive life in this autochthonous breed can be expected by whatever of them, however it will be higher by NC trait due to its high heritability.

In the third chapter, a genetic study about accumulated productivity of the cow (ACP) considering calf body weight at weaning and number of offspring (Grossi et al., 2008) was analysed by RRM across the different ages of the cow. The results showed the existence of an important genetic component, heritabilities were of medium-high magnitude (0.25 to 0.41). Therefore, the use of this trait, which is directly related to the profitability of the breeding stock as a selection criterion would allow a more effective improvement in reproductive parameters related to fertility, which generally have a very low heritability, as well as those of growth calf, for which its use as independent criteria does not have any type of problem.

Two types of evolutionary patterns EBV cow's curve were detected, on the one hand, animals with decreasing or increasing it with respect to the average of the population when increasing its age (plastic animals), on the other hand, animals which are able to maintain this productivity constant until older years (stable animals). That is, they provide enormous flexibility to select the most appropriate kind of animal at the desired replenishment rate.

Finally, we found large differences in the evolution of the average productivity curves between breeders, suggesting a deep revision of the productive system of some of them.

In the fourth chapter, the effect of inbreeding on the fertility of the Retinta bulls has been objectively analyzed for the first time. Using automated and objective sperm analysis (CASA) in highly inbred bulls was showed that the spermatozoa from highly inbred bulls have motile defects, presenting a movement pattern coincident with those observed in hyperactivated spermatozoa, but in advance. This may lead to a depletion of their energy reserves early, which could lead to a decrease in their fertility, a fact that would explain the results obtained when analyzing the calving intervals of 5,230 cows matted with 743 sires (159 semen donors), which show an average increase of 19 days of the calving interval when bulls intervened whose level of inbreeding exceeded 13% (Dorado et al., 2013).

However, those differences showed a clear differential pattern of heritabilities among calves reared in summer and in the winter season, and a convergent pattern of growth heritabilities after three months of age.

Finally, the last chapter of this PhD work has been based on the detection of a genetic component in the degree of resistance to thermal stress. We analyzed 7,753 live weight records collected for nine years from 3,162 Retinto calves, born of 1,249 dams and 85 sires raised in the Andalusian region. By a THI comfort index study (Finocchiaro et al., 2005), which combines temperature and humidity and solar radiation, two climatic seasons were differentiated corresponding to the cold and hot months, in which the (co)variance components of weaning weight were estimaed by a "norm-reaction" model, solved by random regression techniques. Overall assessment did not show significant effects of the genotype-environment interaction, however, a highly significant evidence of genotype-climatic condition interaction as the found by Santana et al. (2016) was found during the calf´s early months of growth with genetic differences between the two climatic periods, higher heritabilities were found when the animals were exploited in cold conditions relative to when they did so in warm conditions. These results open a very important line of research due to the increasingly pronounced effects of global warming; It is becoming increasingly necessary to include variables that allow to select the more resistant animal to climatic stress, especially those who are raised in extensive areas severely punished by heat, as it is the case of Andalusia.

As a final conclusion, we emphasize that the methodologies set out in the present PhD study for the analysis of new selection criteria in the Retinta breed could be incorporated into their Breeding Program collaborating to the genetic progress of the breed, although in some cases it is necessary to expand the studies carried out and to make a greater control of some aspects related mainly to the reproductive behavior.

INTRODUCCIÓN GENERAL Y JUSTIFICACIÓN

INTRODUCCIÓN GENERAL

El sector del vacuno de Carne en España

El sector vacuno de carne representa el 16,5% de la producción final ganadera española, en el año 2016 alcanzó un valor económico de 2.765 millones de euros, constituyendo el 8% del valor total producido en la unión europea (Eurostat). La importancia de este sector se ve reflejada en el hecho que la carne vacuna española ocupa el quinto lugar en la Unión Europea en cuanto a censo y producción, solo por detrás de países con una larga tradición en este sector como Francia, Alemania, Reino Unido e Irlanda. Según los datos de SITRAN (Sistema Integral de Trazabilidad Animal) en ese mismo año el censo español ascendía a 6.327.450 cabezas. (Mapama, 2015). En España, este ganado ha sido seleccionado durante las últimas décadas utilizando como principales objetivos de selección el crecimiento y la aptitud maternal (Serradilla, 2008). Estos objetivos se ven claramente diferenciados entre los dos principales componentes de este sistema productivo: el de las vacas madres y el del cebo. La primera etapa es la fase más costosa y delicada, su objetivo de producción es generar vacas nodrizas capaces de suministrar terneros vivos, sanos y homogéneos, lo suficientemente desarrollados como para poder comportarse de manera eficiente en el cebadero, donde se transformarán en animales adultos aptos para ser faenados. Una de las principales razas empleadas en esta etapa en productiva es la raza Retinta, caracterizada por una su buena aptitud maternal, siendo una raza autóctona muy adaptada a las condiciones productivas y ambientales de la península Ibérica (Jimenez et al., 2007). Es por ello que la misma se emplea tanto en pureza como mediante cruzamientos con razas de crecimiento rápido como la Charolesa y la Limusine para la producción de cruces con destino a matadero (Acero-Adámez, 2009).

En la actualidad, el sistema extensivo de producción de carne le brinda una marcada importancia al peso al destete de los terneros, debido a que está altamente correlacionado con su evolución y crecimiento y a su uso como predictor de la evolución del peso al sacrificio y como componente esencial de la productividad de la vaca. Este rasgo es completado con otros caracteres que miden el comportamiento en cebo, la calidad cárnica en matadero, su morfología y su eficiencia reproductiva (A.N.C.G.V.S.R.R., 2010), así como la ausencia de anomalías genéticas relacionadas con la infertilidad (Moreno Millan and Genero, 2008).

La Raza Retinta

La raza Retinta, incluida en El Catálogo Oficial de Razas de Ganado de España como raza de fomento, presenta un censo nacional aproximado de 200.000 vacas, de las cuales más de un 10% están inscritas en su Libro Genealógico (ARCA, 2016). Estos datos convierten a la Retinta en la segunda raza autóctona con mayor censo de toda España y en la raza predominante en el cuadrante suroccidental peninsular, siendo las comunidades de Extremadura y Andalucía las áreas en las cuales están distribuidos el 96% de sus animales (Jimenez et al., 2007). Son varios los tipos de sistemas de explotación extensivos presentes en estas comunidades, pero el que da cobijo a la mayor parte de la producción de bovino extensivo, es el ecosistema de la dehesa.

La dehesa es un sistema de explotación sostenible de los recursos agroganaderos y forestales, sin precedentes en Europa. Se trata de un modelo de alto valor natural, que se caracteriza contribución al equilibrio entre el medio ambiente y la actividad ganadera, así como por la marcada estacionalidad de sus pastos, la cual condiciona el manejo del ganado. Es por ello que además de su producción ganadera per se, la raza Retinta cumple un papel fundamental en la conservación y al mantenimiento del medio natural y a la fijación de población rural (Jiménez et al., 2007).

Esquema de Selección y Mejora genética

La Raza Retinta es una de las primeras razas españolas en poseer un sistema de evaluación genética sistematizado, el cual fue aprobado por primera vez por resolución de la Dirección General de Producciones y Mercados Ganaderos, el día 29 de enero de 1992. Con el transcurso de los años, las mejoras productivas y reproductivas conseguidas fueron evidentes, lo que provocó que la respuesta a la selección fuese bastante más limitada, ante la falta de un programa de mejora integral y moderno. Esto, sumado a la aparición de nuevas tecnologías y metodologías genéticas (Schaeffer, 2004; Dekkers, 2012) hizo imprescindible 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 la raza y al uso de metodología y técnicas actuales. Es por ello que con fecha 22 de septiembre de 2016 se aprobó una resolución en la que se detalla el actual Programa de Mejora de La Raza Bovina Retinta (BOE de 5 de octubre de 2016), cuyos objetivos se centran en mejorar, mediante valoraciones genéticas sistematizadas, la eficacia productiva de esta raza, manteniendo la rusticidad y adaptación al sistema de explotación extensivo en que se desenvuelve. Es por ello que se han incluido por primera vez no sólo aquellos aspectos permiten incrementar la productividad, como el crecimiento de los terneros o las características reproductivas tanto de hembras como de machos, sino que también se han incluido parámetros productivos relacionados con la mejora en la conformación de los animales y la calidad de la canal y de la carne.

Además, este esquema de selección promueve y resalta el mantenimiento de la cría de animales en condiciones de pureza racial, pero sin olvidar el encuadre de la raza Retinta dentro de las razas maternales, así como su uso frecuente en cruzamientos interraciales para obtener una mayor producción cárnica.

El presente programa de mejora contempla los siguientes objetivos específicos:

- ✓ La mejora del crecimiento durante el periodo predestete en la explotación y postdetete y de la eficiencia alimenticia en cebadero.
- ✓ La mejora de la aptitud reproductiva.
- ✓ La mejora de la conformación de los animales en vivo, y la calidad de la canal y de la carne.
- ✓ La ausencia de alteraciones cromosómicas y enfermedades hereditarias.
- ✓ El mantenimiento de la rusticidad y sus buenas características maternales, así como de su aptitud para el cruzamiento con otras razas paternales.

Para la consecución de estos objetivos, se lleva a cabo un programa sistematizado de valoración el cual consta de tres fases secuenciales:

(1) Selección al destete en la explotación.

(2) Valoración individual de candidatos a semental en el centro de testaje.

(3) Valoración genética combinada a partir de los controles de rendimientos en explotación, cebadero y matadero.

Los controles de rendimientos productivos y reproductivos, necesarios para llevar a cabo este sistema de valoración, son realizados mayoritariamente por los veterinarios oficiales de la asociación mediante el uso de unas fichas estandarizadas que permiten recopilar toda la información requerida por el plan de mejora.

Los resultados obtenidos en los controles fenotípicos son corregidos mediante técnicas estadísticas apropiadas que analizan y cuantifican los efectos de los distintos factores que influyen en la producción, haciendo posible junto con la matriz de parentesco, la comparación de los sementales en el proceso de valoración y la combinación de los distintos caracteres a tener en cuenta. Mediante este programa, se pretende favorecer la difusión de la mejora genética lograda en los reproductores.

JUSTIFICACIÓN

En nuestras razas locales, especialmente en las del sudoeste español, aumentar la productividad a lo largo de la vida de los animales se ha convertido en una prioridad, ya que paradójicamente, la retribución que reciben los criadores por kilogramo de carne producida es cada vez más ajustada y el coste de amortización de las reproductoras es cada vez mayor, lo que hace que el sistema deba aumentar su eficiencia para lograr mantenerse. Adicionalmente, las prácticas reproductivas utilizadas por los criadores, más aún en explotaciones con un limitado número de animales, han descuidado el control de la endogamia, utilizando para la reposición toros nacidos en las mismas explotaciones con altos niveles de consanguineidad, lo cual podría repercutir en la eficiencia productiva y reproductiva de los animales. Por otro lado, el cambio climático, que trae asociado un aumento de la temperatura media del planeta, hace que un punto fundamental para lograr animales más productivos sea un incremento en su resistencia al estrés térmico. Es por ello, que estos tres factores (aumento de la productividad, control de la endogamia y resistencia al stress térmico), 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 extensiva.

Hoy en día la significación de estos factores está cobrando una mayor importancia debido a la necesidad de una mayor adaptación de los animales a los sistemas de cría en extensivo. Esto se debe al aumento de la población mundial que genera la necesidad de aprovechar productivamente ecosistemas marginales, los cuales tienen costes productivos menores, y de disminuir la utilización de insumos agrícolas, los cuales pueden ser derivados para la alimentación humana. Todo esto se ve además influenciado en el caso de España, por el posible cambio de la política agraria, lo cual hace que sea aún más necesario adecuar los objetivos de selección utilizados en estos sistemas hacia una mejora de la rentabilidad global de las explotaciones (Alenda and Pérez-Cabal, 2010). Es por ello que el éxito de este tipo de razas locales y eco-adaptadas estará en función de lograr que sus vacas sean capaces de producir y amamantar cada año un ternero, siendo además capaces de mantener niveles productivos aceptables durante el mayor número de años posibles y de que la progenie resultante tenga una elevada capacidad de crecimiento y desarrollo en condiciones extensivas.

A pesar de esta problemática existente, la productividad real de este tipo de explotaciones vacunas no ha sido abordada de forma global y sistematizada. Por el contrario, el vacuno de leche ha tomado en cuenta esta situación, haciendo que la longevidad productiva y los kilos de leche producidos a lo largo de la vida del animal tengan cada vez más importancia en los esquemas de selección (Potočnik et al., 2011; van Pelt et al., 2015).

Modelos de productividad basados en regresión aleatoria

El presente estudio ha llevado a cabo por primera vez la puesta a punto de modelos de regresión aleatoria y modelos de supervivencia en la valoración de caracteres relacionados con la productividad en el ganado Retinto, como modelo para su utilización en sistemas de producción extensivos. Esta metodología estadística tiene la ventaja de permitir un enfoque longitudinal (a lo largo del tiempo de manera continua) tanto en el análisis de la curva de crecimiento del ternero, como en el análisis de la productividad a lo largo de la vida productiva de la vaca.

Los primeros trabajos utilizando esta metodología de Regresión Aleatoria se realizaron evaluando el control diario de producción láctea, mediante una metodología conocida como Test Day Model (TDM) (Schaeffer and Dekkers, 1994). Gracias a dicho modelo, estos autores sentaron las bases metodológicas generales para el procedimiento hoy conocido como RRM (Random Regresion Model). Estos modelos muestran ventajas frente a los modelos clásicos utilizados en la mejora (BLUP) debido a que permiten el análisis de la curva de crecimiento completa, lo cual es una ventaja evidente frente a la utilización de una sola variable que resuma todo el crecimiento (como puede ser el peso tipificado a los 180 días). Entre las ventajas observadas, esta metodología permite una mejor estimación del peso y sus (co)varianzas en cada punto de la curva de crecimiento de los animales, su precisión estará en función de las correlaciones entre los diferentes pesos de cada animal analizado, además no exige un proceso de tipificación individual, el cual siempre está sometido a un cierto grado de error. Los modelos de RMM permiten del mismo modo, estimar la productividad acumulada de cada reproductora hasta la edad actual evitando el tener que controlar los animales hasta el final de su vida productiva para poder obtener evaluaciones fiables.

Estimación genética de la longevidad de los animales

Es bien sabido que la longevidad es uno de los factores más importantes económicamente en vacuno de carne, debido a que el elevado coste de llevar una becerra desde su nacimiento hasta su etapa de reproductora será el mismo independientemente del número de terneros producidos a lo largo de su vida productiva, por lo cual debe ser amortizado en el mayor tiempo posible. Es por ello que la utilización de modelos estadísticos de supervivencia, como los empleados en el presente trabajo, quedan ampliamente justificados y son considerados en la actualidad como el enfoque estadístico más pertinente para la evaluación genética de la longevidad de las vacas (Olechnowicz et al., 2016). Sin embargo, hay que resaltar, que esta metodología se ha utilizado ampliamente en la mayoría de las especies ganaderas, como el vacuno lechero (Famula, 1981; Caraviello et al., 2004; Jenko et al., 2013), vacuno de carne (Rogers et al., 2004), cerdos (Meszaros et al., 2010) y más recientemente en caballos (Sole et al., 2017), pero escasamente en sistemas de producción vacuna extensiva, siendo el número de estudios realizados hasta la fecha limitado a pesar de su importancia económica (Rogers et al., 2004; Dákay et al., 2006; Szabó and Dákay, 2009). De igual manera, el número de estudios que estimen parámetros genéticos para rasgos de longevidad en ganado vacuno de carne, si bien es mayor ((Tanida et al., 1988; Rogers et al., 2004; Dákay et al., 2006; Forabosco et al., 2006; Phocas and Ducrocq, 2006a; Szabó and Dákay, 2009), sigue siendo limitado cuando el objetivo de estudio son sistemas productivos extensivos. Es por ello que el presente trabajo, con el fin de incrementar los conocimientos ya existentes en este ámbito, plantea ser el primero en realizar un análisis de supervivencia utilizando un modelo de riesgo proporcional de Weibull y la puesta a punto de esta metodología mediante el uso del software Survival Kit (V. Ducrocq & J. Sölkner, 1994) en una raza española de vacuno de carne.

La endogamia: un parámetro genético muchas veces olvidado y su efecto en la fertilidad

La endogamia, producida por el cruzamiento de individuos emparentados genéticamente, es otro de los factores que ha sido tenido poco en cuenta en algunos esquemas de selección, tanto en los machos reproductores, como en las hembras. Es bien sabido que el incremento de esta condición genética provoca una menor habilidad de los animales para adaptarse al medio-ambiente y luchar contra las enfermedades, repercutiendo en su eficiencia productiva global (Leroy, 2014). Además, es de resaltar que uno de los primeros aspectos afectados por el aumento de la endogamia es el reproductivo. Este hecho ha sido ampliamente estudiado en vacas mediante la caracterización de índices reproductivos poblacionales obtenidos de explotaciones comerciales y asociaciones de productores (Mc Parland et al., 2009; Stachowicz et al., 2011; Bjelland et al., 2013; Malhado et al., 2013). De la misma manera, existen también estudios que evaluaron el efecto de la endogamia en la calidad seminal de toros, obteniéndose resultados absolutamente contradictorios (Ducrocq and Humblot, 1995; Thompson et al., 2000; Persson and Soderquist, 2005; Sorensen et al., 2005; Maximini et al., 2011; Losdat et al., 2014). Sin embargo, este tipo de análisis fueron realizados en su mayoría en base al análisis de datos obtenidos de centros de inseminación, en los cuales la caracterización del esperma se realiza de manera subjetiva y puede ser afectada por el operador. En este sentido existe solo un estudio experimental en el cual se criaron animales altamente endogámicos para evaluar el efecto de este factor en su calidad reproductiva. Sin embargo el mismo fue realizado hace más de 25 años (Flade and Zeller, 1992), cuando los métodos de análisis espermático estaban pobremente desarrollados. No existe hasta la actualidad ningún estudio que haya caracterizado la viabilidad espermática de toros altamente endogámicos utilizando técnicas objetivas de análisis seminal, como lo es el análisis automatizado asistido por ordenador (SCA) (Rodriguez-Martinez and Larsson, 1998). Es por ello que el presente trabajo tiene como objetivo el realizar, por primera vez, un estudio sistematizado de la calidad seminal de dosis comerciales de esperma crioconservado proveniente de animales con altos niveles de endogamia utilizando técnicas de evaluación espermática objetivas, lo cual permitirá obtener una mayor precisión en la determinación de los efectos de la endogamia en el esperma de los bovinos.

La producción bovina extensiva frente al cambio climático

Finalmente, una importante problemática a la cual se están enfrentando los sistemas de producción animal extensivos de cara al futuro es el cambio climático (McMichael et al., 2007). Según los últimos modelos predictivos (Pachauri and Meyer, 2014), utilizados para determinar sus consecuencias a corto y mediano plazo, Andalucía (y en general el sudoeste español) es la región europea donde la temperatura sufrirá una mayor variación, estimándose incrementos en la temperatura media cercanos a los 3ºC y de hasta 8ºC en las temperaturas mínimas. Esta variación climática se producirá especialmente en las zonas de montañas del interior andaluz, lugar donde se encuentran la mayor parte de las explotaciones dedicadas a la cría del vacuno de carne. A pesar de que este tipo de explotaciones utilizan razas autóctonas eco-adaptadas, este salto violento en las condiciones ambientales provocará sin lugar a dudas un aumento del estrés térmico al que estarán sometidos los animales, con la consecuente pérdida de productividad y descenso de su bienestar general. Debido a ello, la inclusión de evaluaciones objetivas del estrés térmico sufrido por los animales, así como su inclusión como parámetro fundamental dentro de los planes de mejora genética de este tipo de razas, ha sido señalada como una de las prioridades de la mejora del vacuno andaluz. Esta situación hace necesaria, e incluso prioritaria, la puesta a punto de técnicas de evaluación genética, basadas en nuestro caso en metodologías estadísticas de tipo “norma-reacción”, que permitan realizar una evaluación de la interacción genotipo-ambiente (capacidad de adaptación diferencial de determinados animales a distintas condiciones ambientales), optimizadas al estudio del estrés térmico. Para ello, el presente estudio plantea la utilización de los índices de temperatura-humedad (THI) y radiación solar (RS), determinados a lo largo de la totalidad del período de crecimiento previo al destete como variables indicadores y la aplicación de metodologías RMM, permitiendo cubrir una amplia gama de condiciones dentro de un mismo modelo (Schaeffer, 2004).

OBJETIVOS E HIPÓTESIS

OBJETIVOS

El objetivo que se persigue en la presente Tesis Doctoral es optimizar los programas de selección de las razas locales bovinas de aptitud cárnica, utilizando como ejemplo el de la Raza Retinta. Se abordarán unos objetivos específicos esenciales que inciden en la mejora de la rentabilidad de las explotaciones de vacuno extensivo, basados en la mejora genética de la productividad y de la resistencia al estrés térmico:

- La mejora de la estimación de parámetros genéticos del crecimiento al destete de los terneros mediante el análisis de la curva de crecimiento por técnicas de regresión aleatoria.

- La determinación y optimización de criterios que permitan abordar la mejora de la productividad global de las reproductoras, mediante el análisis de la curva productiva y de la productividad acumulada de la reproductora a lo largo de toda su vida, así como de su eficiencia reproductiva, utilizando técnicas de Regresión Aleatoria, modelos de supervivencia y analizando la influencia de la endogamia en dichos caracteres.

- El aumento de la resistencia al estrés térmico de los animales mediante la detección de los factores climáticos que estén dando lugar a una disminución productiva de los animales y el análisis de la base genética de una posible mayor o menor resistencia a dicho estrés ambiental, determinando nuevos objetivos y criterios de selección que produzcan individuos mejor preparados para soportar el impacto del cambio climático en las próximas generaciones.

HIPÓTESIS DE TRABAJO

Por lo tanto, la presente Tesis Doctoral tiene como hipótesis de partida que la utilización de técnicas de Regresión Aleatoria, modelos de supervivencia y el análisis de la influencia de la endogamia permitirán complementar y mejorar los resultados obtenidos con las técnicas de valoración genética clásicas. Teniendo como consecuencia una mejora del vacuno extensivo de carne en su productividad, fertilidad y resistencia al estrés térmico.

CAPÍTULO I

Capítulo I: Direct and maternal genetic effects for preweaning growth in Retinta cattle estimated by a longitudinal approach throughout the calving trajectory of the cow.

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Summary

The direct and maternal genetic effects were estimated for the preweaning growth of Retinta calves with a multitrait model across parities, using a longitudinal approach with random regression models (RRM). The 120 (P120) and 180 days (P180) weights (5972 calves) were considered as different traits in each calving. The heritability of direct effect across parities was on average 0.37 for P120 and 0.58 for P180, slightly higher than the estimates by univariate (0.30 and 0.56) and bivariate models (0.30 and 0.51, respectively). The heritability for maternal effects was 0.16 for P120 and 0.26 for P180 and very similar by uni- (0.16 and 0.23) and multivariate model (0.16 and 0.22, respectively). The correlation between direct and maternal effects by RRM showed a pronounced antagonism 0.64 for P120 and 0.78 for P180), likewise uni- (0.62 and 0.72) and multivariate case (0.64 and 0.74, respectively). The preweaning weights should be considered as different traits across parities, because the genetic correlations were different from unity. The RRM also allowed us to estimate all the parameters throughout the calving trajectory of the cow. The use of multiple traits RRM across parities can provide very useful information for the breeding programmes.

Introduction

The question of estimating the variance components for weaning weight (WW) in cattle has received considerable attention because of its importance in selection and breeding programmes of beef cattle breeds. There is lots of variations in the magnitude (and in some cases in the sign) of the direct and maternal (co)variances (r_{am}), which are the major genetic components of WW. Wilson and Réale (2006) in their meta-analysis of about 50 publications on cattle and sheep concluded that, in evolutionary terms, antagonism between the two genetic effects is a rule rather than an exception in these species.

Eler et al. (1995) argued that due to this antagonism, methods of selection accounting for both direct only on the direct genetic effects. In general, the WW usually has been evaluated using repeatability models. The models assume that WW in different calvings is a manifestation of the same trait. This implies the same (co)variance across the trajectory of the parities of the cow, and therefore, the genetic correlation of one among the weights for different calvings to. In the comprehensive analysis, Wilson and Réale (2006) concluded that it is incorrect to assume constant genetic parameters for the effects at different ages. There are not many results available on the changes of the parameters over the lifetime of the dams. Van Vleck et al. (1996) were pioneers in dealing with the topic using data from several pure beef breeds and their crosses. They concluded that no evidence could be found to indicate differences in r_{am} by the calving age of the cow. By contrast, Okut et al. (1999) showed in sheep that the early growth traits of lambs with respect to different ages or parities of the dam should be considered as separate positively correlated traits. The articles above are based on animals under experimental conditions, where the management and feeding are fairly uniform, and the results could well be different for animals and native breeds under extensive production systems.

The estimates of r_{am} are affected by both the models used and the data structure (Robinson, 1996; Clément et al., 2001; Heydarpour et al., 2008). Koch (1972) showed that a direct-maternal environmental covariance can cause bias in the estimated genetic parameters, when it is ignored or assumed to be zero. To avoid this problem, it is possible to fit a correlation structure in the residual; however, computational complexity is then substantially increased. Therefore, Eaglen et al. (2012), to avoid this potential bias caused by correlated residuals, remove from the data all individuals that appeared as both calf and dam. They reintroduced the animals and the analyses were repeated to evaluate the bias.

Most of the publications concerning beef cattle have been made using breeds widely spread in the world, such as Angus, Hereford, Charolais and Limousin, all of which have been subjected to intensive breeding programmes.

Native breeds are characterized by robustness and adaptation to adverse environmental conditions. There are not many studies on the genetic variation in native breeds from the view point of integrating them into breeding programmes. Maternal effects (and direct-maternal covariance) are increasingly important in genetic improvement in these breeds; for example, Baro et al. (2012) and Gutierrez et al. (1997) carried out studies based on the genetic parameters of maternal traits in hardy breeds like Asturiana de la Montaña and Asturiana de los Valles respectively, assuming that the traits in different calvings are manifestations of the same characteristic. A good example of a hardy breed is the Retinta. It is the main maternal Spanish breed, with a census size of over 200 000 breeding cows and is a prototype breed reared in the Southwest Spain. The animals are raised under the extensive regime of the Dehesa ecosystem, with marginal pasturelands and severe climate. Using the breed as a maternal breed to cross with other breeds like Charolais and Limousin takes full advantage of the high maternal ability yielding profitable crosses.

The main objective of this study was to determine by random regression models (RRM), the change pattern of covariance components in the Retinta breed for direct and maternal genetic effects across the trajectory over the calvings for the live weight of the calf recorded at 4 and 8 months of age and to compare these results to those obtained with the classic univariate models (UVM) and bivariate models (MTM).

Material and methods

The Retinta breed has a selection nucleus with the systematic recording, which has been in use for over 20 years. We used the live weight at 180 days of age (P180) as equivalent to WW. We also used the live weight at 120 days (P120), because the growth of the calf at this age is highly influenced by maternal effects. In the database, altogether 16 401 adjusted live weight records for P120 and P180 were available on calves born between 1990 and 2009 in total of 48 herds. We selected data from the 14 herds participating in the breed improvement programme chosen to maximize the completeness of the production and reproduction records and the genetic links between the herds (achieved using insemination with connecting sires). Calving records without one of the reference weights or records outside the range of 3 standard deviations from the average were excluded. Finally, only the first six calvings of the cows were used. This left a total of 5972 calves with 1680 dams and 129 sires. Of these, 47.7% of mothers and 42.6% of sires were represented in the data vector, which determined an acceptable structure to contribute to the general objectives of this study. The pedigree was extended to include all the available information in the breed database comprising in total 7014 animals.

The data were analysed using three different statistical models. Firstly, two repeatability animal models were used, in which (co) variance components are assumed to be the same across the parities the dam. The dependent variables P120 and P180 were analysed using a univariate (UVM) and multivariate (MTM) animal model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{CN}_{j} + \mathbf{Z}_{1}\mathbf{a}_{d} + \mathbf{Z}_{2}\mathbf{a}_{m} + \mathbf{Z}_{3}\mathbf{p}_{c} + \mathbf{e}$$

where y is the vector of records of P120 and P180 on a calf, b is a vector of fixed effects with incidence matrix X and includes the effects of combined herd-year-season of calving with 433 levels, sex of the calf with two levels, and the jth parity effect (CN) of the dam with six levels (CN_j, j = 1,2,…6 or more calvings). The terms a_d and a_m are sets of random effects caused by (possibly correlated) direct and maternal genetic effects, respectively, and p_c are the random maternal permanent environmental effects. The elements Z_1 and Z_2 are incidence matrices of ‘n’ dimension (number of animals with records and ancestors without records) x t_i traits (i = 1 for P120 and i = 2 for P180). For p_c, Z_3 matrix has a dimension of c x t_i, where c is the number of cows. The term 'e' is the residual with a uniform variance for UTM and correlated for MTM. The expected (co)variance components for the MTM model can be represented by the following three submatrices:

$$V\begin{bmatrix} G_0 \\ P_0 \\ R_0 \end{bmatrix} = \begin{bmatrix} G_0 = \begin{bmatrix} \sigma^2_{d_1} & \sigma_{d_{12}} & \sigma_{d_1m_1} & \sigma_{m_2d_1} \\ \sigma_{d_{21}} & \sigma^2_{d_2} & \sigma_{d_2m_1} & \sigma_{d_2m_2} \\ \sigma_{m_1d_1} & \sigma_{m_1d_2} & \sigma^2_{m_1} & \sigma_{m_1m_2} \\ \sigma_{m_2d_1} & \sigma_{m_2d_2} & \sigma_{m_2m_1} & \sigma^2_{m_2} \end{bmatrix} \otimes A & 0 & 0 \\ 0 & P_0 = \begin{bmatrix} \sigma^2_{c_1} & \sigma_{c_{12}} \\ \sigma_{c_{21}} & \sigma^2_{c_2} \end{bmatrix} \otimes I_c & 0 \\ 0 & 0 & R_0 = \begin{bmatrix} \sigma^2_{e_1} & \sigma_{e_{12}} \\ \sigma_{e_{21}} & \sigma^2_{e_2} \end{bmatrix} \otimes I_n \end{bmatrix}$$

in which G_0 is the genetic (co)variance submatrix for direct (σ^2_d) and maternal (σ^2_m) effects for traits indicated in the subscripts ; σ_{dm} is the covariance between the direct and maternal genetic effects, all these components are multiplied by A, the numerator of the relationship matrix among all animals with records and their ancestors without records. P_0 is the submatrix of the random maternal permanent environmental effect with $\sigma^2_{c_i}$ and $\sigma_{c_{ij}}$ for variance and covariance for the single and pairs of the traits respectively, and all these elements are multiplied by $\mathbf{I}_c$ incidence matrix of the dimension c (number of cows) and t traits. R_0 is the submatrix of residual random error with variance $\sigma^2_{e_i}$ and covariance $\sigma_{e_{ij}}$ for both traits, and these elements are multiplied by $\mathbf{I}_n$ incidence matrix (number of animals and t traits), respectively. The submatrices P and R are of the order 2x2 and G_0 is of the order4x4 when the model is an MTM. For UVM, P and R will have single components and G_0 will be 2x2.

The heritability for the direct (h^2_d) and maternal effects (h^2_m) and the total heritability (h^2_t) and the correlation between the effects (r_{dm}) for each trait, were estimated using the classic formulae (Willham, 1963) for both the UVM and MTM results. The standard errors were estimated as a linear function of the corresponding components.

The third model was applied in a different statistical approach separately for each dependent variable to estimate the same genetic parameters as previously indicated, but across the trajectory of the parities of the dams by a random regression model (RRM). The RRM model can be represented as follows:

$$y = Xb + \sum_{r=0}^{1} \Phi_1 \beta_{1_r} CN_j + \sum_{r=0}^{1} \Phi_2 \beta_{2_r} a_d + \sum_{r=0}^{1} \Phi_3 \beta_{3_r} a_m + Z_3^* p_c + e$$

In this model Xb has the same meaning as previously indicated, and the parity effects were considered as a continuous variable expressed in a standardized form between -1 and +1. They were modelled by a fixed regression β_1 Legendre polynomial of order r =1, which represents the response curve of the population for P120 and P180 across the trajectory of jth CN of the cows. The terms $\beta_2\, a_d$ and $\beta_3\, a_m$ are sets of random regression genetic effects of order r =1, for direct and maternal genetic effects, respectively, and are assumed to be correlated. The total effect for the Legendre polynomial factors are estimated by the addition of the intercept and slope multiplied by the corresponding polynomial coefficients. While in this RRM, the genetic (co)variance components for each trait are estimated in a longitudinal way along the calving trajectory of the cows, the random maternal permanent environmental effects ($Z_3^* p_c$) are a transversal factor because they are expressed only in the set including all the calvings of the cows, with variance σ_c^2 and $Z_3^* = I_c$ as the incidence matrix. The term e is the homogeneous residual variance σ_e^2 with I_n as the incidence matrix. Based on LogL, BIC and AIC information criteria, a similar model, with six levels for heterogeneous residual variance (one for each calving number), did not improve the adjustment of the model. In this RRM model, the incidence matrices are $\Phi_1 = \Phi_2 = \Phi_3$, which contain the coefficients of Legendre polynomial (Φ) of order 1 as elements. The expected (co)variance components in this RRM model are:

$$v\begin{bmatrix} G_0 \\ P_0 \\ R_0 \end{bmatrix} = \begin{bmatrix} G_0 = \Phi_i * \begin{bmatrix} A \otimes K_d & A \otimes K_{dm} \\ A \otimes K_{md} & A \otimes K_m \end{bmatrix} * \Phi_i' & 0 & 0 \\ 0 & I_c \sigma_p^2 & 0 \\ 0 & 0 & I_n \sigma_e^2 \end{bmatrix}$$

in which the meaning of $I_c \sigma_p^2$ and $I_n \sigma_e^2$ were described previously. The solution of this RRM model provides a complex G_0 matrix composed of different **K** submatrices for genetic effects σ_d^2, σ_m^2 with the covariance σ_{dm}. As in the MTM, all these components are multiplied by A, the numerator of the relationship matrix among all the animals with records and their ancestors without records. The $\mathbf{K_d}$ and $\mathbf{K_m}$ submatrices are composed of an intercept (int), a slope (coef) and a covariance (int,coef) for direct and genetic maternal effects. In general:

$$K_i = \begin{bmatrix} \sigma_{int}^2 & \sigma_{int,coef} \\ \sigma_{coef,int} & \sigma_{coef}^2 \end{bmatrix}$$

The elements of the $\mathbf{K_{dm}}$ submatrix are the covariance between int and coef for each genetic effect.

Following the procedure presented by Jamrozik and Schaeffer (1997), the (co)variance for direct and maternal genetic effects at calving j can be estimated by:

$$\sigma^2_{dj} = \Phi_{dj} K_d \Phi'_{dj}$$

$$\sigma^2_{mj} = \Phi_{mj} K_m \Phi'_{mj}$$

$$\sigma_{dmj} = \Phi_{dj} K_{dm} \Phi'_{mj}$$

Following this procedure and using the corresponding (co)variance components, the heritability for the direct ($\mathbf{h^2_d}$), maternal ($\mathbf{h^2_m}$) and total heritability ($\mathbf{h^2_t}$) effects, as well as the correlation between both effects ($\mathbf{r_{dm}}$), can be estimated for P120 and P180 in each calving.

The solution from UVM and MTM can be used to estimate breeding values (EBV$_i$) of all the animals for each dependent variable. For the results of RRM, it is necessary to apply further analysis: for example, for the ith animal, its EBV for the second calving will be:

$$\mathbf{EBV^i_{j2}} = \Phi_{j2} \mathbf{a'_i}$$

In this formula, Φ_{j2} are the coefficients of the polynomial corresponding to the 2nd calving (0.707 -0.980) and a$_i$ is the vector of the genetic function (linear equation) of animal i, which consists of an intercept (i.e. general genetic level) and a slope (i.e. the specific genetic level of the animal), to increase or decrease its EBV as the CN increases. In the formula, only the Φ_j coefficient varies, since a$_i$ is the same for each animal. According to this approach, each animal will not have a uniform EBV, as it will depend on the calving number of the cows. Note that in UVM or MTM, this differentiation is not made. RRM is more complex than UVM and MTM and requires more computer resources, but it provides very useful information, as we will present later.

The correlations (r$_{BV}$) between the EBV estimated following the official procedure (e.g. MTM BLUP) and the EBV estimated by RRM in each calving of the cow, for both dependent variables, were estimated.

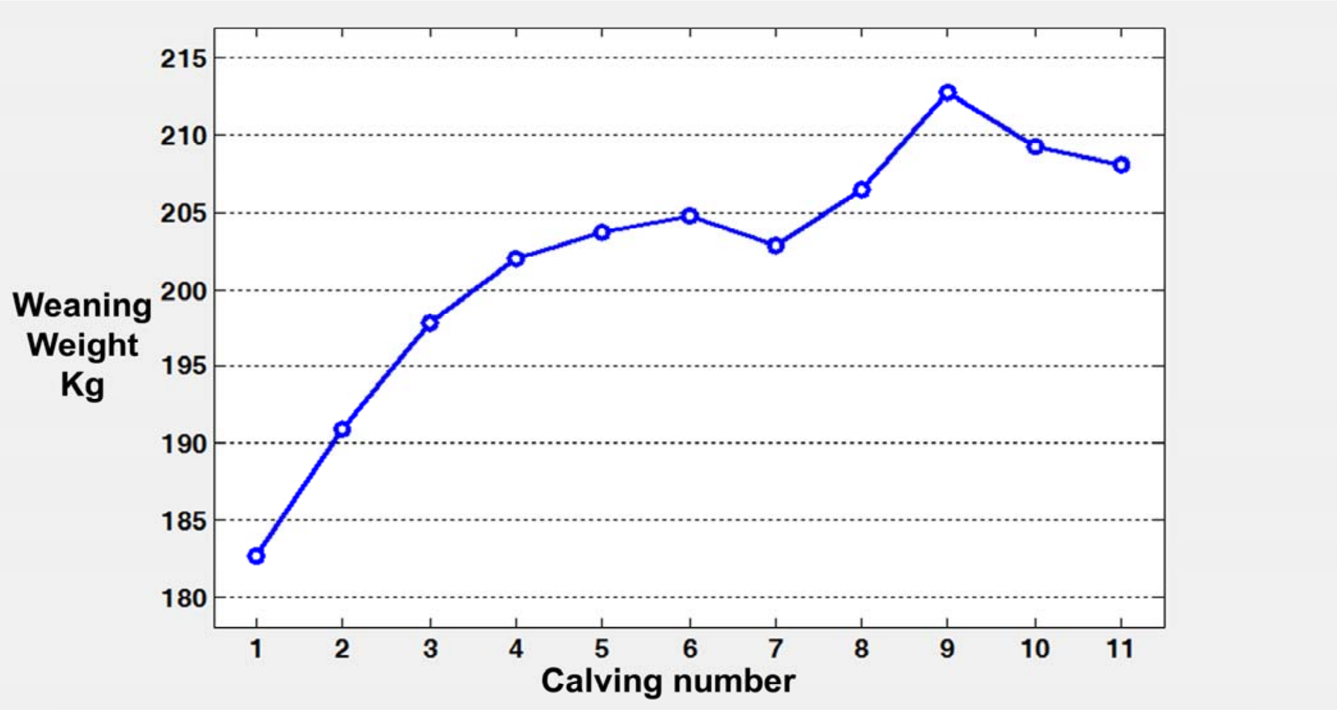
Finally, the r$_{BV}$ for P180 for direct and maternal genetic effects obtained by RRM for each calving were subjected to a principal components analysis. The corresponding eigenvalues (λva) and eigenvectors (λve) were estimated for the resulting matrices (6x6 each) for both genetic effects. To illustrate the possibilities of RRM, the top 500 animals were selected according to their EBV for direct and maternal genetic effects, estimated by the official method (MTM BLUP), and these were compared with the EBV of the same animals estimated by the RRM across the CN of the cow.

All the statistical analyses were carried out using the ASReml software (Gilmour et al., 2009b).

Results

The Retinta cow weaned a calf of 199.9 (±32.8) kg at 187 (±45) days (average daily gain of about 1 kg for male calves and over 900 g for female calves). Male calves were heavier than females (+14.2 kg and +22.8 kg for P120 and P180, respectively). The Retinta breed apparently showed a special pattern of maturity, with a sharp increase in WW (P180) of their progeny as the CN increased (Figure 1), until it reached a maximum at the 9th calving, although the main increase was achieved by the 6th calving (+12.1%, compared with the first calving). The evolution from the seventh calving onwards was influenced by the fact that a large number of cows had been discarded, and only the most efficient in reproduction traits had been kept. This was the reason why the parities from the sixth onwards were treated as one level in the model.

Figure 1. Effects of calving number on live weight at 180 days in Retinta breed.



Univariate and multivariate models

The results of the variance components and genetic parameters for the UVM and MTM models are presented in Table 1. The estimated parameters for both models were very similar for each dependent variable. The variance components for P180 were almost three times higher than those for P120, and h_d^2, h_m^2, and h_t^2 estimates were also higher in P180 compared to P120. The h_d^2 was higher than the h_m^2 for both traits. Proportionally the maternal components were higher for P120 than for P180. For P120, the variances for direct effects were 1.8 times higher than the maternal effects, whereas for P180, they were almost 2.4 times higher.

The results for the correlation between direct and maternal effects (r_{dm}) showed the classic antagonism between direct and maternal genetic effects in both models and traits. The antagonism was more evident for P180. The genetic correlations between P120 and P180 were 0.80±0.10 for direct effects and 0.88±0.11 for maternal effects (results not shown). Finally, the antagonism between the direct effects for one characteristic and the maternal effects for the other were also negative and of the same magnitude as the ones shown in Table 1.

Table 1. Variance components and genetic parameters[1] for live weight at 120 and 180 days in Retinta breed estimated by Univariate (UVM) and Multi-trait (MTM) animal models.

Model	σ_d^2	σ_m^2	σ_{dm}	σ_t^2	h_d^2	h_m^2	h_t^2	r_{dm}
	Live weight at 120 days of age							
UVM	132.8	69.8	-69.8	446.9	0.297	0.156	0.180	-0.625
MTM	136.6	71.5	-63.3	447.9	0.305	0.159	0.208	-0.640
	Live weight at WW (180 days of age)							
UVM	483.7	196.6	-221.6	855.8	0.565	0.230	0.356	-0.718
MTM	465.0	202.7	-226.0	909.0	0.511	0.223	0.312	-0.736

[1] σ_d^2; σ_m^2, and σ_{dm} are variance components for direct and genetic effects and their covariance; σ_t^2 are the total variance; h_d^2; h_m^2, and h_t^2 are heritabilities for direct, maternal, and total effects respectively and r_{dm} is the genetic correlation between both effects.

Random Regression Model.

There were some differences between the averaged variance components of RRM expressed for each calving (Table 2 and Table 3) and those estimated by UVM and MTM (Table 1). Except for the σ^2_t for P120, the remaining variance components and genetic parameters of the two dependent variables were higher than those presented in Table 1. The antagonism estimated between direct and maternal genetic effects was also higher (more negative) in the RRM.

Table 2. Variance components and genetic parameters[1] for live weight at 120 days across the calving number of the cow in Retinta breed, estimated by Random Regression Model.

CN	σ_d^2	σ_m^2	σ_{dm}	σ_t^2	h_d^2	h_m^2	h_t^2	r_{dm}
1	171.3	52.7	-46.6	456.7	0.375	0.115	0.305	-0.490
2	139.7	54.5	-49.6	423.7	0.329	0.128	0.247	-0.568
3	131.2	61.2	-58.4	413.3	0.317	0.148	0.215	-0.651
4	145.9	72.8	-72.9	425.1	0.343	0.171	0.214	-0.707
5	183.8	89.1	-93.1	459.1	0.400	0.194	0.243	-0.727
6	244.9	110.3	-119.0	515.5	0.475	0.214	0.293	-0.724
Average	169.5	73.4	-73.3	448.9	0.373	0.161	0.253	-0.645

[1] σ_d^2; σ_m^2, and σ_{dm} are variance components for direct and genetic effects and their covariance; $\sigma_t^2=\sigma_d^2+\sigma_m^2+\sigma_{dm}+\sigma_c^2+\text{residual}$; h_d^2; h_m^2, and h_t^2 are heritabilities for direct, maternal, and total effects respectively and r_{dm} is the genetic correlation between both effects.

The ratio of variances between direct and maternal genetic effects for P120 throughout the calving trajectory of the cow decreased from the first calving (minimum importance of the maternal effects) to the third (maximum importance of the maternal effects), and then increased until the sixth calving. The trajectory of the variance components and genetic parameters for P120 (Table 2) increased clearly for σ^2_m, σ_{dm} and h^2_m over parities. The other parameters have a different pattern: at the beginning, they decreased from the 1st to 3rd parity, and then they increased until the sixth calving. For P180 (Table 3), the evolution of the variance components and genetic parameters showed a U-shaped pattern, which is typical when Legendre polynomials are used. The antagonism between direct and maternal genetic effects reached the highest values (more negative) in the last calving analyzed (CN_6).

Table 3. Variance components and genetic parameters[1] for live weight at 180 days across the six first calving of the cow in Retinta breed, estimated by Random Regression Model.

CN	σ_d^2	σ_m^2	σ_{dm}	σ_t^2	h_d^2	h_m^2	h_t^2	r_{dm}
1	560.7	204. 9	-257.4	892.0	0.628	0.229	0.382	-0.759
2	459.2	173.0	-207.0	809.0	0.567	0.213	0.354	-0.734
3	410.1	169.9	-194.4	769.3	0.533	0.220	0.327	-0.736
4	413.4	195.4	-219.4	773.2	0.534	0.252	0.306	-0.772
5	469.3	249.6	-282.1	820.5	0.571	0.304	0.294	-0.824
6	577.6	332.5	-382.6	911.3	0.633	0.364	0.291	-0.873
Average	481.7	220.9	-257.2	829.2	0.578	0.264	0.326	-0.783

[1] σ_d^2; σ_m^2, and σ_{dm} are variance components for direct and genetic effects and their covariance; $\sigma_t^2 = \sigma_d^2 + \sigma_m^2 + \sigma_{dm} + \sigma_c^2$+residual; h_d^2; h_m^2, and h_t^2 are heritabilities for direct, maternal, and total effects respectively and r_{dm} is the genetic correlation between both effects.

The ratio of variances between direct and maternal genetic effects for P180 throughout the calving trajectory of the cow decreased from the first calving (minimum importance of the maternal effects in relation to the direct effects) until the sixth (maximum importance of the maternal effects).

The genetic correlations for either direct or maternal genetic effects across calvings are shown in Table 4 (P120) and Table 5 (P180). All of them were positive. Therefore, selection made at any calving will have a positive impact throughout the rest of the productive life of the cow, particularly between adjacent calvings (the wider apart the parities are, the lower are the correlations).

Table 4. Correlation for genetic direct effects and for genetic maternal effects on live weight at 120 days across the calving number (CN_i) of the cows in Retinta cattle estimated by Random Regression Model.

	CN_1	CN_2	CN_3	CN_4	CN_5	CN_6
CN_1		0.967	0.854	0.673	0.478	0.309
CN_2	0.977		0.957	0.838	0.684	0.538
CN_3	0.917	0.980		0.959	0.865	0.758
CN_4	0.836	0.933	0.985		0.971	0.911
CN_5	0.751	0.873	0.951	0.990		0.983
CN_6	0.671	0.812	0.910	0.967	0.993	

Table 5. Correlation for genetic direct effects and for genetic maternal effects on live weight at 180 days across calving number (CN_i) of the cows in Retinta cattle estimated by Random Regression Model.

	CN_1	CN_2	CN_3	CN_4	CN_5	CN_6
CN_1		0.979	0.902	0.766	0.594	0.423
CN_2	0.965		0.971	0.880	0.745	0.599
CN_3	0.850	0.958		0.968	0.882	0.772
CN_4	0.677	0.845	0.963		0.972	0.906
CN_5	0.497	0.706	0.879	0.975		0.980
CN_6	0.342	0.575	0.785	0.922	0.985	

The positive trends mentioned above might be cancelled out if the found existence of antagonism between direct and maternal genetic effects, also described above, is not taken into account. The antagonism was observed both with the repeatability model across calvings (Table 1), and with considering each calving of the cow separately (Table 2 and Table 3), or analysing the relationship pattern across calvings. There are details on r_{dm} levels given in the supplementary Tables A and B. These showed the consistency with respect to negative r_{dm} for both dependent variables and a contrary trend from the first to the sixth calving for P120 and P180.

Supplementary material: Table A and Table B here

<u>Estimation of the breeding values</u>

The reliability of the EBV's, shown in Table 6, was on average 0.94 for P120 and 0.85 for P180 with the highest value at CN_3. There was a similar trend for maternal effects, although the level of r_{BV} for P120 was always higher compared with that of P180.

The first eigenvalue (λva) of r_{BV} for P180 (results not shown) accounted for 90% of the variance for direct effects and 89% of the variance for maternal effects, while the second λva left a gap of around 10%. The first eigenvectors (λve) were all positive, while the second ones were negative for CN_1 to CN_3 and positive for the remaining calvings. The patterns were similar for direct and maternal genetic effects.

Table 6. Correlation between EBV estimated by the official MTM procedure (for direct and maternal effects) and the EBV of the same animals estimated by Random Regression Model across calving numbers of the cows in Retinta cattle.

	Direct Effect		Maternal Effect	
CN	P120	P180	P120	P180
1	0.785	0.811	0.927	0.832
2	0.895	0.849	0.935	0.886
3	0.943	0.861	0.935	0.889
4	0.928	0.840	0.929	0.851
5	0.874	0.788	0.922	0.793
6	0.809	0.717	0.912	0.732
Average[1]	0.942	0.855	0.932	0.873

[1]Average correlation across calving numbers

Supplementary material

Table A. Correlation between genetic direct effects and genetic maternal effects on live weight at 120 days across calving number (CN_i) of the cows in Retinta cattle estimated by Random Regression Model.

	CN_1	CN_2	CN_3	CN_4	CN_5	CN_6
CN_1	-0.490	-0.522	-0.530	-0.521	-0.502	-0.479
CN_2		-0.568	-0.609	-0.625	-0.625	-0.616
CN_3			-0.651	-0.696	-0.717	-0.724
CN_4				-0.707	-0.748	-0.770
CN_5					-0.727	-0.761
CN_6						-0.724

Table B. Correlation between genetic direct effects and genetic maternal effects on live weight at 180 days across calving number (CN_i) of the cows in Retinta cattle estimated by Random Regression Model.

	CN_1	CN_2	CN_3	CN_4	CN_5	CN_6
CN_1	-0.759	-0.741	-0.662	-0.537	-0.404	-0.289
CN_2		-0.734	-0.714	-0.640	-0.543	-0.451
CN_3			-0.736	-0.726	-0.677	-0.617
CN_4				-0.772	-0.776	-0.753
CN_5					-0.824	-0.838
CN_6						-0.873

Discussion

There are still relatively few studies on genetic parameters with random regression models in autochthonous beef cattle. Most of the studies on the genetic variation of production traits by UVM or MTM have implemented a transversal approach with repeatability model.

We have analyzed the direct and maternal genetic effects for pre-weaning growth in Retinta calves using a longitudinal approach across the CN. The results with RRM show that simpler models could produce biased results and therefore, the trait should be analyzed longitudinally likewise in dairy cattle where different lactations are treated as separate although correlated traits (Thompson et al., 2005). The RRM may also provide a more suitable model for environmental effects. (Molina et al., 2007) identified in the Merino sheep by RRM a substantial genetic variation, not only in the general breeding values but also in the shape of the lamb growth curve. Such an analysis will therefore provide more information to breeders in selecting animals that better fulfill the market requirements in slaughter age and weight. According to (Nobre et al., 2003), RRM could be useful in beef cattle genetic evaluation because weights at any age can be used, and expected genetic differences can be predicted for any age.

In biological terms, the results on growth can be explained by the maturation rate. The genetic basis of the topic received considerable selection. Despite its importance very little attention has been given attention in the mid 1970's and Fitzhugh Jr (1976) shows the properties of the methods for modifying the growth curve by to this, although the magnitude of these effects has been well illustrated by Norman et al. (2005) in the evaluation of the U.S. Holstein sires.

The genetic parameters estimated by the three models were similar in our study reflecting the statistical properties of the models (Van Der Werf et al., 1998). This is also true for the reliabilities of EBV's (last row of Table 6). The RRM can extract more information from the available data and is providing specific breeding values at any calving of the cow. Compared to the official methods (BLUP MT), RMM offers the possibility of identifying different types of response across the calving trajectory of the cows. Some cows maintain the same production level throughout their productive life, while others experience changes.

Due to its superior modelling of variances and genetic parameters, RMM requires a better data structure and better links between the production units, and may produce abnormal results with problematic data (Nobre et al., 2003). Models in beef cattle may be more complicated than in dairy cattle, because of correlated direct and maternal effects.

The estimates of h^2 for direct and maternal genetic effects were relatively high and within the range expected from the study by (Molina et al., 1999) for this breed. The results were also similar to those of the rustic breeds with no intensive breeding program, a relative low number of animals and exploited in specific geographical regions of Spain (Gutierrez et al., 1997; Menéndez-Buxadera et al., 2008; Baro et al., 2012).

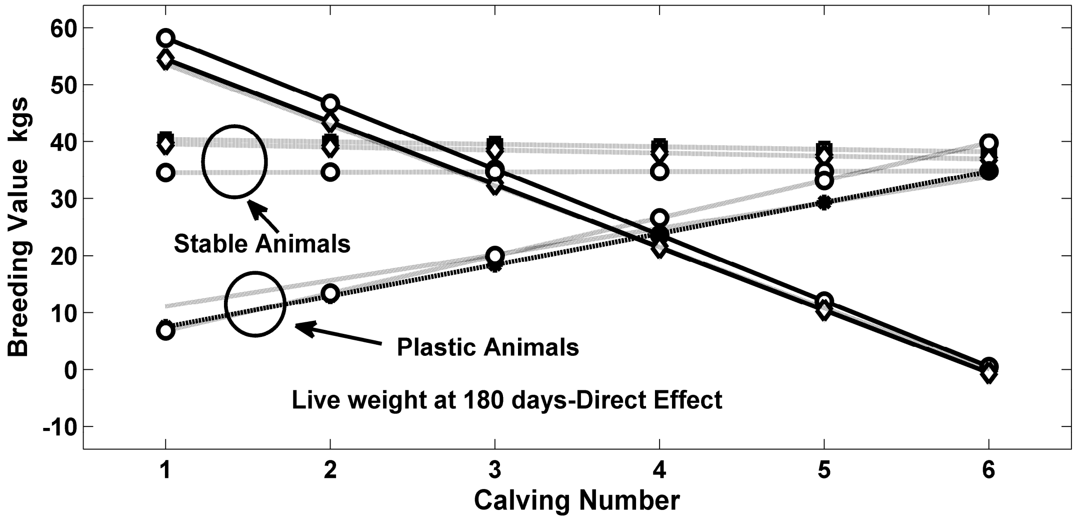
The coefficient of the total additive genetic variation ranged from 10.2% and 12.2% for P120 and P180, respectively, indicating a wide range of possibilities for the improvement of these traits. These are slightly lower than in other Spanish breeds (Gutierrez et al., 1997; Menéndez-Buxadera et al., 2008). Because of the positive genetic correlations any selection based on P120 and P180 would have a positive impact throughout the productive life of cows. However, the greater the difference between calving numbers is, the lower is the correlation.

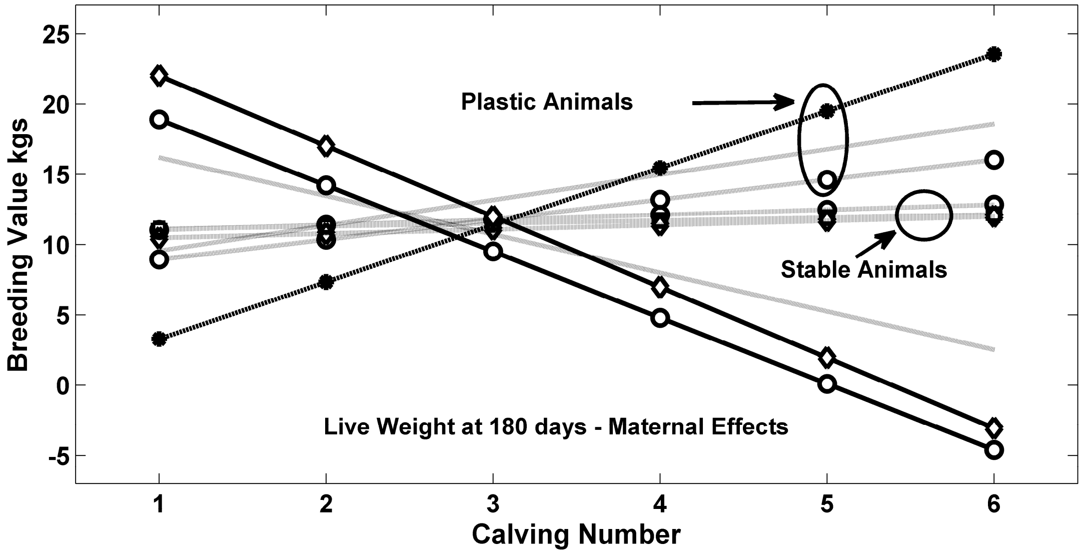
Our results were also consistent about a marked antagonism between direct and maternal genetic effects, which needs attention in selection. The literature on this subject is abundant and controversial covering the entire possible range of values. The observed antagonism could be due to a bias produced by, for example, an environmental link between maternal effects of cows and their female offspring (Meyer, 1992; Robinson, 1996; Quintanilla et al., 1999). In addition, the data structure has been suggested as one of the causes of the negative covariance (Clément et al., 2001; Heydarpour et al., 2008). In our data, 45% of the parent animals were represented in the vector of phenotypic values, suggesting that the data structure would not affect the general pattern of the negative relationship between direct and maternal genetic effects found in our study. In addition, it was found that the antagonism decreased as the CN increased, especially for P180.

More recent studies, like the meta-analysis published by Wilson and Réale (2006) concluded that the antagonism between direct and maternal genetic effects is real. The studies on cattle raised in restricted environmental conditions and with no intense selection programs, also reveal a negative r_{dm} (Nobre et al., 2003).

In the correlation matrix for EBV throughout different calvings of the cow, the first λva accounted for about 90% of the variance for direct and maternal genetic effects, while the second λva accounted for 10%, which might indicate possible changes in response along the calvings of the cow. The coefficients of the first eigenvector (λve) can be interpreted as a general size vector, uncorrelated with the second λve, which represents a vector form. If selection favours one of the eigenvectors, it will bring about significant changes in the shape of the growth curve (Kirkpatrick et al., 1990). For the top 500 animals were selected according to their EBV, estimated by the official method (MTM BLUP) the EBV evolutions throughout the calving trajectory were analyzed by the RRM. From the group, 18 animals which showed different type of response across calvings of their dams for direct and maternal genetic effects for WW are represented in Figure 2.

Figure 2. Different types of animals across the parities of the dams for direct and maternal genetic effects for weaning weight in the Retinta breed.





The nine animals represented in the top part of the Figure 2 do not differ from each other (with an average EBV of around +38 kg for direct effects estimated by MTM and RRM). In addition, in the lower part of Figure 2, nine animals selected on the EBV for the maternal effects (EBV≈ +15 kg) are shown. This is the only information that can be obtained by MTM, and any of them could be selected to be parents in the next generation. However, when the changes in EBV obtained by RRM are taken into account, two types of animals can be identified:

- **Stable animals.** Stable performance over the whole trajectory, as a consequence of an intermediate genetic merit for the intercept and the slope.
- **Plastic animals.** Low genetic level for the intercept but high genetic ability to increase their potential (high slope) as long as the CN increases.

The curves are consistent for the first and second λve. This information can prove very useful the terms of the breeding objectives as it can provide specific EBV for each animal along the time scale (in our case, the calving number). An example on such differences was presented by Menéndez-Buxadera et al. (2008) in the Asturiana de los Valles breed. Breeders may select stable animals to ensure a reasonable level of productivity along the productive life of the cow, while others can select for faster profits, with animals which are extremely productive in the first few years, but are quickly disposed of when their productivity decreases in later several calvings.

Meyer and Kirkpatrick (2005) have provided many arguments about the advantages of the longitudinal approach for the traits whose variation and importance varies over time or environment, defined by Meyer and Kirkpatrick (2005) as Function Value Traits (FVT). Deland and Newman (1991) argued that the lifetime productivity of cows is an important consideration in cow–calf production, because the costs of maintaining breeding animals per progeny produced decreases with increasing numbers of progeny (calving number). With RRM, animals could be selected according to production system focussing on plastic animals. In the same way, Martinez et al. (2004b) reported how the longer productive life may increase profits by decreasing the annual cost of replacing cows, increasing herd production through an increase in the proportion of cows in higher-producing age groups, decreasing the number of replacements to be reared, and increasing voluntary culling. These arguments have been supported by Balieiro et al. (2008), who argued that the length of productive life and reproduction traits of a cow are complex traits that directly affect the profitability and efficiency of production systems, because the characteristics are positively correlated with the number of calves obtained per cow. They also stated that selection for these traits would be possible although with moderate response due to low heritability (0.04-0.05). Our results show that the Retinta cow performed acceptably well, weaning a calf whose WW represented approximately 36% of its live weight.

The use of genetic evaluation based on RRM introduces a flexibility that allows some breeders to select stable animals to ensure a reasonable level of productivity along the productive life of the cow, while others opt for faster profits, with animals which are extremely productive in the first few years, but are quickly disposed when their productivity decreases in later calvings.

Conclusion

The results with the three different statistical models are consistent, and allow us to identify an important additive genetic variability in Retinta breed animals that can be used to enhance its breeding program. However, the possibilities cannot be fully exploited because of the major antagonism between direct and maternal genetic effects throughout the cows' productive life. The correlations between breeding values estimated by the three models were high (over 0.85). The longitudinal approach with RRM revealed a wide variation in the EBV's along the trajectory of different calvings of the cows. The methodology is very useful for genetic evaluation, providing more information with the data available, which makes it possible to differentiate the cows' genetic potential throughout the calving trajectory and yield for greater flexibility in selecting female breeders according to the desired replacement rate.

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CAPÍTULO II

Capítulo II: Breeding beef cattle for an extended productive life: Evaluation of selection criteria in the Retinta breed.

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Summary

We characterized genetically the longevity and the productive life of beef cows considering three different traits, length of true life (LTL), length of productive life (LPL) and number of calvings (NC), in Retinta breed. Data considered in the analysis were collected in 30 Spanish herds and consisted of 3,187 cows born between 1993 and 2013: 1,802 cows had complete carriers while 1,385 cows had censored information. Pedigree information accounted for 7,359 individuals and the genetic evaluation was performed under an animal model using the Weibull proportional hazard model in a survival analysis. Results indicated that cow effects (age at first calving, herd, season-year of cow birth) as well as some calf effects (breed, season-year of birth) were significant ($P<0.05$) for all traits; however, sex of calves did not affect the traits. The heritabilities obtained were very moderate for LTL and LPL (0.14 ± 0.01 and 0.14 ± 0.01 respectively) and more significant for NC (0.30 ± 0.01). These results suggest that an elevated response to selection to increase the productive life in this autochthonous breed can be expected for NC trait due to its high heritability.

Keywords: Beef cattle, Functional longevity, Survival, Weibull.

Introduction

The lifespan of livestock females is divided into two well-differentiated parts: (i) the period from birth to first parity, in which their economic return is zero, and (ii) the productive period, from their first calving to their disposal. This second period, in which the individual effectively produces and generates an economic income, is commonly called longevity (Essl, 1998). In general, beef breeding programs are focused to increase live weight or short-term weight gain in order to produce more meat kilograms per individual. However, it has hardly been studied how those criteria affect cow longevity. Cow longevity is an economically important trait directly related to the productive efficiency and meat yield in beef production systems (Van Melis et al., 2007a). A shorter productive life of the cows forces to keep more heifers in the herd for replacement (Lopez de Maturana et al., 2007) and decreases the possibility of obtaining a higher number of calves during the cow productive life. As a result, the costly period from birth to first parity will be best amortized in cows with an increased longevity because the cost per weaned calf will decrease proportionally (Dákay et al., 2006). The inclusion of this trait in beef cattle breeding programs would allow selecting heifers with an increased chance of remaining in the herd for a longer period of time and, at the same time, farmers would be able to determine the age of culling depending on their breeding objectives (Caetano et al., 2013).

The cow longevity is a highly significant trait in Retinta, an autochthonous breed widely utilized in the Southwest of the Iberian peninsula. Nowadays, its census is slightly over 200,000 breeding cows, which are reared under the extensive regime of the Dehesa ecosystem, characterized by marginal pasturelands and dry and hot climate (Serrano et al., 1992). Although purebreeding is largely preserved in Retinta breed, the breed is also widely used in crossbreeding as a maternal line with other continental breeds, such as Charolais and Limousin, yielding highly profitable crossbred individuals. To maximize the herd profit under the extensive and low-input production systems, cows should have a long productive life to produce a large number of calves. It would be also necessary to know the economic optimum age to cull cows. From simulation studies, maximum herd lives ranging from 8 to 11 years (Rogers, 1972; Melton, 1980).

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 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). It has been widely performed in most livestock species, such as dairy cattle (Famula, 1981; Caraviello et al., 2004; Jenko et al., 2013), beef cattle (Rogers et al., 2004), pigs (Meszaros et al., 2010) and more recently in horses (Sole et al., 2017). Venot et al. (2013) carried out a study to incorporate productive live, through longevity and productive efficiency assessed by the number of calvings at a target age, in a new genetic evaluations of French beef cows. However, this analysis is still frequently overlooked in beef cattle breeding programs and despite their economic importance the number of applied studies performed to date is scarce (Rogers et al., 2004; Dákay et al., 2006; Szabó and Dákay, 2009). Similarly, there are few studies estimating genetic parameters for longevity traits in beef cattle (Tanida et al., 1988; Rogers et al., 2004; Dákay et al., 2006; Forabosco et al., 2006; Phocas and Ducrocq, 2006a; Szabó and Dákay, 2009).

One of the reasons for this lack of information is the fact that a large number of animals is still alive during the genetic evaluation and therefore, only the lower bound of their eventual productive life is known (censored information). The exclusion of these records from the evaluation or their incorrect use as definitive values would lead to biased results (Raguž, 2014). This problem could be corrected using survival analysis (Ducrocq, 1997). This methodology combines the information on dead (uncensored) and alive (censored) individuals, and enables a proper statistical treatment of censored records by accounting for nonlinear characteristics of longevity data (Vukasinovic, 1999). In dairy cattle, the length of productive life (LPL) has been defined as the number of days from first calving to death or culling, having a substantial impact on the net returns of dairy production (Reinhardt, 1996). Ducrocq (1994) defined two types of LPL: true LPL is the ability of a cow to avoid culling no matter the reasons, being estimated as the period of elapsed time between first calving and disposal of the cow; functional LPL is the ability of a cow to avoid involuntary culling, and corresponds to LPL corrected for the level of production. True LPL is strongly related to the production performance of the cow. On the contrary, functional LPL is more related to the ability of the cow to avoid non-productive causes of culling, such as infertility, mastitis, lameness or any other disease.

The more accurate and widely used model in the genetic evaluations for this trait is the Weibull proportional hazard models (Sewalem et al., 2005; Mészáros et al., 2008; Bonetti et al., 2009; Strapáková et al., 2013). Due to a lack of exhaustive recording of reproduction records and cow presence inventory in beef cattle herds, the number of longevity studies of native breeds is very limited and integration of longevity as selection criteria into beef cattle breeding program is scarce.

Herein, we performed the genetic characterization of the productive life of Retinta breed cattle analyzing three different selection criteria (LTL, LPL and NC) as measures of longevity-related traits using a survival analysis based on the Weibull proportional hazard model.

Material and methods

We analyzed the reproductive data recorded in the selection nucleus of the Retinta breed. Data were collected between 1995 and 2016 by the National Retinta Breeders Association. A total of 31,639 calving records from 6,212 cows belonging to 30 genetically linked herds were available. Genetic links were due to the use of artificial insemination sires that connected the 30 herds. Data were initially filtered following two standardization criteria: 1) only cows whose age at first calving ranged between 20 and 42 months were considered in the analysis, and 2) cows whose calving records fell outside the ± 3 SD range from the average calving interval were excluded. After editing, 16,100 calving records from 3,187 dams and 398 sires were considered in the analysis. Pedigree of the cows was extended to include all the available information in the stud book breed database (7,359 animals). The cows were classified as presenting uncensored (dead) or censored (alive) records. Right-censored data (43.46%) included animals alive or with an unknown status at the time of analysis and less than 3 years since the last calving. Our dataset did not present left-truncated records because only cows born in or after 1993 with calvings started after 1994 (at the age of 2 or more years) were included.

Beef cattle longevity was evaluated using three different productive traits: length of true life (LTL), estimated as the number of months between the birth of the cow and the birth of the last calf on record or censoring, LPL, estimated as the number of months between the birth of the first and the birth of the last calf on record or censoring (Meyer, 2009); and number of calving (NC), estimated as the number of calvings for each cow until its last calving or censoring time.

A preliminary analysis was performed using a Weibull hazard survival model to determine the significance of the effects included in the model using a likelihood random test with Survival Kit v6 software (Meszaros et al., 2013). The effects evaluated were *age at first calving*, *herd*, *season-year of cow birth* as time-independent effects, and *age at calving*, *calf breed*, *season-year of calving* and the *combination of sex and type of calving* (simple or twin births) as time-dependent effects. Comparisons were performed between the full model and the same model but excluding one effect each time. Only the *combination of sex and type of calving* was not significant ($P > 0.7$) and therefore, excluded from the analysis. Calving difficulty was not tested in this study since Retinta is a maternal reed in which calving problems are negligible : less than 0.2% of calvings exhibited some difficulties (MAPAMA, 2016).

All these factors potentially associated with cow longevity were analyzed with the following model:

$$h(t,x) = h0(t)exp\{ageftrst_i + herd_j + cow * year * season_k + breed_l + year * season_m + age_n + g_o f\}$$

where $h0(t)$ is the baseline hazard function, $agefirst_i$ is the time-independent effect of the age at first calving (monthly intervals from 20-26.5; >26.5-32.5; >32.5-38.5; >38.5); *Herd* is the time-independent effect of the herd (30 herds); $cow{*}year{*}season_k$ is the time-independent effect of the season combined with the year of cow birth (79 classes); $breed_l$ is the time-dependent effect of the calf breed (1= Retinta, 2= RetintaxLimousin, 3=RetintaxCharolais, 4= cross with others breeds); $year{*}season_m$ is the time-dependent effect of the season combined with the year of calf birth (83 classes); age_n is the time-independent effect of the age at calving (monthly intervals from 20-45; >45-70; >70-95; >95-120; >120-145; >145-170; >170 m.); g_o is the random animal additive genetic value.

Genetic parameters and expected breeding value (EBV) estimations were based on the Weibull proportional hazards method (Ducrocq et al., 1988). The three dependent variables (LTL, LPL and NC) were examined with the same model described above using Survival kit 6.0 (Meszaros et al., 2013). Such models are equivalent to a fully parametric model, in which the baseline is estimated at every discrete time point and the definition of hazard is modified to consider a discrete time scale (Ducrocq, 1999). A special case of proportional hazard models are the grouped data models, where failure times are grouped into intervals $A_i = [a_{i-1}, a_i)$, $i = 1 \ldots r$, with $a_0 = 0$, $a_r = +\infty$, and λ as the hazard function:

$$\lambda(t, z_i) = \lambda_0(t) \exp(z_i'\beta)$$

where $\lambda_0(t)$ is the baseline hazard function and z_i is the design vector for explanatory variables β for cow i. The last calving of the cow or censoring during the time interval A_i is denoted as t_i.

Rates of last calving risk were expressed via risk ratios, which denoted the relative risk of a cow in a certain class to end its productive life compared with cows belonging to a reference class with a risk ratio equal to 1.

The heritabilities (h^2) of the traits analyzed were estimated using the methodology described by Yazdi et al. (2002):

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

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

The reliability R^2 of each estimated breeding value (ebv) was based on the prediction error variance for each estimate as $R^2 = 1 - \frac{pev}{\sigma_a^2}$

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

Results

Table 1 shows the distribution of censored and uncensored records in each trait studied (LTL, LPL and NC). Average censoring ages after first calving 87.62 were and 54.95 months for LTL and LPL respectively; the average number of calves produced per cow was 4.71 for NC. Average failure ages after first calving were 97.23 and 65.02 months for LTL and LPL, and 5.31 calvings for NC.

Table 1. Statistical data of the different traits related to survival (LTL, LPL and NC) analyzed in the Retinta breed.

	LTL	LPL	CN
Right-censored cows	1385	1385	1385
Minimum censoring time[1]	21	0	1
Maximum censoring time[1]	212	189	16
Average censoring time[1]	87.619	54.949	4.713
Uncensored cows	1802	1802	1802
Minimum failure time[1]	22	0	1
Maximum failure time[1]	238	208	16
Average failure time[1]	97.227	65.015	5.312

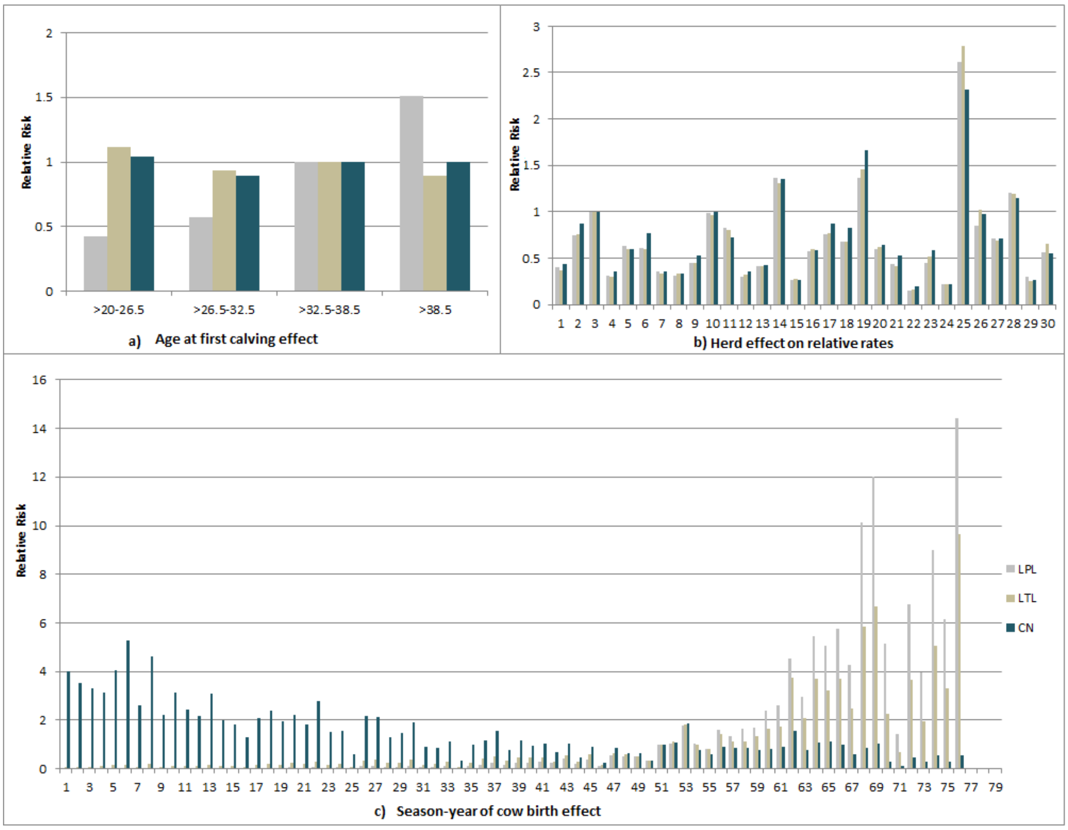
[1](months of life after for LTL, months of life for first calving for LPL and calving number for CN)

Table 2. Likelihood ratio last test statement for the different traits (LTL, LPL, and NC) in Retinta survival analysis.

	LTL				LPL				CN			
	CHI^2	Delta DF	Prob > CHI^2	R^2 Maddala	CHI^2	Delta DF	Prob > CHI^2	R^2 Maddala	CHI^2	Delta DF	Prob > CHI^2	R^2 Maddala
Age at first calving	3.101	3	0.376	0.64	147.97	3	<0.001	0.662	3.122	3	0.373	0.325
Herd	263.17	29	<0.001	0.610	242.2	29	<0.001	0.652	235.2	29	<0.001	0.279
Season-year of cow birth	183.81	75	<0.001	0.619	236.64	75	<0.001	0.652	139.8	75	<0.001	0.295
Calving age	847.69	6	<0.001	0.531	756.35	6	<0.001	0.591	83.4	6	<0.001	0.308
Calf breed	10.665	3	0.014	0.639	12.168	3	0.007	0.676	20.59	3	<0.001	0.321
Season-year of calf birth	257.82	78	<0.001	0.61	295.78	78	<0.001	0.646	179.5	78	<0.001	0.286
Time unit	1496.7	80	<0.001	0.425	2262.4	93	<0.001	0.343	29.54	16	0.021	0.319

Likelihood ratio test results for each effect included in the model are presented in Table 2. All the effects were highly significant (P<0.001) except for age at first calving in LTL and NC. It is noteworthy that higher hazard ratios for the end of productive life were observed in cows which were older at first calving (Fig 1-a). Moreover, the highest risk (1.51) was for cows whose first calving age was above 38 months, while the lowest risk (0.42) was for cows starting to calve at early ages (>20-26.5). The relative risks showed large differences among herds, which reflected the importance of this effect; these were from 0.16 to 2.78 for LTL, from 0.15 to 2.62 for LPL and from 0.19 to 2.31 for NC (Figure 1-b). There was also a wide variation in the relative risks from one to another cow birth season-year, from 0.01 to 9.65 for LTL, from 0.01 to 14.41 for LPL and from 0.01to 5.28 for CN (Figure 1-c). The highest risk for age at calving was for >170 months for the three traits and for LTL also for 20-45 months (Figure 2-a). Regarding breed of calf, the Limousine-Retinta crossbreeding showed the highest risk of failure, and the Retinta pure breeding the lowest (Figure 2-b). Relative risks based on season-year of calf birth ranged from 0.001 to 43.23 for LTL, from 0.001 to 365.83 for LPL and from 0.001to 1.82 for CN (Figure 2-c).

Figure 1. Time-independent effects expressed as hazard ratios for the different traits (LTL, LPL and NC) in Retinta survival analysis.

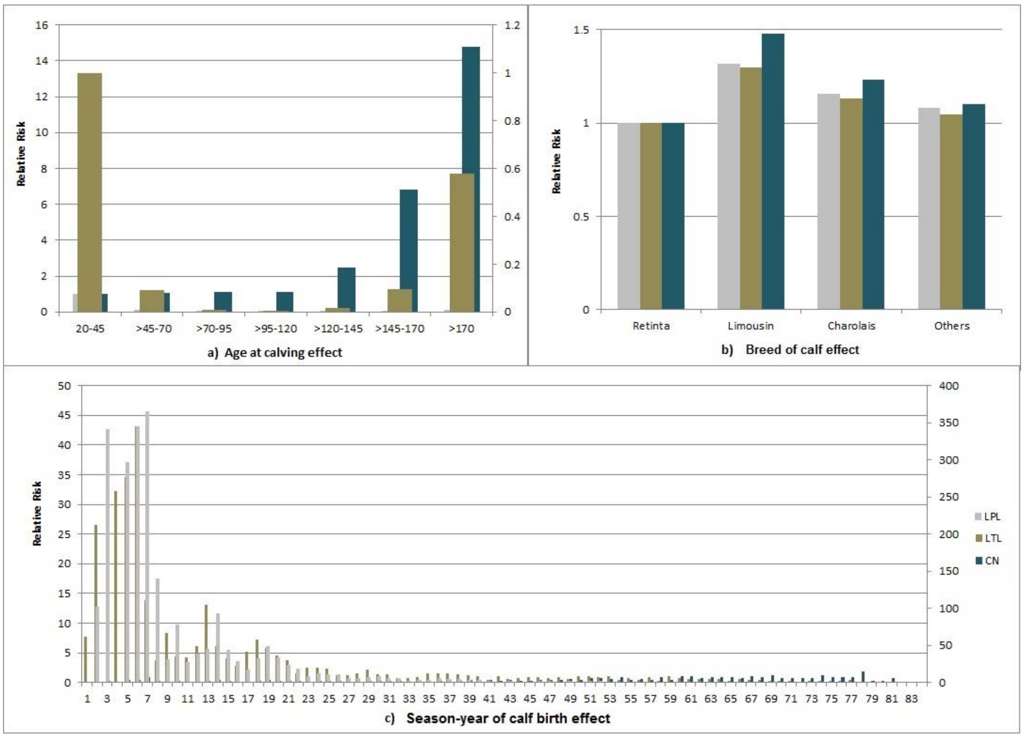


a) Age at first calving effect

b) Herd effect on relative rates

c) Season-year of cow birth effect

Figure 2. Time-dependent effects expressed as hazards ratios for the different traits (LTL, LPL and NC) in Retinta survival analysis.



Heritability, EBV averages and relative risk averages were estimated for all the traits studied (Table 3). The ebv reliability frequency distribution of the cows is shown in Figure 3. Correlations between EBV of all the pedigree animals of the three traits analyzed were very high, 0.99 for LTL and LPL, 0.97 for LTL and NC and 0.96 for LPL and NC. The standardized EBV average evolution of the cows is shown in Figure 4. A scale change has been made so that the EBV average of cow born in year 1994 takes the value of 100. A positive genetic trend was found over the 20 years of the study.

Table 3. Estimates of parameters from Weibull analyses for the different traits LTL, LPL and NC in Retinta survival analysis.

	LTL	LPL	CN
Proportion uncesored/total	0.565	0.565	0.565
Estimated adittive variance	0.292	0.292	0.292
Standard error	±0.01	±0.01	±0.01
h^2	0.142	0.142	0.302
Reliability average	0.710	0.710	0.733
Reliability average uncensored cows	0.669	0.668	0.694
Reliability average censured cows	0.765	0.767	0.783
EBV average	0.113±0.79	0.113±0.79	0.125±0.75
EBV average uncensored cows	0.167±0.77	0.159±0.77	0.120±0.73
EBV average censured cows	-0.476± 0.82	-0.467±0.83	-0.443±0.78
Risk average	1.078	1.079	1.029
Risk average uncensored cows	1.370	1.362	1.276
Risk average censured cows	0.698	0.710	0.708

Figure 3. Frequency distribution of reliability for the different traits (LTL, LPL, and NC) in Retinta survival analysis.

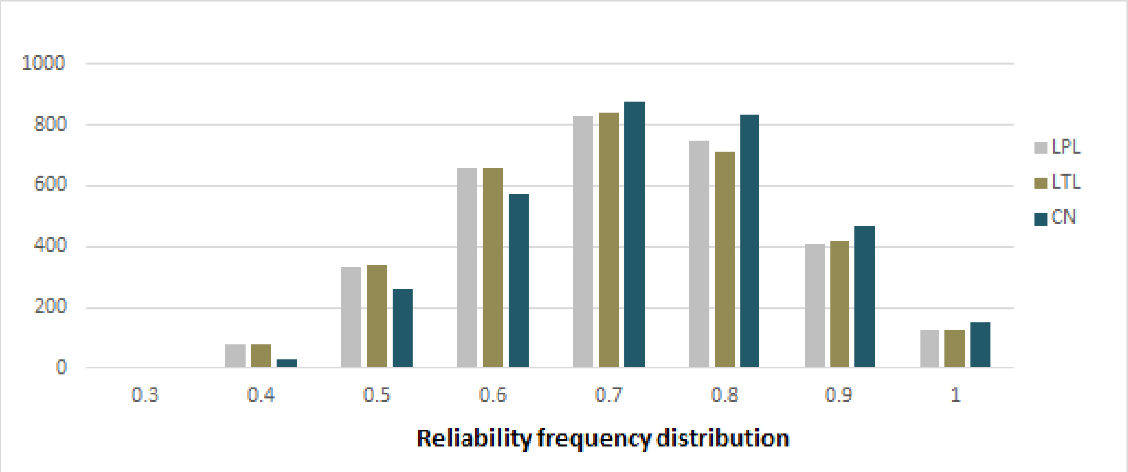
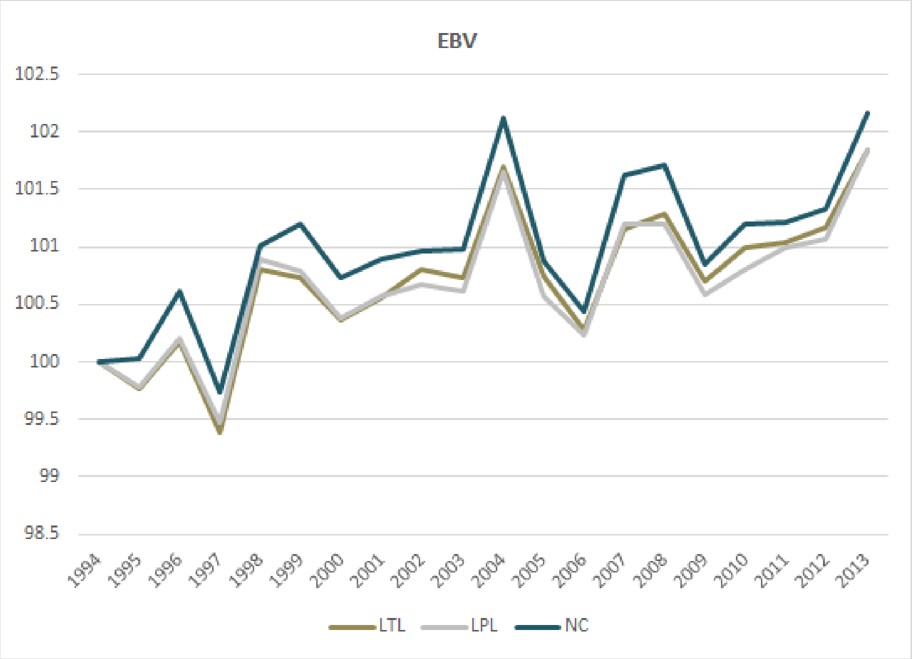


Figure 4. Standardized EBV average evolution of the cows per birth year for the different traits (LTL, LPL, and NC) in Retinta survival analysis.



A scale change has been made so that the year 1994 average takes the value of 100.

Table 4 showed positive but moderate correlations between EBV of the current growth selection (weight at 120 and 180 days) and EBV for the three longevity traits (, LTL, LPL and NC) in Retinta breed.

Table 4. Correlation for genetic direct and maternal values on live weight at 120 and 180 days of the cows in Retinta cattle estimated by classic univariate models and EBV for the different traits (LTL, LPL and NC) in Retinta survival analysis.

	LTL	LPL	CN
P180D	0.165	0.182	0.247
P180M	0.145	0.159	0.155
P120M	0.144	0.153	0.217
P120M	0.078	0.079	0.068

Discussion

In the present study, we analyzed three different traits to determine their interest as longevity selection criteria to be included in a breeding program.

The accuracy of genetic evaluation by survival analysis is highly influenced by the ratio of censored and uncensored records available, being increased as the proportion of censored records decreases. In our case, 43% of the data employed was censored, fitting into the limits proposed by Vukasinovic et al. (1997), who recommended not much more than 40% of censored records to obtain accurate results. Estimations of genetic variance in survival models have been usually based on sire or sire-maternal grand sire models (Tarres et al., 2006). In our case, we adopted an animal model despite it was believed it could not fit with the Survival Kit because of this alleged poor performance of the Laplace approximation. However, with an appropriate data structure, it has been shown that this concern was not justified (Ducrocq, 2006). In this sense, Meszaros et al. (2010) suggested that the use of this models would produce a lower estimation of the genetic variance and heritability. However, the same authors also suggested that the results obtained would be more accurate due to a better correction of environmental effects and be less contaminated by other genetic effects.

According to our results, longevity traits were heavily influenced by several factors associated with the productive cycle. Among them, the age of first calving showed that cows delivering for the first time at older ages (>38 months) had higher hazard ratios of ending their productive life at early stages of their LPL. This observation agrees with Rogers et al. (2004), who demonstrated that beef cows younger than 24 months at first calving had fewer chances of being culled than cows delivering at older ages. Phocas and Ducrocq (2006) reported that Charolais cows having their first calving below 28 months of age had 10% less risk to be culled than heifers calving between 28 and 39 months.On the contrary, Ducrocq (1994) and Vukasinovic et al. (2001), among others, suggested that the percentage of variation in longevity explained by the age at first calving for dairy cows was minimal, and therefore, removed this effect from the analysis.. In our case, the age at first calving was non-significant for LTL and CN, however it was significant for LPL Therefore, the results obtained in this study should be taking into account in the modelling of these traits for including them in future breeding programs.

In our study, culling risk was highly influenced by the herd, the year-season of cow birth, and the year-season of calf birth. However, our data do not allow us to disaggregate the causes of the variability observed. In any case, there are large differences among herds that should be included in breeding programs. Additionally, a more detailed analysis should be necessary to determine the origin of these differences in order to adjust the management practices employed to improve the longevity of the cows.

Retinta cows were widely used as maternal line in two-breed crosses with Charolais and Limousin bulls by farmers due to the high yield observed in the offspring. In this system, the average weaning weight (determined at 180 days) was 199.8 kg for pure Retinta, 206.4 kg for RetintaxLimousin (RL), 209.6 kg for RetintaxCharolais (RC) crosses, and 185.1 kg in Retinta crosses with other breeds. However, RL and RC crosses increased the risk of premature culling by 32.1% and 15.9%, respectively. These results suggest that despite their decreased weaning weight, the breeding of pure Retinta individuals could increase the whole productivity of the system since the total number of calvings was increased.

Previous studies determined that heritability of longevity traits in beef cattle ranged between 0.04 to 0.21 (Sewalem et al., 2005; Phocas and Ducrocq, 2006b; Mészáros et al., 2008; Bonetti et al., 2009; Strapáková et al., 2013). In our case, heritability estimates were of low-moderate magnitude for LTL and LPL (0.14). These results suggest that the genetic improvement of these traits will be difficult. This hypothesis was also suggested by Rogers et al. (2004) in crossbred cows and by Snelling et al. (1995) in Angus cattle, supporting our findings. Another interesting point is that ebv correlations among the three traits were higher than 0.96, showing that the traits are biologically similar. However, the h^2 determined in NC was higher (0.30) and, therefore, this trait could be used as an interesting selection criterion to obtain a faster genetic improvement of longevity. In addition, the evolution of NC at each age of the cow (relative productivity) could allow a close monitoring of the development of each individual throughout the productive life.

Finally, we also found a positive genetic trend in the traits analyzed over the last twenty years (Figure 4). Cows born in recent years had a higher probability of achieving a longer life and, as a consequence, a higher probability of getting an increased number of calvings. This improvement can be due to the current selection for weaning weight due to the existence of moderate positive correlations between weaning weight and longevity traits (Table 4). However, Martinez et al. (2004b) found that selection for weights at weaning and yearling ages had little genetic effect on any measure of lifetime production inn Hereford cows.

One possible way to increase breeding values reliability is to combine longevity with other positively correlated traits measured early in life, such as conformation traits. So far, little is known on the relationship between longevity and conformation traits in beef cattle. Forabosco et al. (2004) found that muscularity could be used as an early predictor of longevity in Chianina breed. Van Melis (2010) found that heifer pregnancy rate can be used as early predictor of longevity as well as post-weaning weight and muscle score in Nellore breed.

Conclusion

According to the results obtained herein, age at first calving, herd and season-year of cow birth as well as calf breed and season-year of birth were important factors affecting longevity in Retinta beef cattle. Producers can increase productive life by modifying these parameters. Since differences among herds are very large, it is important to take care of the reproductive, sanitary and feeding management and to choose the more appropriate breed for crossbreeding purposes.

The high heritability for NC indicates that the number of calving is the more relevant selection criterion for a beneficial response to direct genetic selection for longevity. The high correlations among the breeding values of the three traits entail that the same kind of biological improvement would occur by selecting for one or another. Nevertheless, we would recommend NC because of its higher heritability and major reliability, and because the collection of information of the number of calvings is easier, more accurate and with a lower error percentage.

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CAPÍTULO III

Capítulo III: Genetic analysis of accumulated productivity of Retinta breeding cows.

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Summary

The accumulated productivity of the cow (ACP), is a productive parameter which considers the weight of the calf at weaning and the number of offspring produced per cow during all his productive life. In this study, we estimated the genetic component of the ACP trait using random regression models (RRM), across the different ages of the Retinta cow. In general, individuals showed a highly increased productivity at older ages but large differences between breeders were observed. Heritabilities estimated were from medium to high magnitudes, ranging from 0.25 to 0.41 between 4 and 14 years of age, with a polynomic trend which determined maximum productivities in the early and older ages. Two types of evolutionary patterns of productivity curve were detected in the population analyzed. On the one hand, a group of animals which were highly productive in their early years of life but with a clear decreasing trend. On the other, animals were less productive in their early years of life, but they were able to maintain hi productivity constant until older years. All those results suggest that ACP can be successfully applied and included as an important trait in the selection scheme, providing an enormous flexibility to select the most appropriate individual phenotype according to the necessities of each particular herd.

Key Words: Accumulated productivity, Retinta cattle; genetic parameters; random regression models.

Introduction

Economic performance of extensive beef cattle production highly relays on the total amount of meat produced per cow. However, beef breeding programs are usually focused on increase live weight of the individuals, using growth traits like weight and average daily weight gain as selection criteria. A few year ago, Grossi et al. (2008) affirmed that selecting only for these traits can have unfavorable effects on other traits also associated with the economic importance, such as dam size, early fat deposition, and reproductive traits. It was largely proposed the fact that reproduction is one of the important components for productive efficiency, since it has a great effect on the number of kilograms of weaned calves, due to the number of calves birth (Eler et al., 2008). Additionally, reproductive traits are normally neglected in the selection schemes since its heritabilities range from low to very low (Grossi et al., 2008), normally due to the fact that all those traits are very influenced by the farm management, feed, health, etc.(Pereira et al., 2002). On the contrary, weaning weight is determined directly by the calf's genotype and indirectly by that of the dam (milk production and maternal ability), Meyer (1992). Therefore, growth measurements in pre-weaning are affected not only by the genetic potential of the animal but also by the maternal effect of the dams and therefore, they need to be used carefully. In extensive cattle production systems, cows with extended calving intervals or that deliver light calves are not useful and frequently culled. By this reasons, an interesting determination related to productive efficiency and meat yield is the longevity of the cow, which also has an economically important in beef production systems (Van Melis et al., 2007b). In addition, Morales et al. (2017) found that the evolution of the number of calvings at each age of the Retinta cow (relative productivity) could allow a close monitoring of the development of each individual throughout the productive life.

Accumulated productivity of the cow (ACP) is an index proposed by Grossi et al. (2008), which evaluates female productivity. It is based on the consideration of the calf body weight at weaning and number of offspring per cow and indicates the ability of the cows to calve at young ages, to maintain the calving regularity, and to wean heavy calves. The ACP depends directly on age at first calving, on the calving interval, and on the amount of time that the cow remains active in the herd. Schwengber et al. (2001) reported a heritability estimate of 0.15 for this trait, and therefore, suggesting the inclusion of ACP in beef cattle breeding programs since this index additionally encompasses many important traits in the selection of females and expresses genetic variability.

Native breeds have a unique adaptive characteristic to the natural environment and specific production systems (Rodero-Serrano et al., 2013). Among them, the most important maternal breed employed in Spain is the Retinta cattle. Nowadays, that breed has a census size of over 200 000 breeding cows which are extensively reared in the Southwest Spain under a severe climate and marginal pasturelands. Only 10% of the cows are raised as purebred, being the rest of them used as a maternal breed to be cross with other breeds like Charolais and Limousine. These crossbreed calves take full advantage of the high maternal Retinta ability yielding profitable crosses with an ample acceptation in the Spanish meat market (Morales et al., 2013).

By all those reasons, in this study, we aimed to estimate for the first-time genetic parameters of the accumulated productivity trait in Retinta cows using advanced random regression models (RRM). This methodology will allow determining this productive trait across the different ages of the cow, in order to evaluate their performance along with their entire life. Finally, we aim to develop and provide genetic tools for improving its productivity, which can be included in the current breeding selection scheme.

Material and methods

All the data analyzed in this study were obtained from individuals belonging to the breeding scheme of the Asociación Nacional de Criadores de Ganado Vacuno Selecto de Raza Retinta (ANCRE). In total, 5,834 birth records derived from 1,656 cows (3.5 births per cow in average) and 129 bulls were analyzed, producing 5,972 weaned calves during a period of 10 years in 14 different farms. Those calves were weighted between born and early post-weaning (at 245 days of age in average) producing 15,844 live weight records. A parentage matrix was determined all the pedigree information available, with a final result of 2997 individuals represented and 49.1% of the cows included in the data vector.

Estimation of the age-accumulated cow´s productivity

In this analysis, we calculated the kilograms of weaned calf (using 180 days corrected weight) produced per cow on a monthly basis in each of the years in which the cow has delivered. To this end, we utilized data from the weaned calves, the age at first calving and the periods of time between deliveries up to the weaning age. Only cows with productivity record longer than 4 years and lower than 14 years were employed since the number of individual records outside this period were negligible.

Statistical analysis

A random regression model was employed as follows:

$$\mathbf{y \approx fixed_i + \sum_{r=0}^{2} \Phi_r b_{lr} + \sum_{r=0}^{2} \Phi_r a_{dr} + Z_1 w_m + R}$$

where **y** is a vector with **n** APC observations of during the cow´s life.

$\mathbf{fixed_i}$ is a fixed effect vector including the combination of herd – year – birth season and calf sex, with 420 levels.

$\mathbf{b_1}$ is a Legendre polynomial ($\mathbf{\Phi}$) fixed co-variable with order **r** = 2, included to estimate the age of the cow effect in the **y** variable.

$\mathbf{a_d}$ and $\mathbf{w_m}$ are random effect vectors including $\mathbf{a_d}$, which is the effect of the individual and its ancestors without estimations and $\mathbf{w_m}$, which is a permanent environmental effect produced by the repetitions of the same character in the same individual.

Finally, $\mathbf{Z_1}$ is an incidence matrix (with 0 or 1 as elements) to connect the effect mentioned in the sub-index and the dependent variables. This matrix is replaced by the elements of a Legendre polynomial ($\mathbf{\Phi}$) with order r = 2 to estimate the (co)variance components along the age of the cow and **R** is the residual common error in all the observations.

The variance components expected in this model are:

$$\mathbf{var}\begin{bmatrix}\mathbf{a}\\\mathbf{w}\\\mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathbf{A}\otimes\mathbf{G_a} & \mathbf{0} & \mathbf{0}\\\mathbf{0} & \mathbf{I}\otimes\mathbf{W_m} & \mathbf{0}\\\mathbf{0} & \mathbf{0} & \mathbf{R}\end{bmatrix} \text{ where } \mathbf{G_a}=\mathbf{\Phi_i}\begin{bmatrix}\sigma^2_{ao} & \sigma_{aso} & \sigma_{qo}\\\sigma_{aos} & \sigma^2_{as} & \sigma_{aqs}\\\sigma_{aoq} & \sigma_{asq} & \sigma^2_{aq}\end{bmatrix}\mathbf{\Phi_i'}$$

Where **A** is the relationship matrix, y **I** is an identity matrix with **m** orders (number of cows with data) and $\mathbf{W_m}=\sigma^2_m$ and $\mathbf{R}=\sigma^2_e$ are the permanent-individual environmental and residual variances respectively. In our model, **Ga** is the matrix which includes elements related to intercept, the linear and quadratic genetic effects coefficient with variances σ^2_{ao} ; σ^2_{as} ; σ^2_{aq} ; σ_{aso}; σ_{asq} and σ_{aoq} as their respective covariances.

The estimation of the co-variance components of the cow´s productive life along $\mathbf{i_{th}}$ calvings was performed using the methodology employed by Jamrozik and Schaeffer (1997) as follows:

$\sigma^2_{ai}=\mathbf{\Phi_i G_a \Phi_i'}$ are the genetic variances; and

$\sigma_{a_{ij}}=\mathbf{\Phi_i G_a \Phi_j'}$ are the genetic (co)variances.

Heritabilities ($\mathbf{h^2}$) and genetic correlations ($\mathbf{r_g}$) were estimated using those values along the cow´s $\mathbf{i^{th}}$ years of age, obtained from the coefficients of the Legendre polynomial ($\mathbf{\Phi_i}$) taking into account the permanent environmental and residual variances, as follows:

$$\mathbf{h_i^2}=\frac{\mathbf{\Phi_i G_a \Phi_i'}}{\mathbf{\Phi_i G_a \Phi_i'}+\sigma^2_m+\sigma^2_e} \quad \text{and} \quad \mathbf{r_{g_{ij}}}=\frac{\mathbf{\Phi_i G_a \Phi_j'}}{\sqrt{\mathbf{\Phi_i G_a \Phi_i'} * \mathbf{\Phi_j G_a \Phi_j'}}}$$

With this methodology, we were able to estimate the expected breeding values (EBV) at any $\mathbf{i^{th}}$ point of the productive life of the cow using the following procedure:

$$\mathbf{VGE_{a_i}}=\mathbf{\Phi_i a_i'}$$

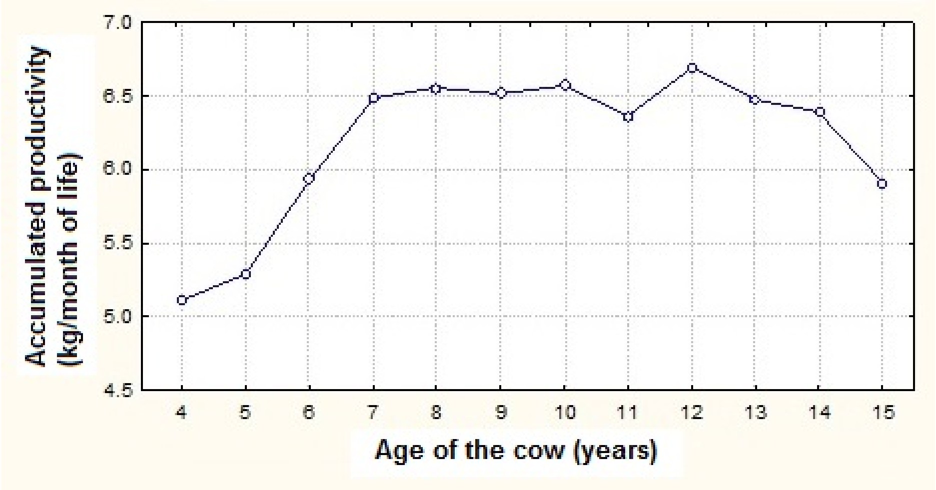
Where $\mathbf{\Phi_i}$ are the coefficients of the polynomial at the $\mathbf{i^{th}}$ year of the cow and $\mathbf{a_i}=[\mathbf{a_o} \quad \mathbf{a_s} \quad \mathbf{a_q}]$ is the genetic function of the individual previously described.

All the statistical analyses were carried out using the ASREML software (Gilmour et al., 2009a)

Results

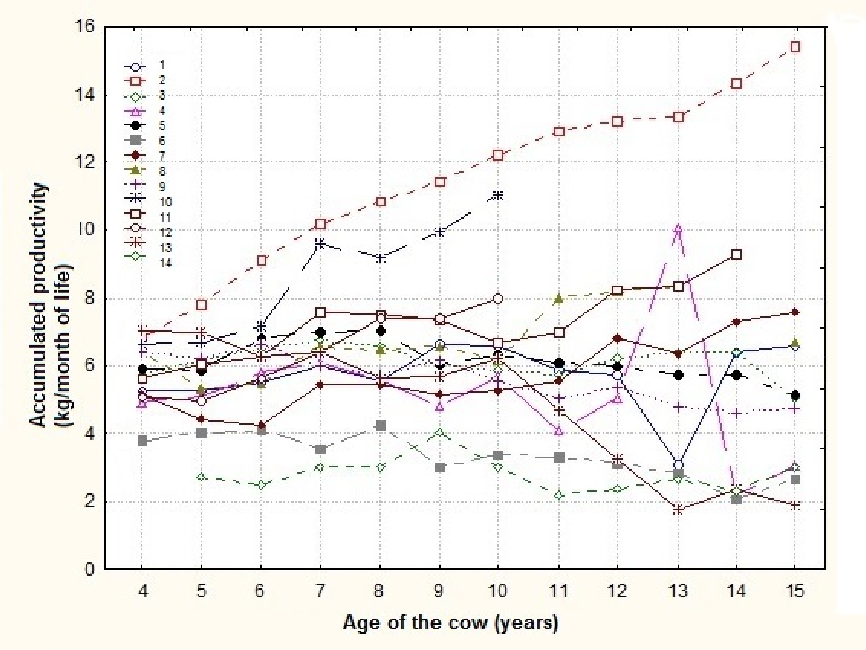
Figure 1 shows the evolution of the average accumulated productivity per cow (ACP) between 4 and 15 years in the analyzed population. In is noticeable an important increase in the productivity at 7 years of age, remaining steady until the 14 years.

Figure 1. Evolution of the average accumulated productivity per cow.



However, the analysis of average ACP showed a great variability among the different herds analyzed (figure 2). Three different evolution patterns of the ACP were observed: an ascendant pattern, characterized by the increase of the ACP during the life of the cow (herd 2); a stable pattern, in which ACP is maintained without great variation during the life of the cow (herd 5) and a decreasing pattern in which the young individuals showed an increased ACP than the older individuals (herd 10).

Figure 2. ACP analysis of the individuals grouped per herd.



ACP heritabilities were estimated along all the productive period analyzed (Figure 3). In general, all the estimations showed a high heritability in this parameter, ranging from 0.27 to 0.41. However, a second-grade polynomial pattern was observed (figure 3) with a minimum value observed at the middle ages of the cows (about 9 years old) and maximum values in young (4years old) and old (14 years old) individuals.

Figure 3. Heritability evolution for ACP across the different ages of the cow

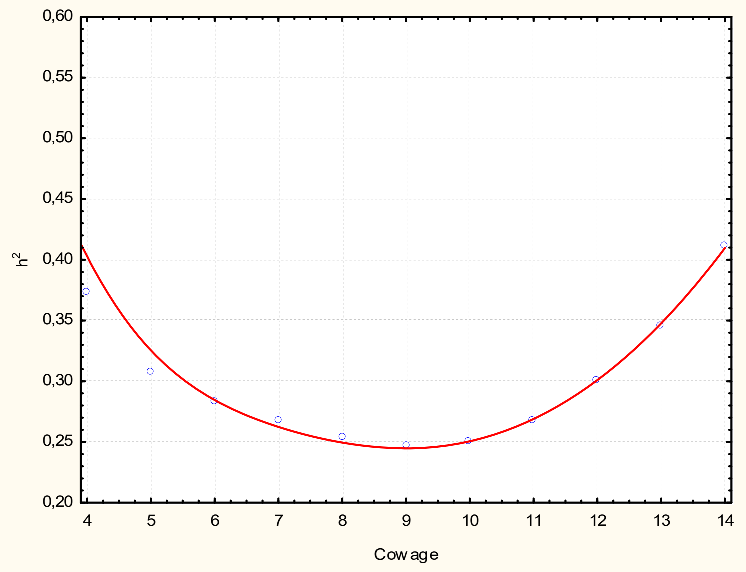
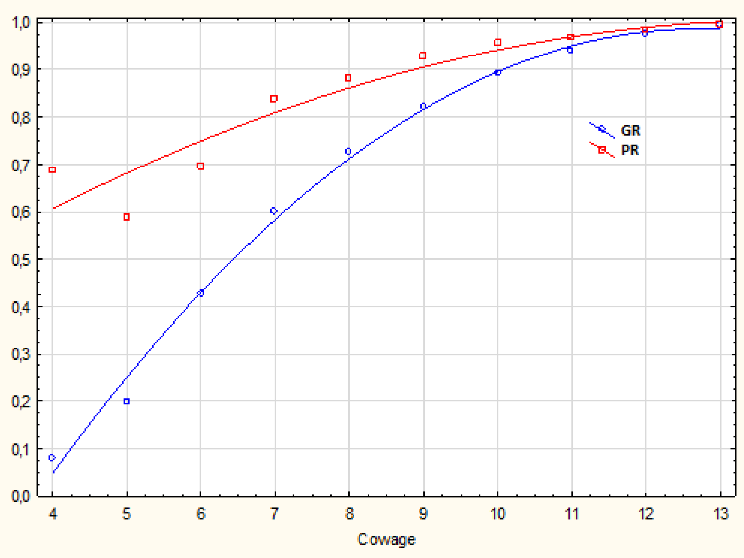


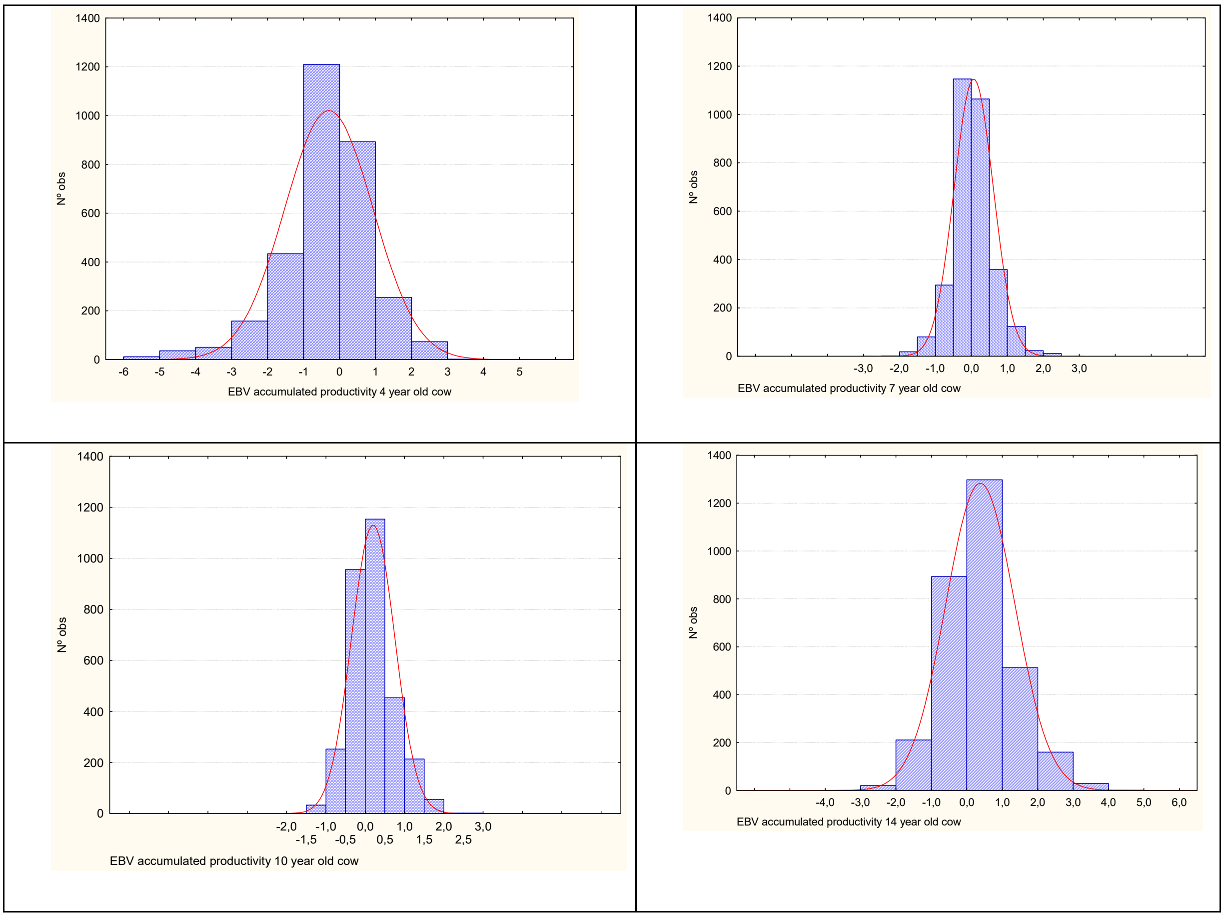
Figure 4 shows the phenotypic (PR) and genetic (GR) correlations between ACP at each age and the ACP determined at 14 years, which is the end of the productive life of the individuals. In both cases, correlations were low at young ages of the cows, being higher than 0.75 after 6 (PR) and 8 (GR) years of age.

Figure 4. Evolution of the genetic (GR) and phenotypic (GR) correlations between ACP at different individual ages and ACP estimation at 14.



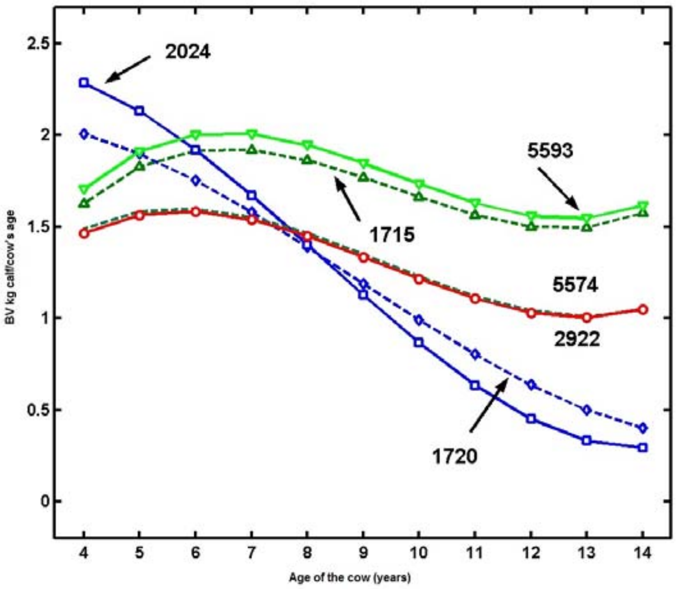
It is noteworthy the variability observed among the correlations, and the difference between PR and GR, mostly at young ages. In this sense, figure 5 showed the histogram of ACP estimated at 4 different ages (4, 7, 10 and 14 years of age), in which variability is higher at young and old ages, being ACP more stable at middle age.

Figure 5. Frequency histogram of ACP estimated at 4 different ages of the cows.



Additionally, 200 animals were selected according to their EBV at 4 years old, the EBV evolutions throughout the different ages of the cow were analysed by the RRM, the analysis showed clear differences in the evolution pattern of ACP along with the cow´s life. We represented 6 of them on figure 6, to show the differences among patterns, two of them were higher than the average ACP at 4 years but evolved to be the lowest ACP at 14 years. On the contrary, the remaining cows were average at 4 years but maintained those values relatively stables until the age of 14.

Figure 6. ACP evolution of six different Retinta cows.



Supplementary material

Supplementary table 1. Heritabilities (diagonal row), genetic (above the diagonal row) and phenotypic (below the diagonal row) correlations of ACP along the life of the cow in Retinta breed.

Cow's age	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
4	**0.374**	0.960	0.865	0.745	0.614	0.479	0.341	0.207	0.086	-0.011	-0.078
5	0.973	**0.308**	0.970	0.900	0.807	0.699	0.582	0.462	0.352	0.262	0.199
6	0.856	0.975	**0.283**	0.978	0.925	0.849	0.758	0.660	0.565	0.485	0.427
7	0.803	0.888	0.981	**0.268**	0.983	0.939	0.875	0.800	0.722	0.654	0.600
8	0.694	0.843	0.914	0.987	**0.254**	0.986	0.949	0.895	0.835	0.778	0.728
9	0.680	0.764	0.868	0.955	0.992	**0.246**	0.988	0.957	0.914	0.867	0.822
10	0.596	0.725	0.839	0.916	0.965	0.995	**0.250**	0.990	0.965	0.930	0.891
11	0.636	0.745	0.876	0.927	0.958	0.981	0.996	**0.268**	0.992	0.971	0.940
12	0.684	0.694	0.825	0.886	0.938	0.965	0.985	0.997	**0.300**	0.993	0.973
13	0.665	0.623	0.778	0.855	0.906	0.945	0.978	0.988	0.997	**0.345**	0.993
14	0.688	0.589	0.694	0.838	0.880	0.928	0.955	0.968	0.981	0.993	**0.411**

Discussion

The selection of animals with high productivity, reproductive precocity and the ability to remains in the herd for longer periods maintaining high productivity levels is essential to achieve the maximum benefit in beef cattle production. This allows to the breeders to determine the age of culling depending on their breeding objectives (Caetano et al., 2013). In this sense, the use of the ACP index could be an interesting option for the breeders since they can determine their optimum replacement rate and select individuals well adapted to this end. Our study demonstrated the existence of individuals with a peak of productivity during their first years of life, which will be more fit in intensively managed herds, and the existence of individuals with a lower productivity at young ages, which is increased in older ages and more stable during all the life of the individual.

Retinta is considered a breed with an extended productive life, reaching maximum levels at the age of 7, being stable up to the age of 12 -13, with a decay until the age of 15, where still maintains fairly acceptable values. In this sense, ACP index could be an interesting tool, since it can predict the productivity of the cow along all their productive life. However, it is noteworthy that the estimation of this index requires a careful productive characterization of the individuals, including all information regarding all the calves produced per each cow.

This trait depends to reproductive management decisions by breeders (mainly, age first mating of the cow and period length in which stallions stay with cows), which are highly variable and could be a source or error in our model, despite the fact that the RRM employed are able to correct herd and birth year of the cow effects, this variable is still highly conditioned by specific changes in this routine of reproductive management. However, the genetic basis predicted in our models is strong, which implies that if the breeders do not produce theses pronounced changes in the reproductive management, the confidence of our predictions will remain high. On the other hand, we observed a large variability among herds, which suggest the existence of ones, which, because of their genetic profile or their productive system (reproductive, food and sanitary management) are unable to maintain elevated productivity levels in the cows with advanced ages. In this case, the use of younger high producer cows could produce an increase their productivity potential, being their genetic improvement possibilities very high.

In this study, we demonstrated that ACP heritabilities were high, ranging from 0.27 to 0.41, being higher than previous studies performed by Grossi et al. (2008), (from 0.14 to 0.25) and Schwengber et al. (2001) (0.15), both performed in Bos Indicus cattle (Nellore). In the same breed, Faria et al. (2007) found a 95% confidence interval for ACP heritability estimates of from 0.19 to 0.31 using a Bayesian inference and Eler et al. (2014) estimated a heritability of 0.16 for the PRODAM index (kilograms of weaned calf per cow per year). In the same way, Grossi et al. (2016) concluded that productivity could contribute to decreasing the mean calving interval in Nellore cattle. In all those cases, h2 was highly superior tan those related to reproductive parameters, such as first calving age, fertility, calving interval and percentage of weaned calves.

Another important fact is that ACP allows evaluating females regardless of the reproductive age and number of calves (Chud et al., 2014). This is important in extensively produced breeds in which the only reproductive information available in most of the cases is delivery date, since extensive pasture management difficult the collection of animal data, supporting the use of ACP as a proper selection trait. Furthermore, Martinez et al. (2004a) found positive results in the selection for cumulative weaning weight in Hereford cows and Grossi et al. (2016), Grossi et al. (2008) found a genetic correlation in this trait with the age at first calving (0.33). This last correlation it is also important, MacGregor and Casey (1999) demonstrated that the most fertile and reproductively efficient cows have lower fist-calve ages, but they continue calving periodically and Bernardes et al. (2015) also demonstrated that precocious cows produce more kilograms of weaned calves, however the genetic variability detected in our study along the different ages of the cow suggests that more research about this fact are needed.

Our study showed, as it was clearly expected, that the correlation with future cumulative productivity is greater at older the reproductive ages. Those results indicate that if the selection of future breeders is performed too early, the response to selection may be lower, or at least more erratic, for this variable. However, the absence of specific studies on this trait (our study is the first one performed in extensively bred cattle) suggest that the selection of the next generation breeding animals should not be performed previously to the 6 years of age under no circumstances, since an early selection would not compensate the loss of precision produced.

Conclusion

In our study, we demonstrated the existence of a major genetic component which modulates the evolution of the accumulative cow productivity in the Retinta cows, producing two clearly differentiated phenotypes. We determined their genetic correlation with phenotypes along the productive life of the cow by using advanced modeling techniques. Furthermore, we also determined that these productive traits are highly heritable, showing h^2 ranging from moderate to high. By those reasons, we suggest that the use of ACP as a regular trait to be included in Retinta selection scheme is an interesting option which will give more options and flexibility to the breeders in the planning of genetic base of their herds. However, a systematized and well-planned collection of reproductive data in each herd is necessary to the successful implementation of this program.

These results are extremely important since they involve the existence of herds, which, because of their genetic profile or their productive system (reproductive, food and sanitary management ...) are unable to maintain good levels of productivity at more advanced ages, even if they can Producing higher yields in the case of younger animals, and therefore their potential for improvement (environmental and genetic) are very high.

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CAPÍTULO IV

Capítulo IV: Effect of inbreeding depression on bull sperm quality and field fertility

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Summary

The present study investigated the effect of inbreeding depression on sperm quality using automated and objective methods and subsequent effects on beef bull field fertility. Individual inbreeding coefficient (F) values and field fertility data were determined using a dataset of AI bulls belonging to the Spanish Retinta Breeders Association (Asociación Nacional de Criadores de Ganado Vacuno Selecto de Raza Retinta (ANCRE)). Animals were clustered in two groups according to the F values as follows: (1) a high inbreeding group (HI; F ≥ 13.5%, mean 16.3); and (2) a noninbreeding group (NI; F ¼ 0%). In total, 17 different assessments were performed in both experimental groups, including evaluation of sperm morphology, acrosomal and DNA status, sperm plasma membrane integrity and function (hypo-osmotic swelling test), 10 kinetic parameters and the structure of sperm subpopulations. Sperm morphology, acrosomal and DNA status and osmotic tolerance were similar in both groups. Three velocity parameters (curvilinear velocity, straight line velocity and average path velocity) and the amplitude of lateral head displacement were higher in HI ($P<0.05$). Cluster analysis of kinematic parameters revealed three different sperm subpopulations (sP1, sP2 and sP3), with the proportion of the sP1 population (highly active but non-progressive spermatozoa) being significantly ($P<0.05$) higher in the HI group. Field fertility was assessed using two calving record datasets. In a smaller database including only bulls evaluated in the present study, there was a significant increase in the calving interval of cows sired with HI bulls. Conversely, in an extended genetic analysis of the ANCRE database, inbreeding only explained a small part of the variation in calving interval, and the results of regression analysis were not significant among bulls. The findings of the present study suggest that high inbreeding levels have a moderate effect on bull semen quality, with an increased percentage of highly active but non-progressive spermatozoa in this group, but only when F values reached a certain threshold. This motility pattern could explain, in part, the higher calving interval observed in inbred bulls.

Introduction

Sperm quality is one of the most important traits defining the reproductive potential of bulls. It is normally determined by a group of characteristics including morphology, motility, viability and DNA function (Söderquist et al., 1996; Gil et al., 2000). It is well known that sperm quality is affected by environmental factors, such as the age of the animal, fitness and absence of diseases (Brito et al., 2002). However, sperm quality is also affected by the genetic pool of the individual, but shows only low to moderate heritability (Mathevon et al., 1998), which is why it is rarely included in cattle selection schemes (Karoui et al., 2011). In practice, candidate sires are evaluated before they are included in AI programs, discarding those that do not meet certain minimum sperm quality standards because of genetic causes (Rodriguez-Martinez and Larsson, 1998).

Inbreeding depression, a consequence of breeding related individuals, results in reduced viability and adaptability in a given population (Kristensen et al., 2010). According to Charlesworth and Willis (2009), the genetic causes of inbreeding depression may be due to three different possibilities: (1) increased expression of deleterious recessive alleles (partial dominance); (2) fitness superiority of heterozygotes over homozygotes (overdominance); or (3) increased possibility of favourable gene combinations in heterozygotes (epistasis). Although the relative contribution of each cause to inbreeding depression remains unclear, it is well known that inbred animals show reduced flexibility in coping with environmental challenges (Lacy, 1997; Leberg and Firmin, 2008), decreased fitness and mean phenotypic traits and impaired reproductive success across wild, captive, domestic and experimental populations (O'Grady et al., 2006; Leroy, 2014). This phenomenon is particularly important in cattle, where the high intensity of current selection programs and the use of autochthonous populations with reduced census have brought about a rapid increase in genetic relationships among individuals(Hansen, 2000; Rodero-Serrano et al., 2013). In these animals, inbreeding depression is expressed in different ways, such as reduced viability and lifetime performance in beef cattle (Smith et al., 1998) and decreased lifetime milk production in dairy cattle (Thompson et al., 2000). Nevertheless,this genetic trait has not been considered to any great extent in selection schemes, which primarily focus on improving production traits (Gandini et al., 2014), leading to a slow but steady increase in inbreeding depression over time (Sorensen et al., 2005; Stachowicz et al., 2011).

There is general agreement that fertility is negatively affected by inbreeding (Keller and Waller, 2002). This impairment is particularly important in endangered wild animals, for which inbreeding levels are very high (Cassinello et al., 1998; Ruiz-Lopez et al., 2010). However, only a few studies have analysed the effect of inbreeding on bull sperm quality and contradictory results have been reported (Losdat et al., 2014). For example, Flade and Zeller (1992) demonstrated that sperm quality was not affected in high inbreeding bulls (inbreeding coefficient (F) = 25%, produced experimentally) compared with their non-inbred half-brothers (F = 0%). In contrast, Maximini et al. (2011) more recently described a low negative correlation between inbreeding and sperm quality in Simmental bulls.

On the basis of this background information, the aim of the present study was to perform a comprehensive evaluation of the effects of inbreeding on bull sperm motility (using computer-aided sperm analysis (CASA)) and DNA integrity (using flow cytometry). Concurrently, we assessed sperm viability and the status of both acrosomal and plasma membranes. Finally, we determined the effects of inbreeding on *in vivo* fertility in our experimental animals as well as in a reproductive dataset of AI commercial beef bulls with broad genealogy and reproductive records over several seasons.

Material and methods

Animals

Genealogical data from 159 sperm donor bulls belonging to the Spanish Retinta Breeders Association (Asociación Nacional de Criadores de Ganado Vacuno Selecto de Raza Retinta (ANCRE)) AI program were analysed. Individual F values (Wright, 1931) and the number of fully traced, maximum number of generations traced and the equivalent complete generations (ECG) for each animal were estimated by ENDOG v4.8 (Gutierrez and Goyache, 2005) using all known generations. Thereafter, 11 bulls with at least two complete generations and 2.5 ECG and available frozen semen doses were selected and classified into two groups based on F values as follows: (1) animals with at least 13.5% consanguinity (mean (± s.e.m.) F = 16.3 ± 0.9%; minimum 13.5%, maximum 18.7%), which were classified as the high endogamy (HI) group ($n = 6$); and (2) animals without consanguinity (F = 0%), which were classified as the non-inbreeding (NI) group ($n = 5$). The mean (± s.e.m.) ECG for the HI and LE groups was 5.2 ± 0.6 and 4.1 ± 0.6, respectively. Minimum consanguinity in the HI group (F = 13.5%) was higher than the equivalent to a half-sibling cross (12.5%), which is considered the threshold value from which serious fitness problems derived from inbreeding depression appear (Sewalem et al., 2006).

Semen samples

In all, 55 frozen semen samples (five per bull) were analysed. Semen was collected from individuals between 20 and 30 months of age with a positive breeding soundness examination score and was frozen at the Centro de Selección y Reproducción Animal (CENSYRA; Badajoz, Spain) following the procedures of ANCRE's AI program. Frozen semen was thawed at 37°C in a water bath for 1 min and diluted in Biladyl A (Minitüb, Tiefenbach, Germany) to reach a working concentration of 25×10^6 spermatozoa mL^{-1}. Only samples with acceptable post-thawing sperm membrane integrity and motility (>40% sperm membrane integrity and >50% total motility) were used.

Semen evaluation

Sperm morphology

The percentage of spermatozoa with abnormal morphology was estimated on Diff-Quik-stained smears (Baxter DADE Diagnostics, Düdingen, Switzerland), as described previously (Hidalgo and Dorado, 2009). The proportion of spermatozoa with normal morphology (NSM) and abnormal morphology (ASM) was recorded. Two independent replicates of at least 200 spermatozoa were assessed for each sample.

Plasma membrane integrity

Sperm plasma membrane integrity was assessed using a Vital-Test kit (Halotech, Madrid, Spain) according to the manufacturer's instructions under a fluorescence microscope (BX40; Olympus, Tokyo, Japan) using a 460–490-nm excitation filter. Two staining patterns were discerned: (1) spermatozoa with a green-stained head were determined to be viable spermatozoa (VS); and (2) spermatozoa with red-stained heads were recorded as dead spermatozoa (DS). Two independent replicates of at least 200 spermatozoa were assessed for each sample.

Plasma membrane function

The function of the sperm plasma membrane was assessed using the hypo-osmotic swelling (HOS) test (Revell and Mrode, 1994). Samples were incubated for 1 h at 38.5°C in hypo-osmotic solution (100 mOsmol mL^{-1}) containing 1 : 1 (v/v) fructose : sodium citrate. Thereafter, 20 μL solution was smeared on a clean slide, dried and evaluated at a magnification of ×400. Spermatozoa with unaltered tail morphology were classified as negative (HOS–), whereas those showing a coiled tail were classified as positive (HOS+). Two independent replicates of at least 200 spermatozoa were assessed for each sample.

Acrosome membrane integrity

Acrosome integrity was assessed using a standard protocol (Demyda-Peyras et al., 2012). A droplet of diluted sample was smeared onto a microscopic slide, air dried, fixed and permeabilised with 70% (v/v) ethanol for 30 s. Thereafter, 30 μL of staining mixture (1 part propidium iodide (PI; 0.1 mg mL^{-1}) and 2 parts isothiocyanate-labelled peanut (*Arachis hypogaea*) agglutinin (0.1 mg mL^{-1})) was spread over each smear and samples were incubated in a dark and humid chamber at 4°C for 30 min. Preparations were subsequently washed, mounted with Vectashield (Vector Laboratories, Peterborough, UK) and scored under an epifluorescence microscope (BX40; Olympus) at ×400 magnification. Two sperm subpopulations were identified: (1) spermatozoa with a uniform green fluorescence of the acrosomal cap (acrosome-intact spermatozoa (AIS)); and (2) spermatozoa with a disrupted, patch-like, green fluorescence staining in the acrosomal cap, a fluorescent band at the equatorial segment or no fluorescence (acrosome-reacted spermatozoa (ARS)). All spermatozoa showed red fluorescence because of counterstaining with PI. Two independent replicates of at least 200 spermatozoa were assessed for each sample.

Chromatin integrity

The percentage of altered DNA (strand breaks) was assessed using the acridine orange (AO) sperm chromosome structure assay (SCSA; (Evenson and Jost, 2000). Immediately after thawing, samples were placed on ice and diluted separately in TNE buffer (0.015 M NaCl, 0.01 M Tris and 0.001 M EDTA, pH 6.8) to a final concentration of 1 × 10^6 spermatozoa mL^{-1}. A 200-µL aliquot of sperm solution was treated with 400 µL acid detergent solution (0.08 M HCl, 0.15 M NaCl and 0.1% (w/v) Triton X-100, pH 1.2) and then after exactly 30 s 1.2 mL AO staining solution was added (6 mg AO per mL buffer (0.037 M citric acid, 0.12 M Na_2PO_4, 1.1 mM disodium EDTA and 0.15M NaCl), pH 6.0). Samples were analysed in an EPICS XL cytometer (Beckmann Coulter, Miami, FL, USA) containing a 488-nm dichroic long-pass filter, a 488-nm blocking filter, a 550-nm dichroic long-pass filter and a 525-nm band pass filter for the first fluorescent channel (FL1), a 600-nm dichroic long-pass filter and a 575-nm band pass filter for the second fluorescent channel (FL2), a 645-nm long-pass filter and a 620-nm band pass filter for the third fluorescent (FL3) channel and a 675-nm long-pass filter for the fourth fluorescent channel (FL4). Fluorescence was recorded at FL1 and FL4. Two independent replicates per bull of at least 20000 spermatozoa were assessed for each sample at an average flow rate of 200 spermatozoa per second. Data were collected individually in list mode and transformed to plain text using MFI (Martz, 1992-2001). The chromatin damage index (DNA fragmentation index (DFI)) and high DNA stainability (HDS) were determined by analysing the ratio of red : green fluorescence, as described by Rybar et al. (2010).

CASA

Sperm motility was assessed using a CASA system (Sperm Class Analyzer; Microptic, Barcelona, Spain). Three consecutive 5-µL drops of each semen working sample were evaluated using a phase contrast microscope (Eclipse 50i; Nikon, Tokyo, Japan) with a prewarmed stage at 37°C (×100 magnification). Three drops and two microscopic fields per drop were randomly analysed, including a minimum number of 200 spermatozoa. The analysis was performed on 25 consecutive digital images captured over a period of 1 s from a single microscope field.

Parameters of the analysis software were set according to (Kathiravan et al., 2011). Briefly, spermatozoa with mean average path velocity (VAP) <10 µm s^{-1} were considered immotile. Spermatozoa with a VAP >90 µm s^{-1} were considered rapid, and spermatozoa deviating <25% from a straight line were designated as linear motile. The following kinetic traits were assessed: curvilinear velocity (VCL), the total distance travelled by the sperm head per unit time; straight line velocity (VSL), the net distance gain of the sperm head per unit time; VAP, the length of a derived 'average' path of sperm head movement per unit time; wobble (WOB), calculated as (VAP/VCL) × 100; linearity (LIN), calculated as (VSL/VCL) × 100; straightness (STR), calculated as (VSL/VAP) × 100; beat cross frequency (BCF), the number of times the curvilinear path crosses the average path per unit time; approximation of the flagellar beat frequency for seminal sperm (in Hz); and amplitude of lateral head displacement (ALH), the width of the head movement envelope.

Classification, ordination and identification of sperm subpopulations

Motility data from all individual spermatozoa assessed were included in this analysis and initially grouped in two categories based on F values (22 190 spermatozoa from HI bulls and 23 097 spermatozoa from NI bulls). A four-step clustering procedure was used to classify the spermatozoa in the dataset (45 287 in total) into a reduced number of subpopulations according to their motility patterns as was previously described by Martinez-Pastor et al. (2005). All determinations were performed using SAS/STAT software package release 9.0 (SAS Institute, Cary, NC, USA). First, the PRINCOMP procedure was used for principal component analysis (PCA). Thereafter, a non-hierarchical cluster analysis (FASTCLUS procedure) was performed using the selected principal components as variables. Then, the processed data were reclustered by hierarchical methods (CLUSTER procedure) using the average linkage method (AVERAGE) for joining clusters. To determine the final number of subpopulations (sP; Step 4), we studied the evolution along the clustering process of three statistics provided by CLUSTER (pseudo-t2, pseudo-F and cubic clustering criterion) looking for certain types of consensus among them, specifically local peaks of the cubic clustering criterion and pseudo-F statistics combined with a small pseudo-t2 value and a larger pseudo-t2 for the next cluster fusion.

Statistical analysis

All statistical analyses were performed using SAS/STAT (SAS Institute). Results are expressed as the mean ± s.e.m. Sperm parameters were compared between groups (HI vs NI) using a nested general linear model (GLM) with group (fixed factor) and bull (nested in group) as the random factor. The parameter SGoF+ (Carvajal-Rodriguez and de Uña-Alvarez, 2011) was used to control the false discovery rate (FDR) of the *P*-values at a significance level of 5% and an FDR of 5%. The percentage sperm subpopulations in the HI and LE groups were compared by Fisher's exact test (FREQ procedure).

Assessment of bull fertility under field conditions

Calving intervals (CI) were estimated based on mating records of the ANCRE. Records from 824 cows inseminated or mated by HI ($n = 490$) and NI ($n = 334$) bulls were compared using GLM. Group (HI or NI) and bull (nested in group) were included as fixed and random factors, respectively. Age of the cow at delivery was included as a covariate.

Genetic analysis

A subsequent broader genetic analysis included the CI of 5230 cows inseminated or mated by 743 bulls (159 semen donors) belonging to the ANCRE dataset. The effects of several factors and the genetic component of CI were analysed with an animal model using Bayesian methodology as follows:

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Z_1a_1} + \boldsymbol{Z_2a_2} + \boldsymbol{Wp} + \boldsymbol{e}$$

where y is observed CI, b is systematic fixed effects, a_1 and a_2 are cow and bull additive genetic effects, respectively (11 445 levels), p is bull permanent environmental effects (743 levels), e is residual effects and X, Z and W are incidence matrices.

The systematic fixed effects (b) included a random contemporary group effect (herd × year × breeding season; 1323 levels) with four different seasons (December–March, April–June, July + August and September–November) defined according to the weather characteristics of the region, and the fixed age effect of the cow. Inbreeding coefficients for both cow and bull were obtained by the tabular method (Tier, 1990) and included as covariates.

The prior distributions of $a = (a_1 \text{ and } a_2)$, p and e were $N(0, A \otimes G_o)$, $N(0, I\sigma_p^2)$ and $N(0, \mathrm{I}\sigma_e^2)$, respectively, where G_o is a (co)variance matrix for the additive genetic components on CI_{12} of cow and bull. Gibbs sampling algorithm was used to make Bayesian inferences for the parameters of interest. Data analysis consisted of a long chain of 10^6 iterations, a burn-in of 500 000 rounds and a thin of 10 iterations using TM software (Legarra et al., 2008).

Results

Sperm morphology and function

Inbreeding did not induce differences ($P > 0.05$) in sperm morphology, acrosomal and plasma membrane integrity or results of the HOS test between the HI and NI groups (Table 1). In addition, inbreeding had no significant effect on DNA structure (DFI), despite the large number of spermatozoa analysed ($P > 0.05$; Table 2), or on the percentage of immature spermatozoa (HDS). The variability in both these parameters was similar between the HI and NI groups.

Motility analysis

Only four CASA-derived parameters were affected by inbreeding (Table 3). VCL, VAP, VSL and ALH were higher ($P < 0.05$) in HI compared with NI bulls. Two principal components with eigenvalues >1 were identified by the PCA, accounting for 84.05% of the variance. Considering the scores of CASA parameters, the first principal component was related to fast linear movement, whereas the second was related to fast but irregular movement.

Table 1. Morphological and functional assessment of sperm samples from inbred (HI; n = 30) and non-inbred (NI; n = 25) bulls

Results are expressed as the mean ± s.e.m. *$P < 0.05$ compared with HI bulls. ASM, abnormal sperm morphology; VS, viable spermatozoa; AIS, acrosome-intact spermatozoa; HOS+, hypo-osmotic swelling test positive

Sperm parameters	HI	NI
% ASM	33.15 ± 2.68	36.07 ± 2.23
% VS	47.70 ± 1.70	50.85 ± 1.94
% AIS	82.97 ± 1.68	80.15 ± 2.09
% HOS+ spermatozoa	42.20 ± 2.07	47.23 ± 3.07*

Table 2. Sperm chromatin structure assay results from inbred (HI; n = 30) and non-inbred (NI; n = 25) bulls

	DNA fragmentation index (%)			High DNA stainability (%)		
	Mean	s.e.m.	Range	Mean	s.e.m.	Range
HI bulls	2.99	1.48×10^{-6}	2.01–5.36	2.09	2.26×10^{-6}	0.17–4.95
NI bulls	3.01	2.43×10^{-6}	0.98–6.02	1.82	2.48×10^{-6}	0.28–3.47

Table 3. Motility analysis of sperm samples from inbred (HI; *n* = 30) and non-inbred (NI; *n* = 25) bulls

Sperm parameters	HI bulls	NI bulls
MOT^{A} (%)	76.68 ± 1.97	79.77 ± 2.10
PMOT^{B} (%)	53.43 ± 1.93	50.86 ± 2.58
VCL (μm s^{-1})	77.73 ± 1.69^{a}	69.64 ± 2.74^{b}
VSL (μm s^{-1})	40.60 ± 0.99^{a}	37.34 ± 2.11^{b}
VAP (μm s^{-1})	55.93 ± 1.41^{a}	50.46 ± 2.29^{b}
Linearity (%)	45.04 ± 0.89	44.48 ± 1.06
Straightness (%)	62.73 ± 0.81	62.34 ± 0.84
Wobble (%)	67.60 ± 1.10	66.64 ± 0.80
ALH (μm)	2.81 ± 0.08^{a}	2.61 ± 0.07^{b}
BCF (Hz)	6.81 ± 0.14	6.46 ± 0.16

Results are expressed as the mean ± s.e.m. Within rows, values with different superscript letters differ significantly at $P < 0.05$ after control of the false discovery rate at 5%. VCL, curvilinear velocity; VSL, straight line velocity; VAP, average path velocity; ALH, amplitude of lateral head displacement; BCF, beat cross frequency

^{A}Total motility (MOT) was defined as spermatozoa with a mean VAP >15 mm s^{-1}.

^{B}Progressive motility (PMOT) was defined as spermatozoa with a VAP >50 mm s^{-1} and straightness >75%.

Three sperm subpopulations were defined using non-hierarchical and subsequent hierarchical classification of 45 287 individual motile spermatozoa and the eight motility parameters (VCL, VSL, VAP, LIN, STR, WOB, ALH and BCF). Summary statistics for the motility characteristics of the subpopulations are given in Table 4.

Table 4. Motility parameters for the three sperm subpopulations (sP1, sP2 and sP3) defined after pattern analysis in semen samples from inbred (HI; *n* = 30) and non-inbred (NI; *n* = 25) bulls

Sperm parameter	sP1	sP2	sP3
No. spermatozoa	19 942	7720	17625
% Spermatozoa	44.05	17.05	38.9
VCL (μm s^{-1})	109.19 ± 0.17^a	62.42 ± 0.26^b	29.81 ± 0.12^c
VSL (μm s^{-1})	63.90 ± 0.21^a	44.21 ± 0.24^b	6.06 ± 0.04^c
VAP (μm s^{-1})	84.07 ± 0.18^a	53.64 ± 0.27^b	15.46 ± 0.09^c
Linearity (%)	56.84 ± 0.15^b	68.16 ± 0.15^a	20.14 ± 0.09^c
Straightness (%)	74.30 ± 0.15^b	81.48 ± 0.14^a	39.30 ± 0.16^c
Wobble (%)	76.04 ± 0.09^b	83.71 ± 0.12^a	51.00 ± 0.12^c
ALH (μm)	3.62 ± 0.01^a	1.97 ± 0.01^b	1.68 ± 0.01^c
BCF (Hz)	9.16 ± 0.02^a	6.71 ± 0.04^b	3.25 ± 0.02^c

Results are expressed as the mean ± s.e.m. Within rows, values with different superscript letters differ significantly ($P < 0.05$). The total number of spermatozoa analysed was 45 287. VCL, curvilinear velocity; VSL, straight line velocity; VAP, average path velocity; ALH, amplitude of lateral head displacement; BCF, beat cross frequency

Subpopulation 1 (sP1) included highly active but non-progressive spermatozoa (highest VCL, ALH and BCF values, together with low LIN and STR values), accounting for 44.05% of the total motile population. Subpopulation 2 (sP2) contained the lowest number of spermatozoa (17.05%) and included spermatozoa with relatively low velocity (medium VCL, VSL and VAP) but high progressiveness (high LIN, STR, WOB and low ALH). Subpopulation 3 (sP3) included spermatozoa with less vigorous movements (low VCL, VAP, ALH and BCF) and less progressiveness (low VSL, LIN and STR) than all other groups and 38.9% of the population consisted of total motile spermatozoa. The proportion of spermatozoa assigned to sP2 (moderately slow but progressive sperm) and sP3 (slow and non-progressive sperm) was significantly lower in the HI group ($P < 0.05$; Table 5), whereas the NI group had a significantly higher proportion of sP1 spermatozoa (highly active but non-progressive).

Bull fertility under field conditions

Analysis of the mating records of the 11 bulls studied showed a CI significantly higher in the HI compared with NI group (15.07 vs 14.44 months, respectively; $P < 0.05$). Bull effect and age of the cow (included as a covariate) were not significant, suggesting that the differences between groups could be explained, in part, by inbreeding.

Table 5. Changes in the frequency of sperm subpopulations sP1, sP2 and sP3 in semen samples from inbred (HI; $n = 30$) and non-inbred (NI; $n = 25$) bulls

	sP1 (%)	sP2 (%)	sP3 (%)
HI bulls	48.2	16.6	35.2
NI bulls	40.0*	17.4*	42.5*

*$P < 0.05$ compared with HI bulls (Chi-squared test)

Results of extended genetic analysis, specifically differences between the best and worst solutions for each effect, in our animal model are showed in Table 6. The largest difference, accounting for nearly 40% of the CI variability, was determined by the contemporary group. This effect is produced by the combination of herd, year, mating time of the year and therefore, environmental effects. A marked influence was also found for cow genetics (4.98% of CI variability) and PEE (permanent environmental effect of the bull; 2.4% of CI variability but with differences up to 7.53 months among bulls). In contrast, the genetic effect of the bull (F) was very limited (0.839%, with differences of 1.48 among bulls). Finally, regression analysis of the effects of inbreeding on CI was significant for cows ($P < 0.05$) but not for bulls.

Table 6. Assessment of field fertility of inbred bulls: differences between the best and the worst solutions for each genetic and non-genetic effect studied

*$P < 0.05$. HYS, herd–year–season of first calving; PEE, permanent environmental effect; Fi, xxx

Effect	Range solutions (months)	Variance components ratio (%)
HYS	17.89	39.83
Cow age	2.63	
Cow genetic	2.43	4.98
Bull PEE	7.53	2432
Bull genetic	1.48	0.839
	Regression coefficient	
Fi^{A} cow	0.176*	
Fi^{A} bull	0.089	

^{A}Inbreeding depression effect (months/percentage increase of inbreeding).

Discussion

Inbreeding has been widely described as a genetic trait that could adversely affect sperm quality in wild mammals (Shivaji et al., 1998; Asa et al., 2007; Ruiz-Lopez et al., 2010), domestic cats (Pukazhenthi et al., 2006), horses (van Eldik et al., 2006) and even cattle (Maximini et al., 2011). However, to our knowledge, the present study is the first comprehensive analysis assessing the effect of high inbreeding values (mean F = 16.3%) on sperm motility traits using computerised methods. In cattle, results from previous studies evaluating the inbreeding effect on spermatozoa are not consistent. For example, Flade and Zeller (1992) evaluated semen of experimentally produced inbred bulls (F = 25% vs F = 0%) and did not find any differences. In contrast, Maximini et al. (2011) demonstrated a correlation between F and four sperm traits (sperm volume, total sperm number, viability and subjective motility). Interestingly, both studies were performed using subjective methods (direct observation and sample classification over a motility scale of 1–5). This methodology has been reported to be less accurate and highly affected by technicians, with differences among rates of up to 30% for the same sample (Amann, 1989; Verstegen et al., 2005). In the present study, such methodological differences were ruled out because kinetic assessments were performed by using an automated computer system (CASA).

Several studies have reported that inbreeding depression increases the number of spermatozoa with abnormal morphology in both wild and domestic animals (Gage et al.; Gomendio et al., 2000; Pukazhenthi et al., 2006; van Eldik et al., 2006; Asa et al., 2007). However, knowledge of the effects of inbreeding depression on cattle spermatozoa is limited (Losdat et al., 2014). In the present study, no significant differences were found between HI and NI animals. The same results were observed for sperm viability and acrosomal status. These results are in agreement with those reported by Flade and Zeller (1992) and Ducrocq and Humblot (1995), because they show a slight but non-significant increase in the percentage of ASM associated with higher inbreeding values. More recently, Godfrey and Dodson (2005) confirmed the absence of such a correlation. In contrast, increased DNA instability or an increased percentage of immature spermatozoa were largely related to increased ASM (Persson and Soderquist, 2005; Enciso et al., 2011a). In the present study, neither DFI nor HDS differed significantly between the HI and NI groups, which is in line with the lack of differences in sperm morphology between groups.

Studies assessing the effects of inbreeding on sperm osmotic resistance in mammals are scarce and, to our knowledge, the present study is the first such study performed in cattle. The findings of the present study indicate that there is no effect of inbreeding on sperm osmotic tolerance in bulls. Previous studies reported decreased tolerance to osmotic stress in inbred wild mice reared in captivity (Malo et al., 2010), but these findings were associated with sperm morphological abnormalities. Conversely, (Garde et al., 2003) found a relationship between F and sperm osmotic resistance in some species of gazelle. However, their findings were highly affected by the species studied and so they cannot be extrapolated across different genera. In the same way, Walters et al. (2005) demonstrated that spermatozoa of inbred strains of mice (C57BL/6 and DBA/2N) were highly sensitive to hypo-osmotic conditions, mostly because of alterations in mitochondrial morphology and function, leading to decreased resistance to cryopreservation. Despite the fact that some of these morphologically altered spermatozoa could regain motility, their ability to fertilise an oocyte may still be compromised (Nishizono et al., 2004). In the present study, there were no differences in the proportion of HOS+ spermatozoa or ASM and VS between the HI and LE groups. Furthermore, although some motility parameters, mostly associated with sperm hyperactivation, were increased in inbred spermatozoa, field fertility of the HI bulls was decreased, suggesting that sperm structure and osmotic resistance are not affected by inbreeding in cattle. Thus, the decreased fertility observed in inbred bulls could be more likely related to kinetic than other sperm traits.

The genetic effect on DFI in cattle spermatozoa was recently studied by Karoui et al. (2012), who reported that only a minimum percentage of the variability (<2.5%) was explained by genetic causes. Similar findings were made in the present study: DFI was not significantly affected by inbreeding, despite the F values were higher in the present study than those reported by Karoui et al. (2012) (16% vs 5.3%, respectively). However, Ruiz-Lopez et al. (2010) and Petrovic et al. (2013) demonstrated a clear correlation between DFI and inbreeding in wild ungulates and rams. This could be explained by differential resistance to oxidative stress and DNA fragmentation of spermatozoa from different species, which was also established by Enciso et al. (2011b). Interestingly, the results of the present study showed a larger than expected variability within groups despite the high number of spermatozoa analysed for each animal (at least 80 000), suggesting that DFI is more affected by bull factors (genetic background plus environmental factors) rather than inbreeding alone. Conversely, the lack of differences in percentage HDS, a marker related to sperm maturation by Rybar et al. (2004), in association with a normal percentage of ASM suggests that inbreeding depression does not affect or impair spermatogenesis.

The negative effect of inbreeding on sperm motility has been well documented in several species, including horses (van Eldik et al., 2006), mice (Songsasen and Leibo, 1997) and wild herbivores (Gomendio et al., 2000). In contrast, results for cattle show a neutral (Flade and Zeller, 1992; Karoui et al., 2011) to very low (Ducrocq and Humblot, 1995) effect. The present study, by assessing an extended set of CASA-derived motility parameters, allowed us to draw more accurate conclusions. The increase in kinetic parameters (VCL, VSL, VAP and ALH) in HI bulls was associated with increased velocity, erratic tracks and unexpected direction changes, typical behaviour of hyperactivated (HA) spermatozoa (Cancel, 2000). Motility results were corroborated by subpopulation clustering, with the proportion of sP1 spermatozoa (highly active but non-progressive), a pattern associated with hyperactivation (Muino et al., 2008), being considerably increased in the HI group. Although this movement is important for egg penetration, premature sperm hyperactivation could impair sperm transport along the lower female reproductive tract (Olds-Clarke and Wivell, 1992). This effect has been reported in mice, in which epididymal motility was increased in inbred strains but fertility was reduced (Carey and Olds-Clarke, 1980), and in donkeys, where individuals with a higher percentage of HA spermatozoa were less fertile (Dorado et al., 2013) . Therefore, we hypothesise that the early sperm hyperactivation observed in HI bulls could hinder access of the spermatozoa to the fertilisation site because of the premature exhaustion of energy reserves, subsequently reducing their fertilisation capacity. This hypothesis is in agreement with the results of the field fertility analysis, which showed significantly increased CI for calves derived from HI bulls. Interestingly, when we selected the animals for the experimental design, we noticed that bulls with such extreme F percentages were used commercially as sires. In our case (Retinta bulls), ANCRE by-laws do not prohibit their use and some breeders, against the genetic counselling provided by the association, only take into account bull morphology and 'pedigree' to select future sires.

It is well known that the genetic response to selection is less efficient for reproductive traits, and even less for fertility, than for several productive traits because reproduction is strongly affected by non-genetic components (reproductive diseases, nutritional status, herd management, year) and has already been affected by natural selection over several generations. However, the results of the present study showed that, in the absence of external factors, HI bulls had an impaired reproductive performance and an extended CI (0.6278 extra months on average) under field conditions compared with NI bulls. These findings agree with those of Charlesworth and Willis (2009), who demonstrated that the increase in homozygosity and the overexpression of deleterious recessive alleles (partial dominance) affect the reproductive performance of animals and suggested that F values must be included in any selection scheme in cattle.

A broader genetic analysis of the ANCRE database (159 bulls) was performed using a REML (restricted maximum likelihood) animal model. This methodology takes into account several genetic and non-genetic effects very efficiently, including all the relationship information among animals at any level. With this analysis, we demonstrated that CI was highly influenced by the. However, most of this effect was explained by non-genetic factors, such as herd–year–season (HYS) of first calving or PPE. These results agree with those of Mackinnon et al. (1990), who found that the male component of fertility under extensive breeding systems with a prevalence of natural mating is larger than in populations with heavy use of AI. In the present study these results were unexpected because Retinta bulls are screened to avoid the use of individuals with poor sperm quality. Therefore, we hypothesise that such differences could be explained by sperm parameters not included in the basic semen analysis performed, such as the detection of premature hyperactivated motility. Conversely, the effect of inbreeding on CI was better explained by the F value of the cow than the mating bull (4.98% vs 0.84%, respectively). This has also been reported by Gonzalez-Recio et al. (2007) and Mc Parland et al. (2009), who found lower pregnancy rates associated with highly inbred cows. However, together, the results of CI analyses (the absence of significance in the extended genetic model and extended CI in HI bulls) may suggest that the effect of inbreeding on sperm is only significant when a certain threshold F value is reached, because the extended analysis included animals with F values ranging from 0% to 18.7%, whereas the lower F value of the HI bulls was 13.5%. These results agree with previous studies performed looking at the productive traits of dairy cows, where an inbreeding 'threshold' was proposed (Hansen, 2000; Sewalem et al., 2006).

Conclusion

In the present study, using objective and automated methodology, we demonstrated, for the first time, that inbreeding affects bull sperm motility. Inbred bulls showed a premature hyperactive-like motility pattern, associated with increased sperm velocity (VCL, VSL and VAP) and ALH. In addition, cows mated with inbred bulls had an increased CI under field conditions. However, we cannot determine whether the reproductive impairment observed was caused by effects associated with the spermatozoa (premature hyperactivation) or inbreeding (partial dominance, overdominance or epistasis). Further complex experiments including genotyping (single nucleotide polymorphism array genotyping or full sequencing) of embryos produced from highly and non-inbred animals are needed to clarify this issue.

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CAPÍTULO V

Capítulo V: Genetic effects of climatic seasons on preweaning growth of beef cattle: a first approach to Retinta calves.

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Summary

Heat stress is a serious concern in agriculture industry, producing serious economic losses in the last years due to the increase in average temperature. We analyzed 7,753 live weight records from 3,162 Retinto calves, born of 1,249 dams and 85 sires raised in the Andalusian region and collected during nine years (equivalent to two generation intervals). During the same period, a comprehensive automated climatological characterization was performed, including data from four different weather stations. The aim of the present study was to perform a first methodological approach for estimating the importance of climatic factors in genetic parameters that may cause genotype-environment interaction problems in growth traits of the Retinto population, using random regression models (RRM). The effect of heat stress on the animals from birth to weaning was measured with the temperature-humidity index, calculated as the combination of ambient temperature and relative humidity. A reaction-norm model following a bivariate random regression model was used to estimate the (co)variance components of weaning weight in two different climatic seasons. Overall assessment did not show significant effects of the genotype-environment interaction. However, a highly significant evidence of genotype-climatic condition interaction was found during the calf´s first three months of growth. Those differences showed a clear differential pattern of heritabilities among calves reared in summer and in the winter season, and a convergent pattern of growth heritabilities after three months of age. Globally weaned calves reared at the cold season showed a greater growth from 70 to 160 days in comparison with the individuals reared at the warm season.

Keywords: Beef cattle, random regression, THI, weather stress, reaction norm

Introduction

Extensive livestock production is characterized by an important dependence on weather conditions. This situation is partially mitigated by the use of autochthonous breeds adapted to the local productive environment at the expense of highly selected individuals which cannot cope with extreme weather conditions. In this sense, McMichael et al. (2007) suggested that most of the livestock individuals reared under extensive conditions will be submitted, on a yearly-increased basis, to augmented heat stress due to the effects of climate change. Furthermore, international consensus indicates that this problem is expected to worsen in the next decades (IPCC, 2014). Additionally, extensive livestock production is also increasing due to the necessity of a reduction in the cost per kilogram produced, the derivation of highly productive lands to agricultural uses and the environmental pollution produced by intensive livestock schemes (Mazzetto et al., 2015).

Heat stress has been reported as a cause of performance decline and important economic losses in livestock animals (Mader, 2003; St-Pierre et al., 2003; Nienaber and Hahn, 2007). The effects of exposure to high temperatures range from a reduction of feed intake and an increase in respiration rate and water intake to changes in hormonal signals that affect target tissue responsiveness to environmental stimuli (Collier and Zimbelman, 2007). The decrease in energy intake due to reduced feed results in a negative energy balance; consequently, the body weight of cows subjected to heat stress goes down (Lacetera et al., 1996). Furthermore, individuals experimenting heat stress showed a diminished immunological capability and a reduced ability to cope with their environmental conditions (Silanikove, 2000).

The first experimental approach to select animals based on stress tolerance was proposed by Misztal (1999) through the evaluation of the productive reaction of individuals to increasing heat loads (reaction-norm model). The main advantage of this procedure is the utilization of accessible productive and reproductive records (usually available from the selection schemes of breeder's associations) in combination with weather parameters, which can also be rapidly obtained from automated stations belonging to national weather systems located close to the farms, as is the case of Spain (Carabano et al., 2017). With these records, a modified reaction norm-model (using random regression methods) can easily determine the genotype-environment interaction, allowing to detect the best genetically adapted individuals to an increased temperature range (Santana et al., 2016).

Most of the studies evaluating the application of reaction-norm models to produce heat tolerance breeding values have been performed in dairy cattle. Intensive selection were based on production traits, intensive and environmentally controlled production systems and poor adaptation to high thermal loads (Ravagnolo and Misztal, 2000; Bohmanova et al., 2005; Sanchez et al., 2009; Brugemann et al., 2011; Carabano et al., 2014). On the contrary, only a few studies have been very recently performed in extensively raised beef cattle (Bradford et al., 2016; Santana et al., 2016). The last one was performed in zebu cattle, which are naturally selected for heat environments since they were established as different breeds. However, heat stress played an important role in both studies, since the animals were exposed to different stressful climatic variables along the year and throughout their entire life in the herds.

Retinta is a small autochthonous breed (200,000 breeding individuals approximately) widely used in the south of Spain due to its excellent adaptation to the hard environment (Morales et al., 2013). Individuals are raised and bred in an extensive regime characterized by pasturelands with scarce production, steep hills and a dry and hot climate (Rodero-Serrano et al., 2013). In these extensive systems, the effect of environmental (nutrition and climatic conditions) and health (parasites and diseases) stresses is rapidly manifested as a depression in weight gain and reproductive parameters (Vercoe and Frisch, 1980). Under these conditions, increased stress tolerance is a highly desirable trait which is visible in most individuals. Despite the fact that breeding in purity is largely preserved in Retinta, the breed is also used as a maternal line in crossbreeding with highly productive continental breeds, such as Charolais and Limousin, yielding highly profitable terminal-cross individuals.

Here we analyzed the influence of several weather parameters on the growing ability of purebred Retinta calves using random regression (reaction-norm) models. More than 3,000 individuals were analyzed in two largely characterized different environments to determine the most reliable parameters to be included in the Retinta breeding scheme. We also aimed to determine the real impact of the genotype-environment interaction in the Andalusian extensive beef production system which could be used as a baseline to be extrapolated to several minority breeds used in this area.

Material and methods

Animals and growth records

Growth records of 3,162 calves from 14 Retinta herds located in the south of Spain were collected between birth and 245 days of age in a nine-year period (approximately equal to two generation intervals). Farms were selected according to the reliability of their records and the importance of their Retinta pedigree and history. In total, 7,753 live weight determinations were performed in calves derived from the combination of 85 sires and 1,249 cows. The pedigree of each individual was provided by the Retinta Breeders Association, obtaining a final figure of 6,053 animals.

Environmental characterization

Climate data were obtained from four weather stations located near the farms. The heat load in each herd was estimated daily using the temperature and humidity index (THI) according to Finocchiaro et al. (2005) as:

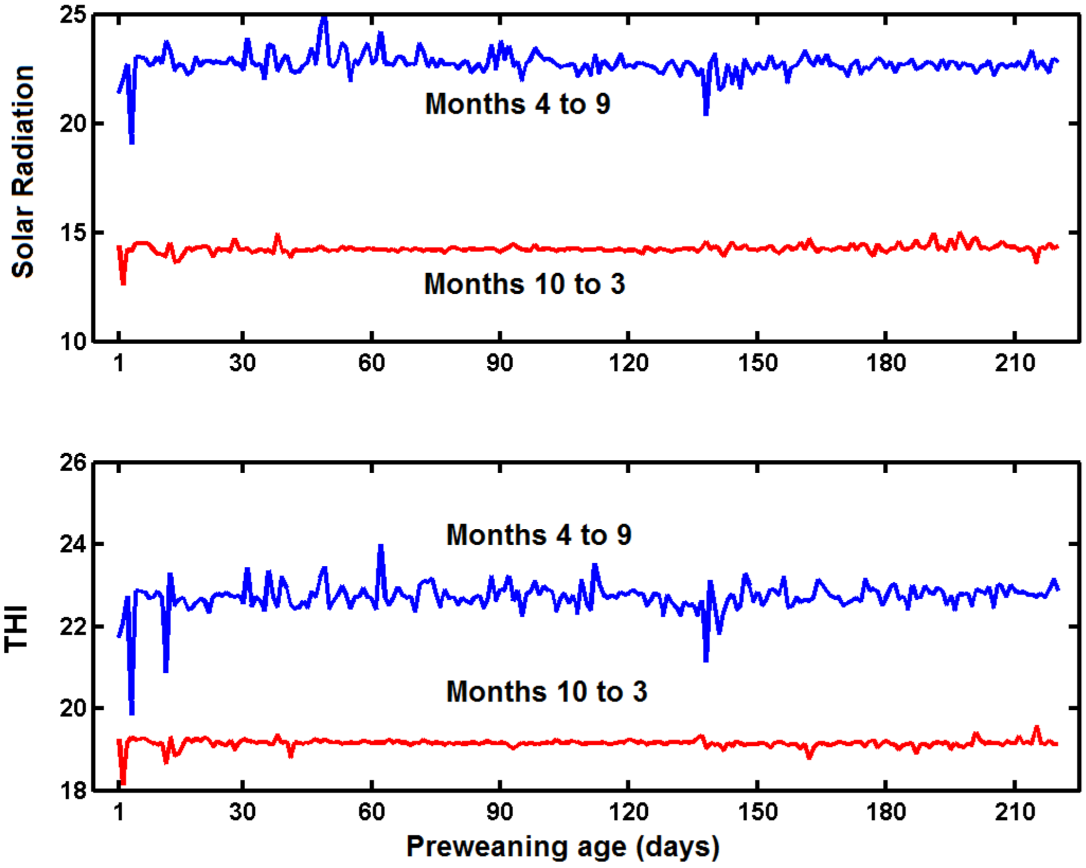
$$\mathbf{THI = Tdb - (0.55 - 0.0055 \times RH) \times (Tdb - 14.4)}$$

where **Tdb** = dry bulb temperature (°C) and **RH** = relative humidity of the air (%).

Solar radiation (SR; MJ/m^2 per day) was also registered to define the annual variation and to determine the existence of weather seasons based on systematic records.

Two clearly differentiated climate periods were identified; a warm or high heat stress (HHS) period from April to September, and a cold or low heat stress (LHS) period from October to March (Figure 1).

Figure 2. Evolution of THI and RS indices during pre-weaning growth of Retinta cattle in the two climatic categories used for the study of heat stress.



Reaction-norm model

Individual live weight results recorded during the HHS and LHS seasons were considered as two different traits. A bi-character random regression model was applied and components of variance were estimated throughout the trajectory of the pre-weaning age intra-stress zone. The model was:

$$y_{ijkl:z} = \text{fixed} + \sum_{r=0}^{3} \Phi_r \beta_{:z} + \left[\sum_{r=0}^{1} \Phi_r \lambda_k a_{i_r} \right]_z + Z_1 p_i + e_{ijkl}$$

Where $y_{ijkl:z}$ is the ith records of live weight in each **z** stress zone, **fixed** is a set of fix effects: sex of the calf with two levels, parity effect of the dam with ten levels (CNj, j = 1,2,…6 or more calvings) and combined herd-year with 355 levels. Age effects were analyzed by a fixed covariable intra **z** stress zone ($\beta_{:z}$) by a Legendre polynomial (Φ) of order r=3.

Genetic effects (a_i) were calculated by a random regression matrix (λ_k) intra stress zone with a Legendre polynomial (Φ) of order r = 1. Z_1 is an incidence matrix of permanent environmental random effects (p_i) due to repetitions of the same trait in the animal. e_{ijkl} is a random error common to all observations. A residual intra-zone stress variance was evaluated but did not contribute to any increase to the model fit. All the statistical analyses were carried out using the Asreml software (Gilmour et al., 2009a).

In this norm-reaction model, the variance can be estimated by:

$$\mathbf{var(y)} = \mathbf{\Phi_1}(\lambda_{\mathbf{k:z}} \otimes \mathbf{A})\mathbf{\Phi_1'} + \mathbf{I_p}\sigma_{\mathbf{p}}^{\mathbf{2}} + \mathbf{I_n}\sigma_{\mathbf{e}}^{\mathbf{2}}$$

in which $\mathbf{I_p}\sigma_{\mathbf{p}}^{\mathbf{2}}$ and $\mathbf{I_n}\sigma_{\mathbf{e}}^{\mathbf{2}}$ are variances of permanent environmental random effects and residual effect, with matrices of identity $\mathbf{I_p}$ and $\mathbf{I_n}$, respectively. These variance components are given directly by Asreml, while the expected (co)variance components through different ages of the cow for each stress-zone can be represented by a further random regression matrix modification $\lambda_{\mathbf{k:z}}$ by the following four sub-matrices:

$$\lambda_{\mathbf{k}} = \begin{bmatrix} \lambda_{\mathbf{h}} = \begin{pmatrix} \sigma_{\mathbf{ih}}^{\mathbf{2}} & \sigma_{\mathbf{is,h}} \\ \sigma_{\mathbf{si,h}} & \sigma_{\mathbf{sh}}^{\mathbf{2}} \end{pmatrix} & \lambda_{\mathbf{hl}} = \begin{pmatrix} \sigma_{\mathbf{ih,il}} & \sigma_{\mathbf{ih,sl}} \\ \sigma_{\mathbf{sc,ib}} & \sigma_{\mathbf{sh,sl}} \end{pmatrix} \\ \lambda_{\mathbf{lh}} = \begin{pmatrix} \sigma_{\mathbf{il,ih}} & \sigma_{\mathbf{il,sh}} \\ \sigma_{\mathbf{ls,ih}} & \sigma_{\mathbf{sl,sh}} \end{pmatrix} & \lambda_{\mathbf{l}} = \begin{pmatrix} \sigma_{\mathbf{il}}^{\mathbf{2}} & \sigma_{\mathbf{is,l}} \\ \sigma_{\mathbf{si,l}} & \sigma_{\mathbf{sl}}^{\mathbf{2}} \end{pmatrix} \end{bmatrix} \otimes \mathbf{A}$$

The diagonal sub-matrices elements ($\lambda_{\mathbf{h}}$ y $\lambda_{\mathbf{l}}$) are used to estimate the variances of live weight over the pre-weaning age on HHS and LHS environment conditions, symbolized as **h** and **l** respectively, while the correspondent (co)variances are contained in $\lambda_{\mathbf{hl}} = \lambda_{\mathbf{lh}}$. The (co)variance estimates were obtained applying a procedure proposed by Jong (Jong, 1995); details of practical application with data of this breed were recently presented by Morales et al. (Morales et al., 2013). Heritability at **j** age and genetic correlations between any pair of ages in both stress zones were determined by classical methodologies.

Results and Discussion

Despite limitations in the experimental design, such as the fact that several environmental factors were not included in this analysis (e.g. nutritional management, livestock load of the farm, grazing strategies) and that the weather range analyzed was included within the hot summer Mediterranean climate (CSA, according to the Köppen-Geiger climate classification; Kottek et al. (2006)), our study aimed at demonstrating the flexibility and potentiality of reaction-norm random regression models to evaluate the genotype-environment interaction in extensive cattle productions systems.

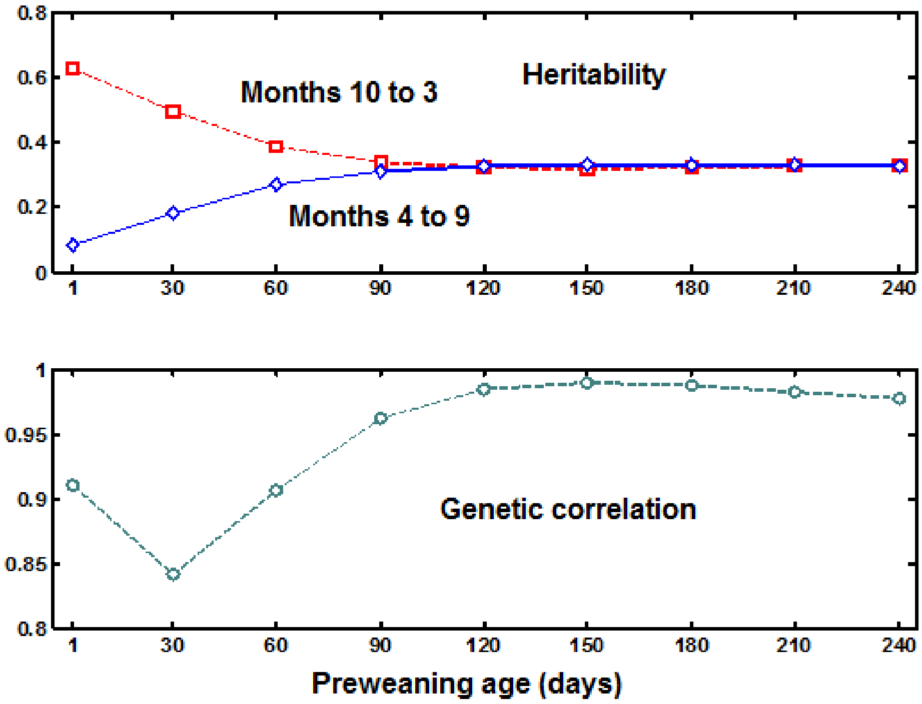
The south of Spain and specifically the Andalucía region has a harsh weather, usually characterized by cold winters and dry and hot summers, and by very abrupt changes between them. This is reflected in the analysis of the weather data collected during nine years, which showed two clearly differentiated climate seasons: a warm season from April to September (HHS) and a cold season from October to March (LHS) (Figure 1).

HHS was characterized by a 40% increased SR and 20% increased THI as compared with LHS. However, monthly THI and RS variations within seasons were negligible.

In this study, we used an analytical methodology previously employed in dairy cattle (Ravagnolo and Misztal, 2000; Aguilar et al., 2009) and swine (Zumbach et al., 2008; Fragomeni et al., 2015) in a Mediterranean grazing beef production system. It is noteworthy that previous reports were performed in species raised in confined systems in which the environmental conditions were tightly controlled with a minimum variation among farms. Our experimental results, performed for the first time under extensive conditions, showed that these methods are also valid and can be utilized in the evaluation of grazing animals.

Live weight variance components and heritabilities were estimated in each climatic season during the pre-weaning period. All the variables analyzed were significant, but the interaction weather season-age of the calf was highly significant, suggesting that climatic conditions could have an increased influence during the first months of life of the calf. Additionally, genetic correlations between both climatic periods were also estimated, showing values under 1 in the first three months of age and close to 1 after this age (Figure 2). These results strongly suggest a highly significant interaction of the environment with the genotype during the calf´s first months of life.

Figure 2. Heritability and genetic correlations of live weight through the pre-weaning trajectory in each climatic class.

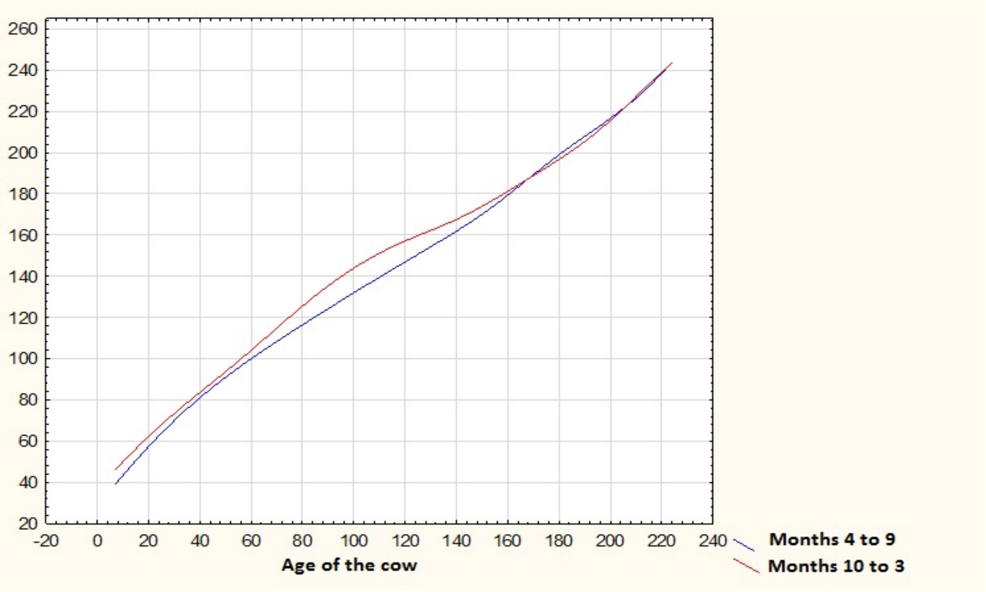


In a previous study, Bradford et al. (2016) determined a heritability close to 0.24 for weaning weight in Angus cattle using reaction norm models with intermediate heat loads.

Results obtained in similar studies but with more favorable environmental conditions and zebu cattle were higher (Cardoso and Tempelman, 2012; Santana et al., 2016). In our case, heritabilities showed a wide range of variation throughout the calf's age, but they were significantly higher during the first 90 days of growth (Figure 2). After this point (end of the third month), the heritabilities observed were not significant, converging to zero after 120 days of growth. This phenomenon could be partially explained by differences in heat stress tolerance between individuals, but it could also be due to differences in the availability and quality of pasturelands acting through the maternal ability (mainly via milk production) which is crucial during this initial period when calf growth is basically dependent on it. Several studies have also demonstrated that milk production is severely affected by the heat stress tolerance of the individual (Bohmanova et al., 2005; Aguilar et al., 2009; Sanchez et al., 2009; Carabano et al., 2014), suggesting that those individuals could be affected by the heat stress tolerance of their genotype, but also by the genotype of their mother. Likewise, it is noteworthy that genetic correlations between climatic periods are extremely high during the last period of growth of the calf, in which the dependence on maternal milk is much lower.

Despite the overall interaction determined in this study was not significant, genetic differences between climatic seasons were significant at particular growing periods of the calf. This phenomenon was also recently described by Santana et al. (2016), who observed a substantial heterogeneity in the (co)variance components for weaning weight analyzing different environmental conditions associated as an evidence of the genotype-environment interaction. Moreover, these authors demonstrated that the best fit animals detected in the less stressful environments were not necessarily the more suitable, and even suitable at all, to be raised in the more stressful environments. In our study, it is clear that individuals that grew during HHS were submitted to a highly stressful environment in comparison with the group reared in LHS. Nevertheless, the number of records analyzed in each category was homogeneous, suggesting that Retinta calves are well adapted to the environmental conditions observed in HHS.

Figure 3. Evolution of live weight in the pre-weaning age trajectory of Retinta calves and in each climatic class.



Based on these studies, we would expect a lower response to selection for weaning weight populations reared under more stressful environments, since a greater growth appeared from 70 to 160 days in animals raised during the cold season (Figure 3). However, globally there are no differences between them, probably because of a compensatory growth that equalizes calf weights after this age, considering that in the pre-weaning phase the dam begins to reduce its amount of milk, forcing to the calf to consume grass. These individuals are reared under extensive grazing conditions in which the animals harvest their own forages. Thus, the effect of calving season and heat load could be more related to the availability of grasses than to the thermal stress of the animal.

Conclusions

In conclusion, we demonstrated differences in the heritability pattern of individuals reared in different environments during the first 90 days of age. However, such differences were not significant at the end of the growing period. Our results confirmed a clear variability among individuals since animals raised during the cold season showed a greater growth from 70 to 160 days and could be used as a baseline for further studies including an ample range of rearing environments as well as the nutritional differences derived from environmental differences.

Acknowledgements

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DISCUSIÓN GENERAL

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La subsistencia del sector vacuno de carne español ha estado ligada en muchos casos a las ayudas comunitarias, pero ante el nuevo enfoque más sostenible de las políticas agrarias de la Unión Europea, se hace más que nunca necesaria una reestructuración del sector orientada hacia un aumento de su rentabilidad. Este sector se caracteriza, según datos del MAPAMA, por una baja fertilidad y una elevada edad al primer parto. El número de terneros registrados por vaca y año se sitúa en 0,68, siendo la edad al primer parto superior a los 3 años para el 44 % de los primeros partos registrados, lo que supone una baja productividad, y con ello, una elevada pérdida económica (López-Paredes and Alenda, 2015). Con el fin de aportar nuevas herramientas de valoración genética que permitan optimizar los programas de selección de las razas locales bovinas de aptitud cárnica, se ha llevado a cabo la presente Tesis Doctoral. En la misma se ha utilizado como modelo productivo a la Raza autóctona Retinta, la segunda raza española de vacuno de carne en cuanto a censo, y la primera de la España seca.

La raza Retinta, bovino de aptitud eminentemente cárnica, se caracteriza además por una elevada rusticidad y un marcado carácter maternal. Los criterios de selección aplicados dentro de su programa de mejora se han traducido en un progreso de los principales caracteres productivos relacionados con el crecimiento (el peso medio al destete está en torno a 200 kilos y 180 días de edad) y con la reproducción (el periodo medio de interparto se sitúa por debajo de los 15 meses y la edad media al primer parto es de 35 meses debido a que la primera cubrición de las novillas se suele realizar entre 20 y 28 meses de vida). El Real Decreto 2129/2008, de 26 de diciembre, la define como una raza autóctona de fomento y por lo tanto susceptible de acceder a las líneas de ayudas que establece el *Programa nacional de conservación, mejora y fomento de las razas ganaderas (Ministerio de Medio Ambiente, 2009).* En él se pone de manifiesto que los recursos genéticos animales son un patrimonio único, remarcando que las razas autóctonas son las mejor adaptadas al medio ambiente en el que se desarrollan. Pese a ello su censo se ha visto muy reducido, debido fundamentalmente a la introducción de razas foráneas que ofrecen mayores producciones, o un producto más acorde con el mercado actual (especialmente en cuanto al tipo de canal). Sin embargo, en muchos casos, el uso de estos animales supone que estén peor adaptados al medioambiente, lo que conlleva un aumento de los costes en suplementación y sanidad, además del consecuente impacto en los ecosistemas tradicionales al tener que intensificarse su sistema productivo.

En las ganaderías de producción cárnica, el coste de producir un ternero y llevarlo hasta matadero, se centra principalmente en el costo del mantenimiento de la vaca (Consortium, 2010), el cual incluye no sólo el coste del periodo productivo sino también el del período desde su nacimiento hasta su primer parto. Tradicionalmente, los esfuerzos de mejora se han centrado en aumentar el crecimiento predestete, que conlleva un aumento del crecimiento postdestete de forma correlacionada. No obstante, una elevada intensidad de selección hacia el crecimiento, y en especial hacia el crecimiento magro, puede tener sus contraindicaciones a medio-largo plazo, ya que nos enfrentamos a un sistema dependiente del medio. Estos sistemas, en los cuales es necesaria la rusticidad de los animales, hacen que el uso de animales altamente seleccionados para el crecimiento, y por tanto menos adaptados, pueda determinar un deterioro del rendimiento reproductivo y de la longevidad productiva de las reproductoras.

El Plan de Mejora del ganado vacuno de raza Retinta tiene como objetivo último la mejora de las cualidades cárnicas de los animales como vía de contribución a la rentabilidad de las explotaciones de esta raza, haciendo especial hincapié en la explotación en pureza, pero sin olvidar su carácter maternal ni su frecuente uso en el cruzamiento industrial. Hasta el momento su Esquema de Selección se ha centrado en la mejora del crecimiento, de la conformación de los animales, así como de los caracteres reproductivos tanto de la hembra como del macho. Una vez conseguidos unos niveles productivos más que aceptables en estos parámetros, se apostó también por una mejora en la calidad de la carne mediante la puesta a punto de la metodología de detección del polimorfismo genético de genes con un efecto demostrado en la terneza de la carne (μ-calpaína, CAPN1 y calpastatina, CAST), y en el grado de infiltración de grasa intramuscular en ésta (diacilglicerol O-aciltransferasa 1, DGAT1). No obstante, en la actual coyuntura económica del sector del vacuno de carne, con rentabilidades muy ajustadas, ayudas económicas de la política agraria común (PAC) con una clara tendencia a la desaparición y una creciente competencia en los mercados internacionales, se hace necesaria la mejora de otros caracteres con gran peso en la rentabilidad de las ganaderías, como son los relacionados con la longevidad productiva y la productividad global de las reproductoras. Mediante este tipo de caracteres se permitiría amortizar de forma adecuada los costes asociados a la recría y el mantenimiento de las hembras, como fue demostrado y realizado hace una década en la mejora del vacuno de leche. En este sentido, Martinez et al. (2004a), demostraron que una vida productiva más larga aumenta los beneficios al disminuir el costo anual de la reposición de las vacas, aumentando la producción del rebaño a través de una mayor proporción de vacas en los grupos de edad de más alta producción, disminuyendo el número de hembras criadas para reposición y aumentando los sacrificios voluntarios (lo cual incrementa la longevidad funcional de los animales). Uno de los problemas al que nos enfrentamos al estudiar esta variable es que gran parte de la población del estudio está aún viva y por lo tanto carece de parte de su información productiva, así como de la duración de su vida en el rebaño. El desarrollo de metodologías como el análisis de supervivencia, que combina información de animales vivos (censurados) y muertos, nos ha permitido abordar este problema.

En el segundo capítulo de esta Tesis, se empleó la metodología de supervivencia con el objetivo de evaluar la posibilidad de incluir estas técnicas en el programa de mejora. Utilizando el paquete Survival Kit, un software específico actualmente considerado como el estándar de referencia a nivel mundial (Ducrocq and Sölkner, 1994), y un modelo de distribución de Weibull (Mészáros et al., 2013) se analizaron tres variables asociadas a esta característica: duración de la vida real (tiempo desde el nacimiento hasta el último parto conocido), duración de la vida productiva (tiempo desde el primer parto hasta el último parto conocido) y número de partos (número de partos entre el primero y el último conocido). Las tres variables mostraron estar muy influenciadas por factores asociados al ciclo productivo, como los efectos de la ganadería (en los que se incluyen diversos factores de difícil definición como el manejo reproductivo, alimenticio o sanitario), el año y la época de nacimiento de la vaca y del ternero. También se encontraron diferencias en el tipo de raza usada para el cruzamiento, manifestando aquellas vacas dedicadas a la cría en pureza un menor riesgo de ser eliminadas del rebaño (capítulo 2, figuras 1 y 2). Este hecho debería estudiarse más en profundidad y determinar su verdadero alcance, ya que podría ser más conveniente dejar de utilizar cruces con razas de crecimiento rápido si conseguimos un aumento de la vida de la reproductora tal, que supere el global de kilos de carne producidos (pese a producir terneros menos pesados). En detrimento de este hecho, está la penalización que hace el mercado al animal puro de razas autóctonas, muy por encima de lo que los datos objetivos recomendarían, en relación a los animales cruzados o puros de razas continentales. Basta recordar que la mayoría de canales procedentes de los animales de razas como la Retinta se clasifican en la categorización SEUROP como R3 (buena), siendo el porcentaje calificado como U (muy buena) muy pequeño. Por el contrario, un animal cruzado RetintoxLimusin o Charolés se incluye normalmente en la categoría U, y hasta en la categoría E (excelente) en algunos casos (Ministerio de Agricultura, 2008).

Las correlaciones genéticas entre las tres variables fueron superiores al 96%, por lo que cualquiera de ellas podría ser utilizada como criterio de selección. Sin embargo, al estudiar las heredabilidades obtenidas, se comprobó que la variable "número de partos" presentaba una heredabilidad mucho mayor a las otras dos (cercana a 0,30), lo que nos permitirá obtener una mejora fenotípica de este carácter mucho más rápido. Por este hecho, el presente trabajo a concluido que esta debería ser la variable a utilizar en las valoraciones genéticas (Capítulo 2, tabla 3).

Al analizar la evolución genética de estas variables a lo largo de los últimos 20 años, se encontró una tendencia positiva (un incremento de la vida productiva, capítulo 2, figura 4). Esto puede ser debido, además de la parte atribuible a la mejora en las condiciones ambientales, a una selección más o menos empírica por parte del ganadero, que, consciente de la importancia de esta variable, ha ido dejando recría propia obtenida de las familias más longevas. Además, debemos mencionar la existencia de una pequeña correlación genética positiva entre estos caracteres y el peso al destete, la cual es una de las principales variables por la que se ha estado realizando la selección en las últimas décadas (capítulo 2, tabla 4).

No obstante, el anterior criterio no tiene en cuenta las características de los terneros obtenidos en cada parto, pudiéndose dar el caso de que un incremento del número de partos sea contraproducente para la productividad global si las características del crecimiento de los terneros producidos no son adecuadas. Por ello nos planteamos en el tercer capítulo de esta Tesis, un análisis longitudinal de esta productividad global en función de la edad utilizando modelos de Regresión Aleatoria.

Nuestro enfoque experimental se centró en la utilización de metodologías de RRM, las cuales permiten el análisis de datos longitudinales (recogidos varias veces a lo largo de la vida del animal) maximizando el uso de la información disponible (Hill and Brotherstone, 1999; Bilal and Khan, 2009), al aprovechar las covarianzas entre los controles del mismo animal. Esto determina un incremento de la fiabilidad de las estimaciones, evitando el uso de una variable resumen ya que la metodología emplea directamente toda la información existente del animal, lo cual evita las desviaciones producidas por la propia tipificación a una edad en concreto lo que permite un control ambiental mucho más específico (Jamrozik and Schaeffer, 1997). Determinante todo ello de un incremento en la estimación de las heredabilidades de los parámetros (Swalve, 1998), lo cual favorece el progreso genético en la población por unidad de tiempo (Uribe, 2001). Adicionalmente, esta metodología permite obtener una función de evolución de los parámetros genéticos (y por tanto de los valores genéticos de los animales) a lo largo de la vida del animal, lo cual es de suma importancia ya que se ha comprobado que la activación, desactivación o modificación del nivel de expresión de diversos genes, así como las modificaciones postrascriptacionales están altamente influenciadas por la edad del animal, lo cual permite realizar predicciones mucho más fiables y con una base genética más ajustada. En ganado de leche, se consideraban a las diferentes lactancias como un mismo carácter. Sin embargo, en la actualidad éstas se asumen como diferentes caracteres positivamente correlacionados pudiendo obtener para cada lactación heredabilidades para cantidad de leche, proteína y grasa, como se recoge en la revisión de Thompson et al. (2005).

La principal limitante del uso de RRM es el aumento en las complicaciones de los modelos y de las necesidades computacionales, las cuales se encuentran muy por encima de las requeridas por los modelos multicarácter (MTM), debido principalmente a que las matrices de incidencia y de coeficientes son más densas y el número de efectos a estimar se ve incrementado de forma exponencial (Uribe, 2001). Aunque Nobre et al. (2003) demostraron que, en análisis complejos, RRM requiere menos memoria y mucho menos tiempo que el análisis de MTM equivalente. Para resolver la complicación de modelar la evolución de estas varianzas y covarianzas a lo largo del periodo analizado se han desarrollado diferentes estrategias (como pe. el uso de Splines, o el de polinomios ortogonales), siendo los más aplicados los polinomios de Legendre (Kirkpatrick et al., 1990).

Para comprobar su eficacia en la estimación de los componentes de la varianza para los efectos genéticos directos, maternos y su covarianza a lo largo de los partos de la vaca, para los caracteres de peso al destete y de peso a los 4 meses de edad del ternero (medida indirecta del potencial lechero de la hembra) se compararon los resultados obtenidos mediante RRM con los de un modelo multivariado que considera los pesos de los terneros de los diferentes partos como variables diferentes, y con los de un modelo univariado para el peso al destete que asume que dichas variables son expresión del mismo carácter en los distintos partos de la vaca (primer capítulo de esta tesis).

Según los resultados de este análisis se puede inferir que la vaca Retinta manifiesta un adecuado comportamiento materno, destetando un ternero cuyo peso representa aproximadamente el 36% de su peso vivo, siendo el coeficiente de variación genético aditivo del orden de 10.2% y 12.2% para P120 y P180 días respectivamente. Estos valores implican la existencia de un amplio margen de posibilidades para realizar un trabajo de selección (Capítulo 1, figura1). En los tres modelos, las h^2 para efectos directos (Ed) y efectos maternos (Em) fueron relativamente altas, aunque dentro del rango de valores publicados en vacuno de carne (Gutierrez et al., 1997; Menéndez-Buxadera et al., 2008; Baro et al., 2012), y semejantes a los publicados por Molina et al. (1999) en esta misma raza (capítulo 1 tablas 1, 2 y 3). Como era de esperar, y como ya fue demostrado por innumerables trabajos previos en vacuno de carne (Koch, 1972; Meyer, 1992; Robinson, 1996; Quintanilla et al., 1999), se encontró un marcado antagonismo entre ED y EM, lo cual puede restringir las posibilidades de selección si este hecho no es tenido en cuenta (Wilson and Reale 2006).

Las correlaciones obtenidas para los valores genéticos (VG) de los animales estimados por los tres procedimientos fueron altas, lo cual confirma que los modelos actuales de valoración que se han seguido en las últimas décadas podrían considerarse aceptables como método de rutina. Sin embargo, ha quedado demostrado que el enfoque transversal de los modelos UVM o MTM, en el cual se asume que los diferentes registros de cada vaca son manifestaciones del mismo carácter, puede producir resultados sesgados ya que, según muestran los resultados del modelo RRM, el comportamiento maternal no es constante entre sus diferentes partos, lo cual sugiere de manera clara que se trata de un rasgo que debe ser analizado en forma longitudinal. Por otro lado, el estudio de la evolución de cada animal presenta un valor añadido muy importante, por cuanto permite detectar diferentes patrones de evolución de gran repercusión a la hora de determinar el momento óptimo de eliminar la reproductora o de seleccionar el tipo de amortización de las mismas (más o menos prolongado) en función del progreso genético que se quiera conseguir (a mayor vida productiva, mayor intervalo intergeneracional y menor progreso genético anual) y de la amortización anual de las reproductoras.

Para ilustrar estas posibilidades se seleccionaron independientemente los 500 animales superiores según su VG para Ed y Em (estimados por el método oficial empleado por la asociación de criadores, modelo UVM) y se los comparó con la evolución de los mismos caracteres en los mismos animales, pero estimados por el modelo RRM durante toda la escala de los partos de la vaca. Los resultados fueron claros y lograron identificar dos tipos de animales (capítulo 1, figura 2):

- Animales Estables: son aquellos que manifiestan un comportamiento constante en toda la trayectoria, producto de un mérito genético en el que la pendiente de la función de valores genéticos (parte del mérito que va variando con la edad) tiene escasa importancia en relación al intercepto (parte estable del mérito genético a lo largo de la vida del animal).

- Animales Plásticos: son aquellos con un peso menor del intercepto en relación a la pendiente de la función. En este caso podemos encontrar animales que van incrementando su productividad en relación al resto de animales de referencia conforme va incrementándose su edad, animales en los cuales la productividad va disminuyéndo al envejecer o incluso animales cuya evolución sigue una forma polinómica (pe. animales que van incrementando su potencial genético relativo hasta una determinada edad para descender a partir de esta).

Resulta evidente que este tipo de información puede ser muy útil para los objetivos del programa de mejora de esta raza, pudiendo seleccionar de manera mucho más ajustada animales más adaptados a cada sistema de producción. Mediante esta tecnología, algunos ganaderos optarán por animales estables, que asegurarán una productividad adecuada a lo largo del máximo número de años posible, mientras que otros elegirán una amortización acelerada para obtener un mayor progreso genético, con animales plásticos, muy productivos en los primeros años de vida, que serán desechados rápidamente al bajar su productividad.

Este estudio, centrado en el peso al destete en los diferentes partos de la vaca, permitió abordar de forma conjunta los dos grupos de caracteres relacionados con la rentabilidad de la explotación analizados de forma separada en los capítulos primero y segundo (evolución de los pesos de los terneros y longevidad). Es por ello que el el tercer capítulo se centró en la realización de un estudio sobre la productividad acumulada (ACP), la cual está definida como la cantidad de kilogramos de ternero destetados a lo largo de las diferentes edades de la reproductora, componente esencial para la rentabilidad de las explotaciones de vacuno extensivo. Este análisis tuvo como objetivo monitorizar el desarrollo de cada individuo a lo largo de su vida productiva, lo que nos permitiría conocer el momento óptimo para el desvieje, mediante la determinación del punto en el cual las vacas dejan de ser lo suficientemente productivas.

A diferencia de los estudios realizados en el vacuno de leche, no se había abordado hasta el momento el análisis directo de la mejora de la productividad global de las reproductoras en el vacuno de carne de producción extensiva, debido entre otras cosas a la mayor complejidad de los factores ambientales que afectan a algunos de los parámetros que intervienen en esta productividad, entre los que podemos resaltar especialmente la edad al primer parto o el intervalo entre partos (Pereira et al., 2002). La heredabilidad de estas variables reproductivas suele ser de una magnitud demasiado baja (en torno a 0,1), lo cual hace que raramente sean introducidas como criterios de selección en los esquemas de valoración (Meyer et al., 1990; Cammack et al., 2009). Por otra parte, los parámetros relacionados con la longevidad del animal exigen monitorizar o censurar los datos de las reproductoras que no han llegado al final de su vida productiva, generando una problemática adicional para su estudio, como hemos indicado previamente.

Desde el ICAR (Internacional Commite for Animal Recording), institución responsable del control animal en la CEE (dependiente de la UE, con participación de la EAAP, la FAO, etc.) se han desarrollado varios indicadores de la productividad, los cuales se basan mayormente en la estimación de los kilos de carne destetados a una edad determinada por cada reproductora, lo cual refleja de manera conjunta la eficiencia reproductiva de la hembra y el crecimiento de sus crías (ICAR, 2006). La utilización de esta variable, además de su relación directa con la rentabilidad de la explotación del vacuno extensivo, presenta la ventaja de tener, a priori, valores de heredabilidad intermedios entre ambos grupos de variables, y por lo tanto es lo suficientemente elevada para poder ser incluida en las valoraciones genéticas (Faria et al., 2007; Grossi et al., 2008). De la misma forma, las recomendaciones del BIF (Beef Internacional Federation; organismo en el que están integradas las principales cooperativas de vacuno de carne a nivel mundial), incluyen como variables a analizar tanto las relacionadas con el crecimiento de los terneros como las relacionadas con la eficacia reproductiva de la vaca, su habilidad de permanencia en el rebaño o la duración de su vida productiva.

Según nuestros resultados, la raza Retinta puede considerarse una raza con una amplísima vida productiva, alcanzándose los niveles de productividad máxima a partir de los 7 años, que se estabiliza o incluso se incrementa levemente (debido a la eliminación de reproductoras menos productivas), hasta los 12 años, para ir descendiendo hasta los 15, donde los valores observados son más que aceptables (Capítulo 3 figura 1). Sin embargo, se ha detectado una gran variabilidad en la evolución de este parámetro entre las diferentes ganaderías analizadas (capítulo 3 figura 2), siendo la posibilidad de mejora (ambiental y genética) muy elevada para las ganaderías que presentan bajos niveles de productividad a edades más avanzadas.

La evolución de la h^2 mostró resultados altos (desde 0,27 a 0,41; capítulo 3 figura 3), lo que asegura un buen progreso genético si se comienza a utilizar como criterio de selección en esta raza, siendo además un parámetro que el ganadero puede cuantificar económicamente de manera simple, lo que conlleva que visualice los beneficios de la mejora de forma directa y que aumente su interés por aplicarlo. Estas heredabilidades son más elevadas que las encontradas por Grossi et al. (2008) y Schwengber et al. (2001) (0,14 a 0,25 y 0,15 respectivamente). Sin embargo, el valor predictivo (fenotipo) del comportamiento del carácter en los primeros años de vida y al final de la vida productiva de la reproductora (14 años) es bajo, con una correlación fenotípica menor a 0,7 hasta alcanzar los 7 años de edad (capítulo 3 figura 4), la cual aumenta, de manera esperable, conforme mayor es la edad de la reproductora. Es por ello que nuestros resultados indican que, desde el punto de vista predictivo, si la selección de las vacas cuya finalidad sea producir futuros reproductores se realiza demasiado precozmente, la respuesta a la selección puede ser baja para esta variable. A falta de otros estudios específicos, pensamos que en ningún caso se deberían seleccionar como madres de futuros reproductores animales menores a los 6 años, debido a que la selección precoz no compensaría la pérdida de precisión observada a edades previas en esta selección.

El análisis de la evolución del componente genético de la productividad de las vacas permitió detectar también curvas claramente diferentes entre los individuos analizados, pudiéndose identificar la existencia de dos tipos de patrones de evolución de este potencial, de manera similar a lo que ocurría con el análisis parto a parto. Tal es así, que en el análisis de las 200 vacas con mayor VG para este carácter a los 4 años de edad, se pudieron distinguir dos tipos de patrones de evolución: unas que van disminuyendo su potencial con respecto a la media de la población al incrementar su edad, presentado en su madurez una peor productividad que el resto, y otras que se muestran más estables a lo largo de su vida productiva (capítulo 3 Figura 6).

Todos estos hallazgos tienen una potencial aplicación productiva muy clara, brindando al ganadero una flexibilidad enorme para seleccionar el tipo de animal más adecuado al ritmo de reposición deseado. A su vez, los productores podrán seleccionar los animales más adaptados a su sistema productivo y a su ritmo de amortización, existiendo animales muy productivos en los primeros años de vida pero que van alargando sus interpartos y disminuyendo el peso de sus terneros frente a otros más longevos que son capaces de mantener una productividad media a más largo plazo.

No obstante, es importante aclarar que para poder aplicar este nuevo criterio de selección es necesario un mayor control de los efectos ambientales de cada explotación, especialmente en la sistematización de la recogida de información sobre aspectos del manejo reproductivo, hoy día no incluidos en el control de rendimientos oficial, como sería la edad a la que se cubren las novillas por primera vez, o el periodo en el cual los machos están dentro de los lotes de hembras en cubrición, ya que estas variables dependen en gran medida del manejo reproductivo de cada ganadería. No obstante, si la conexión genética es fuerte, y durante la campaña no se modifica el manejo reproductivo para un determinado lote de reproductoras, la fiabilidad de los resultados obtenidos con el modelo utilizado es alta.

Existen otros aspectos asociados a la productividad que por su importancia deben ser analizados y considerados para su posible introducción en el programa de mejora de las razas cárnicas. Entre ellos, existe un fenómeno genético, llamado consanguinidad, que se manifiesta en animales resultantes del apareamiento de individuos con relaciones de parentesco muy cercanas, cuya expresión fenotípica es conocida como depresión endogámica (DE). Este parámetro no ha sido tenido en cuenta de manera habitual en los esquemas de selección, los cuales se centran principalmente en la mejora de las características productivas de los individuos. Esto ha producido en algunas razas un aumento lento pero constante de la consanguinidad, con la aparición de los efectos negativos de la depresión endogámica (Sorensen et al., 2005; Stachowicz et al., 2011).

Su principal efecto es la pérdida de rusticidad de los ejemplares que ven reducida su capacidad para hacer frente a situaciones medioambientales adversas (Lacy, 1997; Leberg and Firmin, 2008) dando como resultado niveles de producción inferiores (Leroy, 2014). En ciertas poblaciones de animales silvestres, cuyos niveles de endogamia pueden ser muy elevados, se ha determinado que una de las principales características afectadas es la eficiencia reproductiva (Leberg and Firmin, 2008), principalmente debido a la aparición de una calidad espermática disminuida en los machos.

Para ello en el capítulo cuarto, nos planteamos un análisis de la relación de la endogamia con la fertilidad mediante el análisis de su efecto en los sementales, incorporando así a esta tesis otro componente importante a tener en cuenta dentro de los parámetros reproductivos de la explotación. Este estudio fue realizado analizando efecto de los niveles extremos de endogamia (>13,5%) sobre los parámetros seminales de sementales de la raza, lo cual presenta la ventaja de no estar mediatizado por un gran número de factores ambientales o sanitarios (pe. existencia de traslocación robertsoniana, virosis como el IBR, Campilobacteriosis, etc.), pudiéndose además cuantificar mediante procedimientos laboratoriales muy objetivos, gracias al uso, por primera vez en este tipo de individuos, de sistemas automátizados para el análisis del esperma por medio de imágenes computarizadas, denominados genéricamente CASA (Computer-Assisted Sperm Analysis). Así en esta tesis se ha realizado por primera vez un análisis exhaustivo y objetivo del efecto que ejerce el nivel de endogamia en diferentes parámetros morfológicos, fisiológicos y cinéticos del esperma del toro, lo cual fue posteriormente correlacionado con su efecto sobre la duración del intervalo entre partos y por tanto su influencia en la productividad.

Existen varios estudios que demostraron que la fertilidad del macho es afectada negativamente por el valor de endogamia de los animales, aunque la mayoría de ellos sugieren que su efecto es muy inferior al que determina en las hembras (Gonzalez-Recio et al., 2007). Nuestro estudio ha detectado también un claro efecto de la endogamia sobre la fertilidad de los sementales, el cual esta mediado por diferencias de tipo cinético, sin afectarse la morfología del espermatozoide, su viabilidad, el estado de su acrosoma o la integridad de su ADN (Capítulo 4, tablas 1 y 2). Esto concuerda con estudios previos realizados en otras especies domésticas y salvajes, en los cuales se ha demostrado que el proceso de gametogénesis (producción de esperma) no es afectado por la endogamia (Losdat et al., 2014). Por el contrario, el análisis de la motilidad espermática ha revelado resultados que permiten explicar parcialmente el mecanismo por el cuál la endogamia puede afectar la fertilidad de los sementales, ya que los espermatozoides provenientes de animales altamente endogámicos sufrirían un proceso de hiperactivación temprana, lo cual provocaría que las reservas energéticas de muchos de ellos sean consumidas precozmente, lo que podría producir que la cantidad de espermatozoides que llegaran al lugar de fecundación fuese menor, reduciéndose así la fertilidad del semental (Capítulo 4, tablas 3 y 4).

Estos resultados podrían explicar el alargamiento detectado en el intervalo entre partos en las hembras inseminadas con dichos toros endogámicos. Sin embargo, un análisis estadístico ampliado demostró que no existe correlación entre el porcentaje de endogamia del macho (incluyendo cualquier nivel de F) y la duración del intervalo entre partos. Estos resultados nos hacen pensar que, como fue demostrado en otras especies, la endogamia puede afectar negativamente a los animales a partir de un cierto umbral (13% en nuestro caso), siendo sus efectos prácticamente nulos en animales con porcentajes de endogamia menores. Por todo ello, ha quedado demostrado que el nivel de parentesco debería ser un factor a controlar y tener en cuenta cuando se realiza la selección de los animales que serán utilizados para aparearse con determinado lote de vacas, sugiriendo que un buen asesoramiento genético que tenga en cuenta este tipo de parámetros proveerá de grandes beneficios a los ganaderos durante su labor productiva. En base a nuestros resultados, se ha incluido en la aplicación desarrollada para los ganaderos asociados de la raza Retinta un módulo que permite determinar los niveles de parentesco, y por lo tanto la consanguinidad resultante en los productos obtenidos mediante el apareamiento de dos individuos o grupos de reproductores dados, de manera que el mismo ganadero comience a controlar este fenómeno genético.

Finalmente, aunque el hecho de que la selección de los animales se esté realizando en el propio medio donde se explota la raza asegura que no se pierda capacidad de adaptación (rusticidad) a largo plazo, la clara aceleración de los efectos del calentamiento global hacen cada vez más necesaria la inclusión de variables que sean capaces de cuantificar la resistencia al estrés climático de los animales. Las mismas fueron estudiadas en el capítulo quinto de la presente tesis, con el objetivo de poder determinar cuáles son los caracteres a seleccionar para lograr animales que se adapten mejor a las nuevas condiciones de aumento de temperatura que acontecerán en las próximas décadas. Esto es de vital importancia en aquellas razas que como la Raza Retinta, se desarrollan en el suroeste español y principalmente en las regiones de Andalucía y Extremadura de sierra y montaña, en las que todas las previsiones meteorológicas realizadas determinan un marcado incremento de la temperatura en las próximas décadas. Estas zonas, que ya de por si poseen un clima severo, con grandes contrastes entre verano e invierno, pueden sufrir, en caso de un incremento de las temperaturas medias y máximas, un marcado efecto sobre la disponibilidad de agua y pastos (disminución e incremento de la variabilidad). El sistema de la dehesa, que es el más utilizado para la cría de la raza, se caracteriza por la estacionalidad de sus pastos, condicionando el manejo del ganado, de forma que las cubriciones se realizan en su mayoría estratégicamente entre los meses de noviembre a junio para dar lugar a una concentración de los partos en las épocas de mayor disponibilidad de pastos (de octubre a marzo). El análisis del índice THI (que combina temperatura y humedad) y la radiación solar (RS), calculados a partir de datos meteorológicos recogidos de estaciones automatizadas por un período de 9 años de manera sistemática, muestra claramente dos periodos climáticos diferentes: el periodo cálido de Abril a Septiembre (HHS) y el periodo frío de Octubre a Marzo (LHS) (Capítulo 5, figura 1). La metodología empleada en este estudio, conocida como modelo "norma-reacción", está basada en modelos de regresión aleatoria y ha sido previamente utilizada en vacuno de leche (Ravagnolo and Misztal, 2000; Aguilar et al., 2009). Sin embargo, no ha sido utilizada en razas de vacuno criadas bajo el sistema extensivo. Esta metodología presenta una ventaja comparativa frente a la metodología clásica, ya que considera que un genotipo puede manifestar diferentes fenotipos según su capacidad para adaptarse a las condiciones ambientales imperantes en cada momento, ya que tanto el rendimiento del animal (Ricard et al., 2000), como el ambiente en el que se desarrolla (sanidad, alimentación, clima, manejo, etc.) y sus contemporáneos cambian a lo largo de su vida, debido a que la expresión de los distintos genes varía en respuesta a cambios fisiológicos derivados de la edad o a la influencia de determinados efectos ambientales responsables de una respuesta epigenética. Esto hace que esta metodología "norma-reacción" permita evaluar la capacidad de adaptación de un animal (interacción genotipo-ambiente) para un carácter determinado de manera mucho más eficiente y ajustada a lo largo de su vida. En nuestro caso, hemos demostrado que este tipo de modelos presentan una elevada flexibilidad y potencia para evaluar la interacción genotipo-ambiente también bajo estas condiciones extensivas de producción.

Muy recientemente, Santana et al. (2016), comprobaron la existencia de una interacción genotipo-ambiente al observar una gran heterogeneidad en los componentes de (co)varianza del peso al destete analizando diferentes condiciones ambientales. Nuestros resultados estuvieron en concordancia con dicha hipótesis, demostrando la existencia de una interacción genotipo-ambiente en los primeros meses de vida del ternero, mostrando diferencias genéticas entre los dos periodos climáticos analizados, así como valores de heredabilidad mucho más elevados durante los primeros 90 días de vida (Capítulo 5, figura 2). Este fenómeno podría explicarse en parte, debido a diferencias epistáticas asociadas al estrés climático junto a variaciones en la disponibilidad y calidad de los pastos, actuando indirectamente a través de la cantidad de leche materna, crucial en el periodo inicial de desarrollo. Esto concuerda además con una serie de estudios que han demostrado que la producción de leche está muy afectada por la resistencia al estrés climático del individuo (Bohmanova et al., 2005; Aguilar et al., 2009; Sanchez et al., 2009; Carabano et al., 2014).

Finalmente, otro importante hallazgo descrito en la presente tesis ha sido la demostración de que los animales con los mejores resultados en ambientes sin estrés climático no tenían por qué corresponderse con los mejores en las épocas de estrés. En nuestro caso, los individuos que crecieron en el período cálido estuvieron sometidos a un mayor estrés que los del período frío, mostrando estos últimos un crecimiento mayor entre sus 70 y 160 días de edad (Capítulo 5, figura 3). No obstante, las diferencias globales (al destete) entre ambos grupos no fueron significativas, hecho probablemente explicado por la existencia de un crecimiento compensatorio que equilibra los pesos después de esta edad, dónde la hembra reduce su cantidad de leche forzando a los terneros a consumir pasto.

CONCLUSIONES

CONCLUSIONES

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

Capítulo I

1. El análisis mediante metodologías de regresión aleatoria de los componentes de la varianza para los efectos genéticos directos y maternos del peso al destete y a los 4 meses de edad del ternero en los diferentes partos de la vaca identificó una importante variabilidad genética, presentando además diferentes patrones de evolución a lo largo de la vida productiva de las reproductoras.

Capítulo II

2. El análisis de las variables relacionadas con la longevidad de la reproductora demostró un efecto significativo de diferentes factores relacionados con el manejo productivo de la explotación, pero también con la raza paternal utilizada para la producción de terneros. En este sentido se ha determinado que el riesgo de ser eliminadas del rebaño es menor en aquellas vacas destinadas a la cría en pureza que en las dedicadas al cruzamiento industrial. No obstante, son necesarios nuevos estudios de la productividad ponderal y un análisis económico específico que determine su mayor o menor rendimiento económico dado los criterios impuestos por el mercado actual.

Capítulo III

3. El estudio de la evolución de la productividad acumulada a lo largo de la vida de las reproductoras de la raza Retinta, mostró un componente genético importante, con una elevada heredabilidad durante las diferentes edades de las reproductoras.
4. La utilización de este parámetro como criterio de selección determinaría una mejora de la productividad global de las reproductoras a lo largo de su vida, produciendo además una mejora de aspectos reproductivos de muy baja heredabilidad, como los periodos interpartos, junto con otros de mayor heredabilidad, como el peso de los terneros al destete.
5. La existencia de grandes diferencias en la evolución de las curvas de productividad media de las diferentes explotaciones analizadas hace necesaria la realización de un análisis en profundidad y un posible replanteamiento del sistema productivo de algunas de ellas (alimentación, sanidad, manejo reproductivo etc.).

Capítulo IV

6. El uso de una metodología objetiva y automatizada de análisis de las características espermáticas (CASA (Computer-Assisted Sperm Analysis)), ha demostrado por primera de manera objetiva vez que la consanguinidad afecta a la motilidad espermática del toro retinto. Los toros con alta consanguinidad han mostrado una menor fertilidad, debido a la prematura hiperactivación de los espermatozoides.

Capítulo V

7. El estudio llevado a cabo para detectar un componente genético en la resistencia al estrés térmico mostró una interacción genotipo-ambiente significativa para los primeros tres meses de vida del animal, con una evolución de la heredabilidad diferente para los animales nacidos en los meses fríos y calientes del año.

Conclusión Global

8. En la presente tesis se han puesto a punto metodologías para el análisis de nuevos criterios de selección de las reproductoras de raza Retinta relacionadas con la permanencia de las reproductoras en la explotación y la productividad acumulada durante toda su vida. Los parámetros genéticos obtenidos asegurarían un buen progreso genético en la raza Retinta si fuesen incorporados dentro del Esquema de Selección, dotando de gran flexibilidad la elección del tipo de animal a seleccionar según la pauta de reposición deseada por el ganadero. No obstante, para ello es necesario un más exhaustivo control reproductivo en las ganaderías del núcleo de selección.

CONCLUSIONS

During the development of this PhD work, it has been possible to reach the following conclusions:

Chapter I

1. The estimation of the variance components for direct and maternal genetic effects of pre-weaning weights of Retinta calves across parities by random regression methodologies identified an important genetic variability, presenting additionally different evolution patterns over the productive lives of the dams.

Chapter II

2. The analysis of cow longevity variables showed a significant effect of different factors associated to productive management of the herd. There were also significant differences in the kind of paternal breed used for calf production. In this sense, it has been determined that cows used to purebred had a lower risk of being eliminated than those dedicated to industrial crossing. However, due to the criteria imposed by the current market, further cow productivity studies and a specific economic analysis are required to determine their greater or lesser economic performance.

Chapter III

3. The study of the accumulated productivity evolution throughout the Retinta cow life showed an important genetic component, with a high heritability across the different ages of the cow.
4. The use of this trait as a selection criterion would lead to an improvement in the overall productivity of the cow throughout their lives. Producing also an improvement on very low heritability reproductive aspects, such as calving interval, along with others of higher heritability, such as the weaning weight of the calves.
5. The existence of great differences in the average productivity curves of evolution of different analyzed herds makes it necessary to carry out an in-depth analysis and a possible reconsideration of the productive system of some of them (feeding, sanitation, reproductive management, etc.).

Chapter IV

6. The use of an objective and automated sperm analysis (CASA-Computer Assisted Sperm Analysis) has demonstrated objectively for the first time that inbreeding affects the sperm motility of the Retinto bull. High inbreeding bulls have shown lower fertility, due to premature hyperactivation of spermatozoa.

Chapter V

7. The study carried out based on the detection of a genetic component in the degree of resistance to thermal stress showed a significant genotype-environment interaction for the first three months of life of the animal, with a different heritability evolution for animals born in the hot and cold months of the year.

Global Conclusion

8. In the present Phd study, methodologies have been developed for the analysis of new selection criteria for Retinta cows related to their permanence at the herd and the accumulated productivity during their entire life. The genetic parameters obtained would ensure a good genetic progress in the Retinta breed if they were incorporated into their Breeding Program, giving a great flexibility to select the most appropriate kind of animal at the desired replenishment rate by the breeder. However, this requires a more exhaustive reproductive control in the nucleus breeding schemes.

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PRODUCCIÓN CIENTÍFICA

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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**: Morales, R.**, Menéndez-Buxadera, A., Avilés, C. y Molina, A.

TÍTULO: **Direct and maternal genetic effects for preweaning growth in Retinta cattle estimated by a longitudinal approach throughout the calving trajectory of the cow.**

Revista: J. Anim. Breed. Genet. Año: 2013. Número: 141 (4). Páginas: 277-283.

ISSN: 0931-2668. DOI: ISSN. doi:10.1111/jbg.12038

IF= 1.877 (1er cuartil) en Agriculture, Dairy and Animal Science

AUTORES: Dorado, J.; **Morales, R.**; Molina, A.; Hidalgo, M.; Ariza, J.; Moreno-Millán, M.; Demyda-Peyrás, S.

TÍTULO: **Effect of inbreeding depression on bull sperm quality and field fertility.**

Revista: Reprod Fertil Dev. 2015 Dec 18.:

ISSN: DOI: 10.1071/RD15324.

IF= 2.656 (2º cuartil) en Reproductive Biology

AUTORES: **Morales, R.**, Phocas, F., Demyda-Peyrás, S., Menendez-Buxadera, A.and Molina, A.

TÍTULO: **Breeding beef cattle for an extended productive life: Evaluation of selection criteria in the Retinta breed.**

Revista: Livestock Science. Año: 2017. Sometido

IF= 1.377 (2º cuartil) en Agriculture, Dairy and Animal Science

AUTORES: **Morales, R.**; Menéndez-Buxadera, A. Demyda-Peyrás S. and Molina, A.

TÍTULO: **Genetic effects of climatic seasons on preweaning growth of beef cattle: a first approach to Retinta calves.**

Revista: Livestock Science. Año: 2017. Sometido

IF= 1.377 (2º cuartil) en Agriculture, Dairy and Animal Science

AUTORES: **Morales, R.**; Menéndez-Buxadera, A. Demyda-Peyrás S. and Molina, A.

TÍTULO: **Genetic analysis of accumulated productivity of Retinta breeding cows.**
En preparación

Congresos Nacionales

AUTORES: **Morales, R.**, Menéndez-Buxadera A. y Molina A.

TÍTULO DE LA COMUNICACIÓN: **Optimización del esquema de selección de la raza bovina Retinta. Puesta a punto mediante técnicas de regresión aleatoria de nuevas metodologías genéticas de valoración para caracteres longitudinales y para la resolución de modelos de problemas de interacción genotipo ambiente mediante Norma de Reacción.**

CONGRESO: I Congreso Científico de Investigadores en Formación en Agroalimentación ceiA3.

ENTIDAD ORGANIZADORA: Escuela Internacional de Doctorado en Agroalimentación ceidA3

TIPO DE PARTICIPACIÓN: Comunicación

PUBLICACIÓN: Libro de actas

LUGAR DE CELEBRACIÓN: Córdoba, España.

AÑO: 8 y 9 de Mayo de 2012

AUTORES: Morales R., Menéndez-Buxadera, A., Jiménez J.M., Salado F. y Molina, A.

TÍTULO DE LA COMUNICACIÓN: **Genetic parameters estimation for cumulative productivity in Retinta beef cattle throughout the different ages of the cow by random regression model.**

CONGRESO: XVI Reunión de Mejora Genética Animal

ENTIDAD ORGANIZADORA: Comité organizador de XVI Reunión de Mejora Genética Animal

TIPO DE PARTICIPACIÓN: Comunicación

PUBLICACIÓN: Libro de actas

LUGAR DE CELEBRACIÓN: Ciutadella de Menorca, España.

AÑO: del 31 de Mayo al 2 de Junio de 2012.

AUTORES: Avilés, C., Molina, A., Horcada, A., **Morales, R.** y Peña, F.

TÍTULO DE LA COMUNICACIÓN: **Uso de la ecografía para la evaluación de la composición y características de la canal de añojos de raza Retinta in vivo**

CONGRESO: lV congreso Nacional de la carne de Vacuno

ENTIDAD ORGANIZADORA: Comité organizador del lV congreso Nacional de la carne de Vacuno

TIPO DE PARTICIPACIÓN: Comunicación

PUBLICACIÓN: Libro de actas

LUGAR DE CELEBRACIÓN: Facultad de Veterinaria de la Universidad Complutense de Madrid

AÑO: 21 y 22 Junio de 2012

AUTORES: **Morales, R.**, Jiménez, J., Avilés, C., Salado, F., Amaro, A., Álvarez, F., Pérez, J.A. y Molina, A.

TÍTULO DE LA COMUNICACIÓN: **La raza Retinta, número 1 en la España seca**.

CONGRESO: Fegasur 2012. Feria nacional de ganadería.

ENTIDAD ORGANIZADORA: Diputación de Cádiz, IFECA

TIPO DE PARTICIPACIÓN: Comunicación

PUBLICACIÓN: Libro de actas

LUGAR DE CELEBRACIÓN: Recinto ferial IFECA Jerez, Cádiz, España.

AÑO: 9, 10 y 11 de Noviembre de 2012

AUTORES: Anaya, G., Membrillo, A., Peña, F., Avilés, C., Molina, A., **Morales, R**., Menéndez-Buxadera, A. y Serradilla, J.M.

TÍTULO DE LA COMUNICACIÓN: **Nuevas tecnologías genéticas para los retos de la ganadería en la cuenca del mediterráneo en las próximas décadas.**

CONGRESO: Fegasur 2012. Feria nacional de ganadería.

ENTIDAD ORGANIZADORA: Diputación de Cádiz, IFECA

TIPO DE PARTICIPACIÓN: Comunicación

PUBLICACIÓN: Libro de actas

LUGAR DE CELEBRACIÓN: Recinto ferial IFECA Jerez, Cádiz, España.

AÑO: 9, 10 y 11 de Noviembre de 2012

AUTORES: AUTORES: **Morales, R.**, Menéndez-Buxadera A. y Molina A.

TÍTULO DE LA COMUNICACIÓN: **ANALISIS GENÉTICO DE LA PRODUCTIVIDAD DE LA VACA RETINTA A LO LARGO DE SU VIDA PRODUCTIVA**

CONGRESO: II Congreso Científico de Investigadores en Formación en Agroalimentación ceiA3.

ENTIDAD ORGANIZADORA: Escuela Internacional de Doctorado en Agroalimentación ceidA3

TIPO DE PARTICIPACIÓN: Comunicación

PUBLICACIÓN: Libro de actas

LUGAR DE CELEBRACIÓN: Córdoba, España.

AÑO: 9 y 10 de Abril 2013

AUTORES **Morales, R.**, Avilés, C., Menéndez-Buxadera A. y Molina A.

TÍTULO DE LA COMUNICACIÓN: **Direct and maternal genetics effects for pre-weaning growth in Retinta cattle estimated by a longitudinal approach through the calving trajectory of the cow**

CONGRESO: III Congreso Científico de Investigadores en Formación en Agroalimentación ceiA3.

ENTIDAD ORGANIZADORA: Escuela Internacional de Doctorado en Agroalimentación ceidA3

TIPO DE PARTICIPACIÓN: Comunicación

PUBLICACIÓN: Libro de actas

LUGAR DE CELEBRACIÓN: Córdoba, España.

AÑO: 11 al 13 de Noviembre de 2014

Congresos internacionales

AUTORES: **R. Morales**, A. Menéndez-Buxadera, J.A. Pérez, F. Álvarez, I. Fernández, C. Avilés y A. Molina.
TÍTULO DE LA COMUNICACIÓN: **Estimación de los efectos genéticos directos y maternos para el crecimiento pre-destete en ganado de Raza Retinta mediante un enfoque longitudinal a lo largo de la trayectoria de partos de la vaca.**
CONGRESO: XI Congreso de la Federación Iberoamericana de Razas Criollas y Autóctonas (FIRC)
ENTIDAD ORGANIZADORA: Federación Iberoamericana de Razas Criollas y Autóctonas (FIRC)
TIPO DE PARTICIPACIÓN: Póster

PUBLICACIÓN: Libro de actas

LUGAR DE CELEBRACIÓN: Zaragoza, España.

AÑO: 19 al 21 de Marzo de 2015

AUTORES: J.A. Pérez, J. T. Araújo Filho, **R. Morales** y A. Molina.
TÍTULO DE LA COMUNICACIÓN: **Estudio de la adaptación a la condiciones climáticas y productivas de Brasil. Primera fase.**
CONGRESO: XI Congreso de la Federación Iberoamericana de Razas Criollas y Autóctonas (FIRC)
ENTIDAD ORGANIZADORA: Federación Iberoamericana de Razas Criollas y Autóctonas (FIRC)
TIPO DE PARTICIPACIÓN: Comunicación

PUBLICACIÓN: Libro de actas

LUGAR DE CELEBRACIÓN: Zaragoza, España.

AÑO: 19 al 21 de Marzo de 2015