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Departamento de Genética

TESIS DOCTORAL

CARACTERIZACIÓN DE LAS CURVAS DE CRECIMIENTO DEL OVINO SEGUREÑO EN SISTEMAS CONVENCIONALES Y ORGÁNICOS

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TITULO: *Caracterización de las curvas de crecimiento del ovino segureño en sistemas convencionales y orgánicos*

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La Tesis Doctoral titulada *"Caracterización de las curvas de crecimiento del ovino segureño en sistemas convencionales y orgánicos"*, realizada por la Ingeniera Informática ***TERESA MARTA DUARTE SILVA LUPI DE ORDAZ CALDEIRA***, correspondiente al Proyecto de Tesis aprobado por el Departamento de Genética con fecha de Noviembre de 2011, ha sido realizada en la modalidad de "Compendio de publicaciones". Las referencias completas de los artículos que constituyen el cuerpo de la Tesis son las siguientes:

1. Lupi TM, Nogales S, León JM, Barba C and Delgado JV 2015. Characterization of commercial and biological growth curves in the Segureña sheep breed. animal 9, 1341-1348.
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TÍTULO DE LA TESIS: CARACTERIZACIÓN DE LAS CURVAS DE CRECIMIENTO DEL OVINO SEGUREÑO EN SISTEMAS CONVENCIONALES Y ORGÁNICOS

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(se hará mención a la evolución y desarrollo de la tesis, así como a trabajos y publicaciones derivados de la misma).

La doctoranda inició la realización de esta tesis al incorporarse al Programa de doctorado "Recursos naturales y gestión sostenible".

Esta tesis ha permitido la publicación de los artículos "Characterization of commercial and biological growth curves in the Segureña sheep breed" y "Genetic parameters of traits associated with the growth curve in Segureña sheep" en la revista *animal*, "Analysis of the non-genetic factors affecting the growth of Segureño sheep" en *Italian Journal of Animal Science*, "Modelación de curvas de crecimiento comercial en ovino Segureño", "Estudio de factores no genéticos sobre los parámetros de la función logística en la curvas de crecimiento comercial del cordero Segureño"y "Efecto de factores no genéticos en el peso del ternasco de raza Segureña" en el livro "*Actas Iberoamericanas de Conservación Animal*" (AICA) y "Evolución del control de rendimientos en esquema de selección de la raza ovina segureña" en la revista *Agroforum*, así como 7 comunicaciones en Congresos internacionales.

La doctoranda ha mostrado una alta capacidad analítica, deductiva, de buen manejo y de buen hacer. Ha mostrado iniciativa tanto en la resolución de problemas como al abordar nuevas etapas a las que le ha conducido este estudio y conoce las herramientas necesarias para dirigir su propia investigación.

Por todo ello, se autoriza la presentación de la tesis doctoral.

Córdoba, 29 de Diciembre de 2015

Firma del/de los director/es

Fdo.:_J. V. Delgado Bermejo

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El programa de selección del ovino Segureño ha alcanzado un gran desarrollo en los últimos años, situándose entre los más avanzados de España y de la UE. Por esta razón, el equipo técnico responsable del mismo se ha planteado la búsqueda de nuevos criterios de selección que repercutan positivamente en la competitividad de la raza. Entre estos critérios destaca la utilización del significado biológico de la curva de crecimiento de mejor ajuste, como criterio de selección para mejorar aspectos tales como la edad al sacrificio, la precocidad, entre otros.

En la presente Tesis nos hemos responsabilizado de ese reto y para ello, utilizando los datos entre los años de 2000 hasta 2015 de la base de datos histórica de la Asociación Nacional de Criadores de Ovino Segureño (ANCOS), hemos desarrollado un estudio en tres etapas que nos llevarán a ofrecer los mencionados nuevos criterios de selección al programa genético. En una primera etapa se han analizado modelos no lineales para describir las curvas de crecimiento biológico (del nacimiento hasta la edad adulta) y comercial (del nacimiento hasta la edad de sacrificio) del ovino de raza Segureña. En una segunda etapa se llevó a cabo un estudio para evaluar los efectos de los factores no genéticos (sexo del cordero, época de nacimiento, rebaño, año de nacimiento y tipo de parto) sobre el comportamiento en crecimiento de los animales, con vistas a optimizar los modelos de análisis genéticos a utilizar sobre los parámetros de las curvas. Finalmente, en una tercera etapa de definió la curva de mejor ajuste individual y sobre los parámetros de la misma en cada animal se calcularon parámetros genéticos que nos ilustraron sobre los niveles de variabilidad genética de los mismos en la población; sobre las relaciones genéticas entre los parámetros y sobre todo, sobre sus habilidades como criterios de selección potenciales. Estas tres etapas constituyeron los objetivos específicos de la presente tesis, y cada uno de ellos dio lugar a un artículo específico que se publicó en revistas de impacto. Los contenidos de los mismos se resumen a continuación:

En el primer trabajo (Characterization of commercial and biological growth curves in the Segureña sheep breed. Animal 2015, 9, pp 1341-1348. doi: 10.1017/S1751731115000567. Cuartil 1, Factor de Impacto: 1.841) se analizaron los modelos no lineales para describir las curvas de crecimiento biológicos y comerciales de la oveja Segureña, una de las más importantes razas españolas. Evaluamos los modelos de Brody, von Bertalanffy, Verhulst, Gompertz y logístico a partir de datos históricos de la Asociación Nacional de Criadores de Ovino Segureña (ANCOS). Estos registros fueron recogidos entre los años 2000 y 2013, de un total de 129 610 observaciones de peso que van desde el nacimiento hasta la edad adulta. El objetivo de esta investigación fue establecer el comportamiento matemático del desarrollo corporal durante la vida comercial de esta raza (del nacimiento hasta el sacrificio) y durante la vida biológica (desde el nacimiento hasta la edad adulta); la comparación entre ambas vertientes nos da información importante sobre el mejor momento para el sacrificio, así como asesoramiento dietético según las necesidades de los animales, permite predicciones económicas de producción y, mediante el uso de los parámetros de la curva como criterios de selección, permite mejoramientos en las características de crecimiento de la raza. Los modelos fueron ajustados utilizando el procedimiento de regresión no lineal (NLR) de paquete estadístico IBM SPSS version19. Los parámetros del modelo fueron estimados utilizando el algoritmo de Levenberg-Marquardt. Los modelos en estudio se compararon mediante el coeficiente determinativo, el error cuadrático medio, el número de iteraciones, criterio de información de Akaike y la coherencia biológica de los parámetros estimados. Los modelos de von Bertalanffy y logístico fueron los que mejor se ajustaron a las curvas de crecimiento biológico y comercial, respectivamente, en ambos sexos. El modelo de Brody no es adecuado para el estudio de la curva de crecimiento comercial. Las diferencias entre los parámetros en ambos sexos indican un fuerte impacto de dimorfismo sexual en el crecimiento. Esto resalta el valor de la tasa de crecimiento más elevado en las hembras que indica que alcanzan antes la madurez.

En el segundo trabajo (Analysis of the non-genetic factors affecting the growth of Segureño sheep. Italian Journal of Animal Science 2015; 14:3683, pp 124-131. doi: 10.4081/ijas.2015.3683. Cuartil 3, Factor de Impacto: 0.718) se realizó un estudio para evaluar los efectos de los factores no genéticos sobre el comportamiento de crecimiento de la raza ovina Segureña. Los datos de crecimiento relacionado (peso al destete temprano, peso al destete tardío y peso a los 80 días de edad) fueron tomados de 59 704 corderos pertenecientes a los datos históricos de la Asociación Nacional de Criadores de Ovino Segureño (ANCOS) durante un período de 11 años. Los análisis estadísticos se realizaron utilizando el análisis multifactorial de la varianza del paquete estadístico IBM SPSS v.19. El modelo incluyó los factores no genéticos - sexo (S) de cordero, época de nacimiento (N), rebaño (H), año de nacimiento (A) y el tipo de parto (P) - como efectos principales y la edad de la oveja al parto y la edad del cordero en la toma de peso como covariables, así como las interacciones entre estos factores. Los resultados mostraron que los pesos en todas las etapas de desarrollo fueron afectados significativamente (P <0,001) por todos los factores, a excepción de A y la covariable edad de la oveja al parto en los corderos con 80 días. Las interacciones dobles H×A, H×P y H×N fueron significativas (P <0,001) para todas las variables, así como la triple interacción H×A×P. Los factores no genéticos tienen un papel muy importante en el desarrollo y crecimiento de la raza ovina Segureña, en diferentes edades o etapas de crecimiento, por lo tanto, es necesaria una corrección para aumentar la precisión de la selección directa en el peso de los corderos al destete temprano, al destete tardío y al sacrificio (80 días de edad).

En el tercer trabajo (Genetic parameters of traits associated with the growth curve in Segureña sheep. Animal. Cuartil 1, Factor de Impacto: 1.841) se estudió la importancia genética de los parámetros de la curva de crecimiento y su relevancia como criterios de selección en programas de mejora de ovinos de raza Segureña. Las funciones de crecimiento logístico y de Verhulst fueron utilizados por su mejor ajuste al peso corporal/edad en esta raza; el primero mostró el mejor ajuste general y el segundo el mejor ajuste individual. Se utilizaron los datos de peso vivo de 41 330 animales de los archivos históricos de la Asociación Nacional de Criadores de Ovino Segureño (ANCOS). La progenie de 1464 carneros y 27 048 ovejas se utilizó para estudiar los parámetros genéticos y fenotípicos de los parámetros de las curvas de crecimiento y características derivadas de estas. El manejo reproductivo de la población consiste en monta natural controlada dentro de cada rebaño, con un mínimo del 15% de las hembras fertilizadas por inseminación artificial con semen fresco, con el objetivo de llevar a cabo las conexiones genéticas del rebaño, toda la genealogía de los rebaños se rastreó con marcadores de ADN. Las estimaciones de los parámetros de la curva de crecimiento desde el nacimiento hasta los 80 días se obtuvieron para cada individuo y cada modelo, por el procedimiento de regresión no lineal (NLR) utilizando el paquete estadístico IBM SPSS (v. 21) con el método de estimación de Levenberg-Marquart. Los componentes de (co)varianza y los parámetros genéticos se estimaron utilizando la metodología REML (Restricted Maximum Likelihood Estimation). La heredabilidad del parámetro A se estimó en 0,41 ± 0,042 y 0,38 ± 0,021 con los modelos logístico y de Verhulst, respectivamente, y la heredabilidad del resto de parámetros osciló de 0,41 a 0,62 y 0,37 a 0,61, con ambos modelos, respectivamente. Se encontró una correlación genética negativa entre el parámetro A y tasa de madurez.

En síntesis, la curva de crecimiento que mejor explica el crecimiento biológico (del nacimiento a la edad adulta) del ovino segureño es el modelo de von Bertalanffy, en cuanto que para explicar el crecimiento comercial (del nacimiento al sacrificio) el modelo que mejor se ajusta es el logístico, en ambos sexos. El modelo de Brody no es adecuado para el estudio de la curva de crecimiento comercial. Los factores no genéticos, de una forma general, afectan significativamente el crecimiento del cordero segureño. A través del ajuste individual se determinaron datos con información necesaria para que los productores puedan inferir sobre información económica relevante en relación con el punto de inflexión y la madurez que no son accesibles a partir del análisis de las características de crecimiento simples, tales como pesos a diferentes edades clave (nacimiento, destete y el sacrificio) o ganancias de peso diarias.

The sheep breeding program of Segureño breed has reached a great development in recent years, ranking among the most advanced in Spain and EU. For this reason, its responsible technical team has considered the search for new selection criteria which influence the competitiveness of the breed, in which emphasizes the use of the biological meaning of the best fit growth curve, as selection criteria to improve aspects such as age at slaughter, precocity, among others.

In this thesis we have taken responsibility for this challenge and for this, using data between the years 2000-2015 of the historical database of the National Association of Segureño Sheep Breeders (ANCOS), we developed a study in three stages that lead us to offer the aforementioned new criteria to the genetic program. In a first stage, it was analysed nonlinear models describing biological (birth to adulthood) and commercial (birth to slaughter age) growth curves of Segureña sheep breed. In a second stage a study was conducted to evaluate the effects of non-genetic factors (sex, birth season, herd, birth year and birth type) on the growth behaviour of the animals in order to optimize the genetic analysis models to use of on the curves parameters. Finally, in a third stage it was defined the individual best fit curve and with each animal parameters it was calculated the genetic parameters that illustrated us on genetic variability levels of them in the population, on genetic relationships between parameters and, above all, on their abilities as potential selection criteria. These three stages constitute the specific objectives of this thesis, and each led to a specific article published in journals of impact, and whose contents are summarized below:

In the first paper (Characterization of commercial and biological growth curves in the Segureña sheep breed. Animal 2015, 9, pp 1341-1348. doi:10.1017/S1751731115000567) Non-linear models were analysed to describe both the biological and commercial growth curves of the Segureña sheep, one of the most important Spanish breeds. We evaluated Brody, von Bertalanffy, Verhulst, logistic and Gompertz models, using historical data from the National Association of Segureña Sheep Breeders (ANCOS). These records were collected between 2000 and 2013, from a total of 129 610 weight observations ranging from birth to adulthood. The aim of this research was to establish the mathematical behaviour of body development throughout this breed's commercial life (birth to slaughter) and biological life (birth to adulthood); comparison between both slopes gives important information regarding the best time for slaughter, informs dietary

advice according to animals' needs, permits economical predictions of productions and, by using the curve parameters as selection criteria, enables improvements in growth characteristics of the breed. Models were fitted according to the non-linear regression procedure of statistical package SPSS version19. Model parameters were estimated using the Levenberg–Marquardt algorithm. Candidate models were compared using the determinative coefficient, mean square error, number of iterations, Akaike information coefficient and biological coherence of the estimated parameters. The von Bertalanffy and logistic models were found to be best suited to the biological and commercial growth curves, respectively, for both sexes. The Brody equation was found to be unsuitable for studying the commercial growth curve. Differences between the parameters in both sexes indicate a strong impact of sexual dimorphism on growth. This can emphasize the value of the highest growth rate for females, indicating that they reach maturity earlier.

In the second paper (Analysis of the non-genetic factors affecting the growth of Segureño sheep. Italian Journal of Animal Science 2015; 14:3683, pp 124-131. doi: 10.4081/ijas.2015.3683) a study was conducted to evaluate the effects of non-genetic factors on the growth behaviour of Segureña sheep breed. Growth related data (early weaning weight, late weaning weight and weight at 80 days of age) were taken from 59,704 lambs belonging to historical data from National Association of Segureño Sheep Breeders (ANCOS) during a period of 11 years. Statistical analyses were performed by using the multifactorial analysis of variance of IBM SPSS Statistics v.19 software. The model included non-genetic factors – lamb sex (S), birth season (N), herd (H), birth year (A) and birth type (P) – as main effects, the dam's age at lambing and the lamb's age when weighed as covariables, and the interactions between these factors. Results showed that all weights at developmental stages were significantly ($P<0.001$) affected by all factors, except for A and the covariable age of dams at lambing on lambs aged 80 days. Double interactions H×A, H×P and H×N were significant ($P<0.001$) for all variables, as well as the triple interaction H×A×P. Non-genetic factors have a very important role in the development and growth of the Segureña sheep breed, at different ages or growth stages, therefore a correction is necessary to increase the accuracy of direct selection on lamb weight at early weaning, late weaning and at slaughtering (80 days of age).

In the third paper (Genetic parameters of traits associated with the growth curve in Segureña sheep. Animal) it was studied the genetic importance of growth curve parameters and their relevance as selection criteria in breeding programmes of Segureño

sheep. Logistic and Verhulst growth functions were chosen for their best fit to body weight/age in this breed; the first showed the best general fit and the second the best individual fit. Live weights of 41 330 individuals from the historical archives of the National Association of Segureña Sheep Breeders (ANCOS) were used in the analysis. The progeny of 1464 rams and 27 048 ewes were used to study the genetic and phenotypic parameters of growth curve parameters and derived traits. Reproductive management in the population consist in controlled natural mating inside every herd, with a minimum of 15% of the females fertilized by artificial insemination with fresh semen, with the purpose on the herd genetic connections, all herds genealogy are screened with DNA markers. Estimates of growth curveparameters from birth to 80 days were obtained for each individual and each function by the nonlinear regression procedure using IBM SPSS Statistics (v. 21) with the Levenberg-Marquart estimation method. (Co)Variance components and genetic parameters were estimated by using the REML/Animal model methodology. The heritability of mature weight was estimated as 0.41 ± 0.042 and 0.38 ± 0.021 with the logistic and Verhulst models, respectively, and the heritability of other parameters ranged from 0.41 to 0.62 and 0.37 to 0.61, with the models, respectively. A negative genetic correlation between mature weight and rate of maturing was found.

In short, the growth curve that best explains the biological growth (birth to adulthood) of segureño sheep is the von Bertalanffy model while to explain commercial growth (birth to slaughter) the model that best fits is the logistic, in both sexes. Brody model is not suitable for the study of commercial growth curve. Non-genetic factors, in a general way, significantly affect the growth of segureño lamb. Through individual data adjustment, it was determined data that is informative for breeders as they permit the inference of relevant economic information with regard to the inflexion point and maturity that are not accessible from the analysis of simple growth traits such as weights at different key ages (birth, weaning and slaughtering) or daily gains.

La raza ovina Segureña constituye uno de los tres pilares básicos de la producción cárnica ovina española basada en las razas autóctonas. Ha contribuido en el pasado, así como actualmente, en la fijación de la población rural mediante el mantenimiento de actividades ganaderas centenarias donde, hasta la actualidad, tienen perfecta cabida las prácticas trashumantes y trasterminantes a través de las cañadas y veredas reales que surcan la mayor parte del territorio nacional (Hernández, 2004). Al estar explotada en condiciones extensivas y semiextensivas, es además, uno de los componentes del equilibrio del ecosistema de las regiones que habita, siendo un pilar básico de la sostenibilidad ambiental y social. La raza consigue, en estos ambientes tan duros y desfavorecidos, unos rendimientos muy interesantes (León et al, 2007).

El aspecto general del Cordero Segureño es ágil y grácil con un cuerpo de tamaño medio (los machos alcanzan 90 kg y las hembras 60 kg), y cabeza proporcionada. Su perfil es subconvexo y presenta formas globales alargadas. Una de las características de la raza Segureña es su buena precocidad sexual, pudiendo darse el primer parto, en un grupo bien alimentado, a los doce o catorce meses. Normalmente la prolificidad de las ovejas es alta, llegando algunos rebaño seleccionados a los 175 ejemplares nacidos de 100 partos, aunque lo usual es que se den cifras en torno a los 135 o 140 ejemplares cada 100 partos (Hernández, 2004).

En 1997, la Asociación Nacional de Criadores de Ganado Ovino Segureño (ANCOS) tras la instauración y desarrollo del control de pesadas en los corderos y el programa de valoración morfológica, recibe el apoyo de la Dirección General de Ganadería del Ministerio de Agricultura, Pesca y Alimentación, y de las comunidades autónomas de Andalucía y Murcia, para la puesta en marcha del correspondiente esquema de selección y mejora genética para esta raza, contando con la asesoría del Departamento de Genética de la Facultad de Veterinaria de la Universidad de Córdoba (UCO-ANCOS, 1999).

Esta raza posee unos buenos índices de crecimiento (MAGRAMA, 2012): Nacimiento: 3,5-5 kg.; 30 días: 11-12 kg.; 90 días: 28 kg.Los corderos son de alta calidad para el consumo humano y son sacrificados cuando su peso oscila entre los 24 y los 30 kg. Su rendimiento en el matadero oscila entre 48 y 55% de carne aprovechada (Cano et al., 2003), gracias a una piel de poco peso que representa un 8% del total del cordero vivo (ANCOS, 2015).

El Segureño se encuentra hoy perfectamente estructurado, disponiendo de todos los componentes para el desarrollo de un programa de mejora, como es el libro genealógico, el control de rendimientos y un circuito de inseminación artificial. (MAGRAMA, 2012).

Este gran desarrollo del esquema está estimulando al equipo técnico e investigador a introducirse en el estudio de nuevos criterios de selección que permitan avanzar aún más el esquema. Así es el caso del estudio de las caseínas de la leche como un efecto materno importante que actúa sobre el crecimiento; y la incorporación de caracteres lineales de la morfología del cordero en la edad al sacrificio como un exponente fuertemente correlacionados genéticamente con las características de la carne y de la canal; y por supuesto, la introducción de parámetros de la curva de crecimiento de mejor ajuste, como criterios relacionados con la fisiología del crecimiento de alto significado biológico, de lo que nos hemos encargado en la presente tesis.

La curva de crecimiento es la representación de peso de los corderos frente a la edad, en días, Cuando se toma un conjunto de pesos (o mediciones de altura) en el mismo individuo, desde el nacimiento hasta la madurez, es posible modelar una curva de peso en función de la edad para representar el crecimiento. Esta curva se llama "curva de crecimiento" y está atrayendo el interés de investigadores de diferentes áreas (Oliveira et al., 2000; Echeverri, 2010).

En las primeras etapas de la vida, el crecimiento se acelera y el aumento de peso es mayor que el que se produce próximo de la edad adulta, observándose una curva de evolución sigmoidea ascendente. A medida que el individuo se va desarrollando, la tasa de crecimiento se altera y presenta un cambio en la curvatura, donde se identifica el punto de mayor tasa de crecimiento. Después de este punto de inflexión, el crecimiento disminuye gradualmente y la tasa de crecimiento es cada vez más lenta. Esta tendencia continúa hasta que se estabiliza el crecimiento, hecho que, matemáticamente, coincide con la asíntota horizontal (Agudelo Gómez et al., 2008; Echeverri, 2010).

El término curva de crecimiento evoca la imagen de una curva sigmoidea que describe una serie de medidas de tamaño a lo largo del tiempo. Las curvas de crecimiento se pueden dividir en dos segmentos principales: el primero, de aumento de inclinación, puede ser definido como una etapa de auto-aceleración del crecimiento, y el segundo, de disminución de pendiente, definido como una fase de desaceleración del crecimiento (Brody, 1945). Por esto, el patrón típico de crecimiento sigue la forma de una curva sigmoidea (Echeverri, 2010).

Una de las características utilizadas para representar el proceso de crecimiento de los animales es el peso corporal, que sirve como un sustrato para el análisis de la curva de crecimiento, relacionando el peso con la edad de los animales pudiendo ser utilizado en la definición de programas de alimentación, así como para identificar la edad más adecuada para el sacrificio (Figueiredo Filho et al., 2012).

En general, se estudian las curvas de crecimiento mediante el ajuste de funciones no lineares que permiten sintetizar información de todo el período de la vida de los animales en un pequeño conjunto de parámetros matemáticos con interpretación biológica (Oliveira et al., 2000; Figueiredo Filho et al., 2012). Los modelos más utilizados para describir el crecimiento de los animales son las funciones de Brody, Von Bertalanffy, Verhulst, Gompertz y Logístico (Agudelo Gómez et al., 2008; Sarmento et al., 2006).

Los modelos de crecimiento deben poseer características para poder ser utilizados en los sistemas de producción: deben tener un punto de inflexión, presentar una asíntota horizontal, tener un comportamiento lógico y no permitir valores anormales desde el punto de vista biológico; además, tener una base biológica, es decir, que la ecuación debe derivarse del conocimiento teórico que se tenga de la variable dependiente que se analiza, lo que permite que al incorporar esta base teórica en el desarrollo de la ecuación se obtengan resultados más exactos (Kiviste A., 2002, citado en Agudelo Gómez et al., 2008).

Las curvas de crecimiento permiten evaluar parámetros biológicamente importantes: como es el tamaño del animal, evaluado como el peso al alcanzar la madurez sexual; otro es la relación entre la tasa de crecimiento con respecto a la tasa de maduración sexual. Estos parámetros sólo pueden ser evaluados una vez se haya completado el crecimiento. La estimación temprana de los factores puede servir para proponer programas de selección y mejora pues están asociadas a otras características de importancia económica. (Agudelo Gómez et al., 2008)

La ventaja de utilizar modelos no lineares, en lugar de los lineares, radica en el hecho de que los modelos sintetizan un gran número de mediciones en algunos parámetros y permiten alguna interpretación biológica de los mismos, una vez que utilizan mediciones subsecuentes en el tiempo sobre el mismo individuo (Echeverri, 2010).

Según Fitzhugh (1976) y Silveira (2010), para que un modelo no linear represente de una forma adecuada la relación peso-edad, debe atender a los siguientes requisitos:

interpretación biológica de los parámetros, alta calidad del ajuste y facilidad de convergencia. De un modo general, para que un modelo no linear pueda ser utilizado para describir curvas de crecimiento, debe de tener parámetros con una interpretación biológica relevante, debe presentar ajustes con pequeños desvíos y debe también proporcionar grandes tasas de convergencia, una vez que los modelos no lineares exigen métodos iterativos de estimación. (Silveira, 2010).

En nuestro trabajo hemos tenido que estudiar en profundidad la curva de crecimiento de los corderos Segureños. En primer lugar definiendo la de mejor ajuste poblacional, tanto desde el punto de vista comercial, como vital. Del mismo modo hemos tenido que comprobar la bondad de ajuste individual de las curvas, definiendo parámetros individuales de las curvas que fueran utilizables en análisis genéticos profundos, tanto para la obtención de parámetros genéticos poblacionales, como valores de cría individuales utilizables en selección.

Este trabajo, por tanto, partía con el estudio de la curva de crecimiento del ovino segureño como objetivo genérico y se desarrolló de acuerdo con tres objetivos específicos, que cada uno de ellos dio lugar a un artículo científico en revistas de impacto. A continuación se desarrollan los mencionados objetivos específicos, resaltando las referencias de los artículos correspondientes y el índice de impacto de la revista.

- **Establecer el comportamiento matemático del desarrollo corporal durante toda la vida comercial de esta raza (del nacimiento hasta el sacrificio) y de la vida biológica (desde el nacimiento hasta la edad adulta)**; la comparación entre ambas vertientes da información importante sobre el mejor momento para el sacrificio, informa sobre asesoramiento dietético según las necesidades de los animales, permite predicciones económicas de producción y, mediante el uso de los parámetros de la curva como criterios de selección, permite mejoramientos en las características de crecimiento de la raza. (Lupi TM, Nogales S, León JM, Barba C and Delgado JV 2015. Characterization of commercial and biological growth curves in the Segureña sheep breed. animal 9, 1341-1348. Cuartil 1, Factor de Impacto: 1.841).

- Debido a la falta de información sobre los patrones de crecimiento de corderos segureño, **caracterizar y evaluar los efectos de los principales factores no genéticos,** como el sexo, época de nacimiento, rebaño, año de nacimiento y tipo de parto, y sus interacciones, **en el peso y parámetros de crecimiento de la raza ovina Segureña** nos apoya para el diseño de los mejores modelos para el análisis genético de los parámetros de la curva con un mínimo coste computacional. (Lupi TM, Nogales S, León JM, Barba C and Delgado JV 2015. Analysis of the non-genetic factors affecting the growth of Segureño sheep. Italian Journal of Animal Science, 14:3683, pp 124-131. Cuartil 3, Factor de Impacto: 0.718).

- **La estimación de los parámetros genéticos de los coeficientes de las curvas** nos permite comprobar la capacidad de los mismos para ser introducidos en el programa de cría como criterios de selección. Los componentes de la varianza y de la covarianza, la heredabilidad y las correlaciones genéticas nos dan una información imprescindible sobre los niveles de variabilidad genética aditiva y de las relaciones genéticas entre los parámetros de la curva. Estos parámetros, y especialmente su significado biológico, son informativos para los criadores, ya que permiten la inferencia de información económica relevante en relación con el punto de inflexión y la madurez, información que no es accesible a partir del análisis de las características de crecimiento simples, tales como pesos a diferentes edades clave (nacimiento , destete y sacrificio) o ganancias diarias. (Lupi TM, León JM, Nogales S, Barba C and Delgado JV 2015. Genetic parameters of traits associated with the growth curve in Segureña sheep. animal. Cuartil 1, Factor de Impacto: 1.841)

Articulo 1

Lupi TM, Nogales S, León JM, Barba C and Delgado JV 2015.

Characterization of commercial and biological growth curves in the Segureña sheep breed. animal 9, 1341-1348.

Articulo 2

Lupi TM, Nogales S, León JM, Barba C and Delgado JV 2015.

Analysis of the non-genetic factors affecting the growth of Segureño sheep. Italian Journal of Animal Science, 14:3683, pp 124-131.

Articulo 3

Lupi TM, León JM, Nogales S, Barba C and Delgado JV 2015.

Genetic parameters of traits associated with the growth curve in Segureña sheep. animal.

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Characterization of commercial and biological growth curves in the Segureña sheep breed

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Characterization of commercial and biological growth curves in the Segureña sheep breed

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Non-linear models were analysed to describe both the biological and commercial growth curves of the Segureña sheep, one of the most important Spanish breeds. We evaluated Brody, von Bertalanffy, Verhulst, logistic and Gompertz models, using historical data from the National Association of Segureña Sheep Breeders (ANCOS). These records were collected between 2000 and 2013, from a total of 129 610 weight observations ranging from birth to adulthood. The aim of this research was to establish the mathematical behaviour of body development throughout this breed's commercial life (birth to slaughter) and biological life (birth to adulthood); comparison between both slopes gives important information regarding the best time for slaughter, informs dietary advice according to animals' needs, permits economical predictions of productions and, by using the curve parameters as selection criteria, enables improvements in growth characteristics of the breed. Models were fitted according to the non-linear regression procedure of statistical package SPSS version19. Model parameters were estimated using the Levenberg–Marquardt algorithm. Candidate models were compared using the determinative coefficient, mean square error, number of iterations, Akaike information coefficient and biological coherence of the estimated parameters. The von Bertalanffy and logistic models were found to be best suited to the biological and commercial growth curves, respectively, for both sexes. The Brody equation was found to be unsuitable for studying the commercial growth curve. Differences between the parameters in both sexes indicate a strong impact of sexual dimorphism on growth. This can emphasize the value of the highest growth rate for females, indicating that they reach maturity earlier.

Keywords: growth, models, sex, sheep, Zootechny

Implications

Non-linear models can be an option to establish the mathematical behaviour of body development throughout the life of the Segureña sheep breed. These models require lower computational and faster convergence than other methods. Moreover, in genetic evaluation programmes with large data sets, non-linear models are more advantageous. The results showed a strong impact of sexual dimorphism on growth.

Introduction

According to the official genetic improvement programme, the Segureña breed is one of the three most important Spanish meat sheep breeds. Furthermore, this breed helps boost the local economy of the regions in which it is bred – namely, the highlands of Granada, Sierra de Segura and Las Villas – which are among the poorest regions in Europe. Therefore, this breed is the main reason that people have settled in this region.

Mainly exploited in extensive and semi-extensive conditions, these animals are one of the components that balance the ecosystem of the regions they inhabit, thereby making them a mainstay of environmental and social sustainability. Despite the difficult and disadvantaged environment, this breed has achieved the most competitive and highest production returns (Hernandez, 2004). The carcass yield is between 48% and 55% (Cano *et al.*, 2003), owing to a lightweight lambskin that represents 8% of the total live lamb (ANCOS, 2014). The weight difference between males and females can influence the shape of the growth curve, as has been noted by several authors (Silva and Araújo, 2000; McManus *et al.*, 2003; Sarmento *et al.*, 2006).

The main selection objective and criteria are defined in the official genetic improvement programme. The evaluation herds under selection account for 62 505 animals in total. Every year, around 20 000 new lambs complete the weighting programme, and more than 45 000 new parturitions are

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registered for the analysis of prolificacy. The traits considered for genetic evaluation are the live weight at 30, 45 and 75 days of age and daily gain between 0 and 30, 0 and 45 and 0 and 75 days; prolificacy (number of lambs per birth); the productive longevity (leg and udder morphology); and quality of meat and carcass (MAGRAMA, 2012). The genetic evaluation is based on performances collected on farm. These data are annually evaluated using different variants of the BLUP animal model, obtaining predictions of the breeding values. Based on these predictions, a catalogue is published annually of the best 10 males, selected by a combined selection index.

Growth, described as changes in volume, size or shape of an organism over time, is a very important characteristic of living organisms (Ulutas *et al.*, 2010). Fitting growth curves to growth functions is an interesting method for assessing different management factors or for breeding purposes. Growth curve models provide a set of parameters that describe growth pattern over time and estimate the expected weight of animals at certain ages. In addition, the parameters obtained from growth functions are highly heritable and have been used in selection studies (Daskiran *et al.*, 2010).

The growth curve is represented mathematically as a function of age and live weight, covering all or part of the animal's lifespan (Echeverri *et al.*, 2013). These growth curves show initially a self-accelerating stage (slope increase) followed by a deceleration stage (slope decline) (Brody, 1945). Growth curves have been studied extensively in many types of cattle, and several mathematical models have been proposed to describe the growth behaviour reporting differences of fit accuracy among breeds (Hamouda and Atti, 2011; Tariq *et al.*, 2013). Many mathematical functions have been used to represent growth curves in sheep. In this species, the models that better represent sheep growth are the non-linear Brody, von Bertalanffy, Verhulst, logistic and Gompertz models, as reported in the studies of Topal *et al.* (2004), Hamouda and Atti (2011), Tariq *et al.* (2013), among others. These are the most significant functions in the ovine species according to the existent literature. Other basic models such as linear and quadratic models were preliminarily tested, but their fitting criteria were very bad with respect to the other models achieved in this paper. In order to concrete the discussion of our findings and reduce the extension of the document, these models were removed from the definitive design.

Moreover, Lambe *et al.* (2006), in their study of two contrasting breeds from birth to slaughter, state that the fastest phase of growth, observed in young animals, is often assumed to be linear, and linear regressions or ratios between BW gain and time are used to model growth.

Biological growth can be defined as the weight gain of an animal until it reaches adulthood. In the early stages of life, this growth accelerates and weight gain is greater than when close to adulthood, producing a sigmoid curve. As the animal develops, the growth rate modifies, and a plot of growth rate presents a change in curvature, which identifies the highest growth rate point. After this inflection point, growth gradually decreases and the growth rate is slower. This tendency continues until growth is stabilized, a fact that, mathematically, coincides with the horizontal asymptote of the growth curve (Fitzhugh, 1976; Gómez *et al.*, 2008).

Commercial growth is the weight gain of the animals solely during the period comprised between birth and slaughter (slaughter age is around 80 days). This age is determined by cultural aspects such as the carcass size demanded by consumers, but also by technological criteria such as the level of fattening in the carcass. Therefore, economically this is the most important growth phase. The commercial growth period also varies from one breed to another, depending on genetic and environmental aspects, but is also affected by cultural and technological aspects based on differences in customs among regions regarding the manner and time of slaughter.

Therefore, there is a significant variation among populations and breeds regarding growth behaviour during the animal's biological and commercial lifespan; therefore, the best fitting curve must be determined for each breed or population, taking into account the whole lifespan and the restricted period between birth and slaughter.

The commercial curve is of interest and can be applied for breeding and economic purposes, whereas the biological curve involves physiological, nutritional and technological aspects, among others.

Very few studies have been conducted on the Segureña sheep breed (Hernandez, 2004; León *et al.*, 2005). The relationship between the animal's age, growth rate and maturity can be studied using non-linear empirical models. This information is important for research purposes and for recommendations regarding production, breeding and reproduction. The estimation of biologically interpretable parameters of a growth function, in association with the production characteristics of the animals, can be an alternative for selection programmes that seek precocity with higher weight and carcass quality (Souza and Bianchini Sobrinho, 1994; Ulutas *et al.*, 2010). The main aims of these models are to describe and predict growth and make inferences based on an interpretation of growth parameters (Ratkowsky, 1983). Choosing a suitable mathematical function is crucial in efficiently describing growth evolution during the animal's commercial and biological life; an appropriate choice should, therefore, be based on data from different populations and herds (León *et al.*, 2012).

The objective of this study was to determine the best non-linear growth curve models for the growth performance of the Segureña sheep breed. This important tool can be applied to several aspects of the breed's breeding programme development. The curve parameters can be used as new selective criteria to improve the productive behaviour of the breed – for example, precocity can be inferred from the curve slope, whereas the best time for slaughter can be inferred from the inflection point. This information is also useful for marketing and commercial forecasts, giving information regarding predictions of production, as well as for creating feeding plans, to match feeding supply to production.

Material and methods

The weight-age data for this study were obtained from 60 694 individuals from the historical archives of the National Association of Segureña Sheep Breeders (ANCOS). The data were collected from 2000 to 2013. This archive has all the information regarding lamb weights at different ages of reference – birth, early weaning, late weaning and slaughter – and information about the origin of each lamb (livestock, date of birth, parentage, etc.). Real weighing dates were used to compare with best fitted model-estimated results. Data were grouped as follows: P_0: weighed lambs between 0 and 15 days of age; P_1: weighed lambs between 16 and 35 days of age; P_2: weighed lambs between 36 and 55 days of age; P_3: weighed lambs between 56 and 80 days of age; and adults.

The data file was checked to eliminate outliers. The original data were purged, first, by anomalous dates, then by each weighing date and, finally, all data at least twice the standard deviation above and below the average weight in each weighing were removed. With this restriction, a confidence over 99% of belonging to the distribution is ensured. After this evaluation, only data from 59 937 animals, representing 98.75% of the total, and 129 610 weight observations were retained for this study. All models were fitted using multiple observations of the dependent variable (weights) for each point of the independent variable (day of life). Field data were used to fit the models, and as these data presented too many outliers it was decided that it was better to assume an overvaluation of pseudo R^2 than using data that will distort the results in an uncontrolled manner.

A higher number of females was observed, 35 290 (58.88%), than males, which was 24 647 (41.12%). Table 1 presents information regarding the number of observations and the average weight by sex and age: males were statistically ($P < 0.001$) heavier than females. There were 165 adult females and 68 adult males: 19 animals from 3 to 6 months of age, 12 animals from 6 months to 1 year of age, 37 animals from 1 to 2 years of age, and 165 animals of 2 years and older.

The models used – Brody, von Bertalanffy, Verhulst, Gompertz and logistic – whose mathematical expressions and biological parameters are found in Table 2, were fitted to the data using the non-linear regression procedure from the SPSS version 19 statistical package. In all cases, individual observations were used to fit the correspondent population.

The parameter *a* is defined as the asymptotic value of the function when the time tends to infinity; this value represents the asymptotic weight of the animal, regardless of fluctuation problems due to genetic and environmental effects. The parameter *b* allows calculation of the inflection age. Parameter *k* represents the relative growth rate (rate of exponential growth); high values indicate animals with precocious maturity – that is, animals that attain maturity weight quickly, and low values indicate animals with a delayed maturity or that tend to mature more slowly. Parameter *m* gives the shape of the growth curve and, consequently, determines the inflection point, the beginning of the auto-deceleration stage until the animal reaches adult size (McManus *et al.*, 2003; Echeverri *et al.* 2013; Tariq *et al.*, 2013). Quantitative growth can be characterized using the parameters of each model (Brown *et al.*, 1976; Fitzhugh, 1976; Hamouda and Atti, 2011). The formula for estimating the age at maturity was developed by the authors of the present study, and is presented, for each model, in Table 2.

The growth rate estimates the increase in weight per unit of time (Quirino *et al.*, 1999; Freitas, 2005). The degree of maturity should be treated as the weight change in relation to the weight at adulthood, or as an indicator of the speed with which the animal approaches its adult size (Fitzhugh, 1976; Carneiro *et al.*, 2009).

To select the best curve, there are five principal criteria of adjustment, mentioned by numerous authors (Gbangboche *et al.*, 2011; Echeverri *et al.* 2013; Tariq *et al.*, 2013): determinative coefficient (pseudo R^2), mean square error (m.s.e.), number of iterations, Akaike information criterion and biological coherence of the estimated parameters. For each of these criteria, the optimum was interpreted as follows:

1. The lowest value of the m.s.e. of the studied equation, as a measure that includes the variability of the factors that the investigator has not considered.
2. The highest level of the determinative coefficient (pseudo R^2).

   In its non-linear regression tool, the SPSS package applies the Levenberg–Marquardt algorithm method, which is used in cases where the parameters are closely correlated. When using linear regression models, the quality of fit of the model is represented by the determinative coefficient, known as R^2. In non-linear regression, this is not the correct measure. One problem with the definition of R^2 is that it requires the presence of an intersecting point, which does not exist in most non-linear models. The measure that

Table 1 *Number of observations and weight average (WA) of Segureña sheep distributed by sex and age*

	P_0			P_1			P_2			P_3			Adults		
	n	WA (kg)	CV (%)	*n*	WA (kg)	CV (%)	*n*	WA (kg)	CV (%)	*n*	WA (kg)	CV (%)	*n*	WA (kg)	CV (%)
Females	34 691	3.492	10.8	13 840	8.723	19.9	12 221	13.333	18.3	10 607	18.487	16.0	165	46.390	22.2
Males	23 961	3.521	10.5	13 243	9.141	21.0	11 577	14.164	19.9	9237	20.005	17.6	68	64.041	19.5

P_0 = lambs between 0 and 15 days; P_1 = lambs between 16 and 35 days; P_2 = lambs between 36 and 55 days; P_3 = lambs between 56 and 80 days of age; CV = coefficient of variation.

Table 2 *Mathematical description of growth models, biological parameters and growth evaluators*

	Mathematical expression	Inflection point	Inflection age	Growth rate	Age to maturity ($y \approx a$)	Maturity degree
Brody	$y = a^*(1 - b^*\exp(-k^*t))$	–	–	$v_c = ka\left(1-\frac{y}{a}\right)$	$-\frac{ln\left(\frac{a-y}{ba}\right)}{k}$	
Von Bertalanffy	$y = a^*(1 - b^*\exp(-k^*t))^{**}3$	$y_i = \frac{8a}{27}$	$t_i = \frac{\ln(3b)}{k}$	$v_c = 3ky\left[\left(\frac{a}{y}\right)^{1/3} - 1\right]$	$-\frac{ln\left(\frac{1-\sqrt[3]{\frac{y}{a}}}{b}\right)}{k}$	
Verhulst	$y = a/(1 + b^*\exp(-k^*t))$	$y_i = \frac{a}{2}$	$t_i = \frac{\ln(b)}{k}$	$v_c = ky\left(1-\frac{y}{a}\right)$	$-\frac{ln\left(\frac{a-y}{y-b}\right)}{k}$	$u = \frac{y}{a}$
Logistic	$y = a^*(1 + \exp(-k^*t))^{**}(-m)$	$y_i = \frac{a}{2}$	$t_i = \frac{-\ln(2^{1/m}-1)}{k}$	$v_c = mka\left(\frac{e^{-kt}}{1+e^{-kt}}\right)$	$-\frac{ln\left[\left(\frac{a}{y}\right)^{1/m} - 1\right]}{k}$	
Gompertz	$y = a^*\exp(-b^*\exp(-k^*t))$	$y_i = \frac{a}{e}$	$t_i = \frac{\ln(b)}{k}$	$v_c = kyln\left(\frac{a}{y}\right)$	$-\frac{ln\left(\frac{\ln\left(\frac{y}{a}\right)}{-b}\right)}{k}$	

y = weight, in kg, at age t; t = age in days; a, b, k and m = parameters.

approximates R^2 in non-linear models is the pseudo R^2. This value is slightly lower than the R^2 from the linear model:

$$\text{pseudo } R^2 = 1 - \frac{\text{SSResidual}}{\text{SSTotal}_{\text{Corrected}}} \quad (1)$$

3. The smallest number of iterations needed to reach the value of the model parameters indicates the computational ease of the mathematical function used.
4. The lowest value of the Akaike information criterion (Thomas *et al.*, 2009): this criterion takes into account changes in the quality of fit and differences between the number of parameters in both models (Posada and Noguera, 2007).

$$\text{AIC} = n \times \ln\left(\frac{\text{SSE}}{n}\right) + 2p \quad (2)$$

Where p = number of parameters+1, SSE = sum of squares of the residuals and n = number of observations.
5. Biological coherence of the estimated parameters.

The determinative coefficient should be interpreted with caution, because the models might have limited predictive capacity and present high values of pseudo R^2, which is why this coefficient must not be the only criterion for choosing between models (Noguera *et al.*, 2008). This evaluator is used to compare the goodness of fit of models with different numbers of parameters (Souza, 2010).

Results and discussion

Homogeneity of means and of variances between sexes were analysed to infer whether they showed the same distribution or not, to decide whether a single adjustment was valid for the population or whether the analysis should be made separately by sex. An *F*-test for homogeneity of variances was applied using Microsoft Excel 2010 and, with a $P = 0.09$, it was concluded that the variances for the weights of both sexes were homogeneous. When conducting a *t*-test of homogeneity of means, it was concluded that, with a $P < 0.001$, the averages of the weights between sexes were heterogeneous, implying the need to infer the adjustments separately for each sex. This conclusion was also presented by McManus *et al.* (2003), Ulutas *et al.* (2010) and Gbangboche *et al.* (2011), among others.

Brown *et al.* (1976), Bathaei and Leroy (1998) and McManus *et al.* (2003) emphasized that the most important biological relationship in a growth curve is the relation between the parameters *a* and *k*. A negative correlation between these parameters indicates that early maturing animals tend to grow into animals with smaller mature weights.

Given the quality-of-fit criteria, all models are suitable for describing the growth of the Segureña sheep breed (Table 3). Brody's model is the least suitable, as it has the lowest coefficient of determination (pseudo R^2) and the highest values for m.s.e., Akaike information criterion and number of iterations. Consistent with the findings of Gómez *et al.* (2008) and corroborated by the research of Brown *et al.*

Table 3 *Estimated parameters for each model in the study of the biological growth curve for both sexes of the Segureña sheep breed*

Model	Sex	*A* (s.e.)	*B/M* (s.e.)	*K* (s.e.)	Pseudo R^2	m.s.e.	No. of iterations	AIC
Brody	F	51.343 (0.155)	0.936 (0.000)	0.005 (0.000)	0.915	3.202	27	83 243.45
	M	74.940 (0.353)	0.958 (0.000)	0.003 (0.000)	0.898	4.578	37	88 374.44
von Bertalanffy	F	48.877 (0.137)	0.587 (0.000)	0.010 (0.000)	0.923	2.868	24	75 359.57
	M	67.707 (0.262)	0.628 (0.001)	0.009 (0.000)	0.908	4.098	18	81 933.47
Verhulst	F	44.521 (0.141)	10.249 (0.039)	0.028 (0.000)	0.914	3.236	12	84 000.56
	M	61.633 (0.263)	13.671 (0.068)	0.027 (0.000)	0.897	4.612	12	88 800.69
Logistic	F	46.580 (0.137)	3.657 (0.005)	0.018 (0.000)	0.921	2.957	12	77 558.12
	M	64.054 (0.256)	4.060 (0.007)	0.016 (0.000)	0.905	4.240	21	83 912.71
Gompertz	F	47.489 (0.135)	2.585 (0.003)	0.014 (0.000)	0.923	2.886	18	75 804.87
	M	65.232 (0.255)	2.871 (0.005)	0.012 (0.000)	0.907	4.143	23	82 571.88

s.e. = standard error; pseudo R^2 = non-linear determinative coefficient; m.s.e. = mean square error; AIC = Akaike information coefficient.

(1976) and Gbangboche *et al.* (2011), the von Bertalanffy, Gompertz and Verhulst models overestimate weights at early ages, whereas the Verhulst model underestimates the weight at maturity. The low value of the number of iterations indicates that all models fit the data.

There is a relatively small difference between the estimated parameters *a* and *k* in all models for males and females. According to parameter *a*, all models confirmed that males are heavier than females, which is consistent with the greater average weights of males at all ages of reference, as is evident in Table 1. This was also observed by several authors in the study of different species (Carneiro *et al.*, 2009; Ulutas *et al.*, 2010; Gbangboche *et al.*, 2011).

The parameter *k* represents the animal's rate of maturity and indicates the growth velocity in reaching the asymptotic weight from the initial weight. High values of the parameter *k* indicate that the animals reach maturity earlier (Brown *et al.*, 1976; Carolino and Gama, 1993; McManus *et al.*, 2003), and, as can be observed in Table 3, females have a higher rate of maturity (between 0.005 and 0.028) than males (between 0.003 and 0.027), as was also observed by Bathaei and Leroy (1998), Gbangboche *et al.* (2008), Ulutas *et al.* (2010), and, consequently, have a lower weight at maturity. The growth rates estimated by these models showed that females grow at a higher rate than males, although the differences between males and females were quite small, and always in favour of females, as reported in previous studies (Bathaei and Leroy, 1998; Gbangboche *et al.*, 2006; Ulutas *et al.*, 2010). The Brody model estimated the lowest growth rates for males and females, whereas the Verhulst model estimated the highest growth rates in both sexes.

As presented in studies by several authors on sheep growth (Topal *et al.*, 2004; Gbangboche *et al.*, 2011; Hamouda and Atti, 2011), the model that best fits the observed data to determine the growth curve of animals of both sexes of the Segureña sheep breed is the von Bertalanffy model (Table 3). Accepting this model as the best descriptive model for the growth of this breed from birth to adulthood, an inflection point (Table 2) occurs around 70.4 days for males and 56.6 days for females, at weights of 20.06 and 14.48 kg, respectively. Therefore, it follows that the optimal age of slaughter for females should be around 2 weeks earlier than males to achieve maximum efficiency in the conversion of consumed feed. Logically, the recommended slaughter weights for females must be lower, because after inflection animals tend towards fattening and not muscle growth.

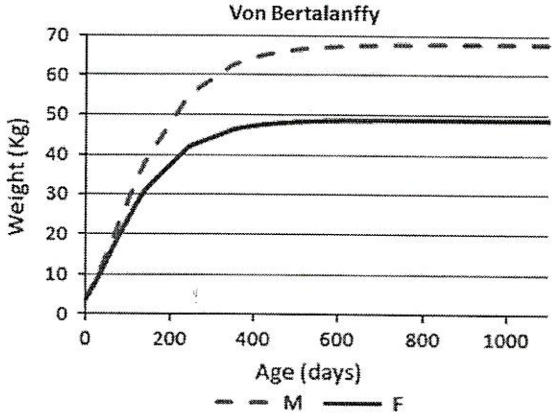

Figure 1 Comparison of biological growth curves for male and female Segureña sheep, with weights predicted by the von Bertalanffy model.

Biological growth curves (males and females) predicted by the von Bertalanffy model are presented in Figure 1. Female adult live weight was lower and was achieved at an earlier age than males. These facts, induced by sexual dimorphism, justify a different zootechnical treatment to reach maximum economic efficiency.

Values obtained for the estimated parameters of each model for the commercial curve, where the weights are used up to slaughter age, as well as the calculated values for the criteria for evaluating the quality of fit, are shown in Table 4. These values show a great variation from one breed to another depending on the traditional consumer demands, determined by cultural aspects. For instance, lambs from dairy breeds are slaughtered significantly earlier than lambs from breeds reared for meat. Segureña lambs are in demand in the market at an age of around 80 days, known as *ternasco* or *recental*.

Table 4 *Estimated parameters for each model in the study of the commercial growth curve for lambs of both sexes of the Segureña sheep breed*

Model	Sex	*A* (s.e.)	*B/M* (s.e.)	*K* (s.e.)	Pseudo R^2	m.s.e.	No. of iterations	AIC
Brody	F	2803.096 (–)	0.999 (–)	$7.284E^{-5}$ (–)	0.917	2.814	>300	73 833.82
	M	3952.560 (–)	0.999 (–)	$5.686E^{-5}$ (–)	0.897	4.237	>300	83 768.31
von Bertalanffy	F	57.252 (0.855)	0.607 (0.002)	0.009 (0.000)	0.920	2.704	12	70 991.26
	M	77.505 (1.754)	0.644 (0.003)	0.008 (0.000)	0.903	4.000	28	80 436.50
Verhulst	F	25.103 (0.087)	6.117 (0.023)	0.039 (0.000)	0.921	2.701	10	70 917.76
	M	28.273 (0.132)	6.871 (0.032)	0.039 (0.000)	0.903	4.004	10	80 496.26
Logistic	F	31.306 (0.190)	3.163 (0.008)	0.024 (0.000)	0.921	2.698	10	70 828.09
	M	36.820 (0.313)	3.378 (0.011)	0.023 (0.000)	0.903	3.996	10	80 373.56
Gompertz	F	38.209 (0.313)	2.394 (0.007)	0.016 (0.000)	0.921	2.700	10	70 878.44
	M	46.145 (0.530)	2.572 (0.010)	0.016 (0.000)	0.903	3.996	16	80 382.80

s.e. = standard error; pseudo R^2 = non-linear determinative coefficient; m.s.e.: mean square error; AIC = Akaike information coefficient.

Table 5 *Predicted weights, in kg, of Segureña sheep at different ages differentiated by sex*

	Observed		von Bertalanffy		Verhulst		Logistic		Gompertz	
Age	M	F	M	F	M	F	M	F	M	F
0	3.521	3.490	3.497	3.475	3.592	3.527	3.542	3.495	3.525	3.487
15	6.421	6.170	6.112	5.931	5.856	5.695	6.033	5.869	6.102	5.812
30	8.949	8.606	9.310	8.847	9.026	8.661	9.326	8.930	9.396	8.686
45	13.147	12.564	12.944	12.069	12.922	12.200	13.187	12.417	13.195	11.915
60	17.836	15.904	16.867	15.454	17.013	15.796	17.253	15.979	17.236	15.278
80	21.986	20.181	22.325	20.022	21.692	19.764	22.379	20.310	22.571	19.638

When fitted to the lamb's weight, the Brody model produces very inadequate parameters. The parameter *a* is estimated with an unacceptable value for these animals (3952.6 for males and 2803.1 for females). The values obtained for all the criteria of fit are the worst among the models under study: it has the lowest pseudo R^2, the highest m.s.e., it fails to converge and it has the highest Akaike information criterion. From this, it can be concluded that, in agreement with Lewis *et al.* (2002), the Brody model does not fit the data for Segureña lambs until slaughter age. This can be explained by the fact that this model predicts more accurately growth at older ages (Brown *et al.*, 1976; Fitzhugh, 1976; Gómez *et al.*, 2008). In the literature, several authors have excluded the Brody model as an explanatory model for sheep growth (McManus *et al.*, 2003; Sarmento *et al.*, 2006).

The remaining four growth models fitted the growth data well (pseudo $R^2 = 0.903$ for males and pseudo $R^2 = 0.921$ for females), confirming their eligibility. The logistic model had the lowest value for all other fitting criteria – m.s.e., number of iterations and Akaike information criterion – in both sexes. As studies by other authors on sheep growth show (McManus *et al.*, 2003; Freitas, 2005; Carneiro *et al.*, 2009), the model that best fits the observed data to determine the commercial growth curve of Segureña lambs, in both sexes, is the logistic model.

Growth rates, estimated by the models for zootechnical growth curves, varied between 0.008 and 0.039 for males and between 0.009 and 0.039 for females. The von Bertalanffy model had the lowest estimates of growth rates in both sexes, whereas the Verhulst model had the highest estimates.

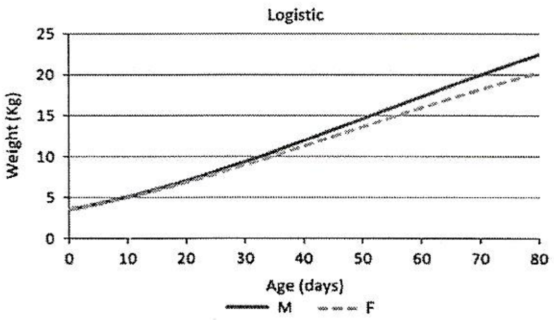

Figure 2 Comparison of commercial growth curves for male and female Segureña sheep, with weights predicted by the logistic model.

Table 5 presents weights predicted by the models at different ages, differentiated by sex. This table confirms the superiority of the weights of the males compared with the females. All the models studied predicted weights at slaughter age consistent with the data presented in the literature, which are indicative of well-fitting models.

Commercial growth curves with weights predicted by the logistic model, for both sexes, are presented in Figure 2, where a slight difference in slope is evident.

In general, we observed that sexual dimorphism is evident in our results, both regarding biological and commercial growth patterns. This is justified by increasing hormonal differences as the lambs approach puberty. Therefore, we recommend that producers take sex into account when establishing fattening feed lots; this procedure would enable the establishment of patterns of feeding and management fitted to the growth behaviour of each feed lot. This is relevant because, at present, feed lot finishing of lambs are not grouped by sex, but by weight or age.

Conclusions

Models considered in the present study – Brody, von Bertalanffy, Verhulst, logistic and Gompertz – are adequate to describe the growth of the Segureña sheep breed, although the Brody model does not converge in the commercial curve.

The most suitable function to explain the biological growth of the Segureña breed, from birth to maturity, is the von Bertalanffy model, for both sexes. The curve parameters showed important differences between sexes, which led us to recognize the strong impact of sexual dimorphism on growth. We highlight the value of the higher growth rate for females, indicating that they reach maturity earlier.

From birth to slaughter, the most suitable function to explain the commercial growth curve of Segureña lambs is the logistic model. During this period, we also observed a sexual dimorphism on growth.

These results, showing the importance of zootechnical applications in terms of the management of both sexes in lamb fattening feed lots, and for making decisions regarding slaughter, may also support selection programmes, as the application of non-linear models can be used for earlier selection and some curve parameters could be introduced into the breeding programme as selection criteria to improve important commercial traits such as the precocity.

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Analysis of the non-genetic factors affecting the growth of segureño sheep

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PAPER

Analysis of the non-genetic factors affecting the growth of Segureño sheep

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Abstract

A study was conducted to evaluate the effects of non-genetic factors on the growth behaviour of Segureña sheep breed. Growth related data (early weaning weight, late weaning weight and weight at 80 days of age) were taken from 59,704 lambs belonging to historical data from National Association of Segureño Sheep Breeders (ANCOS) during a period of 11 years. Statistical analyses were performed by using the multifactorial analysis of variance of IBM SPSS Statistics v.19 software. The model included non-genetic factors – lamb sex (S), birth season (N), herd (H), birth year (A) and birth type (P) – as main effects, the dam's age at lambing and the lamb's age when weighed as covariables, and the interactions between these factors. Results showed that all weights at developmental stages were significantly (P<0.001) affected by all factors, except for A and the covariable age of dams at lambing on lambs aged 80 days. Double interactions H×A, H×P and H×N were significant (P<0.001) for all variables, as well as the triple interaction H×A×P. Non-genetic factors have a very important role in the development and growth of the Segureña sheep breed, at different ages or growth stages, therefore a correction is necessary to increase the accuracy of direct selection on lamb weight at early weaning, late weaning and at slaughtering (80 days of age).

Introduction

The growth described as a change in volume, size or shape with the passing of time is a very important characteristic of living organisms, especially in production animals as meat sheep. Recording a battery of weights during the animal's life is difficult to interpret without a way to summarise them; for this reason it is essential to investigate the best traits to be used in sheep meat breeding (Sarti *et al*., 2001). The use of growth equations provides a good way to summarise information contained in these data into some parameters with biological interpretation (Brown *et al*., 1972; Fitzhugh, 1976).

Not only is information on live weight important for selection purposes, but the degree of maturity and growth rate throughout the animal's life are also relevant due to their association with other characteristics and as they can help to optimise production. Studies on sheep growth have generally been based on live weights over a relevant economic time period, becoming subjects of major interest among animal scientists and producers (Bathaei and Leroy, 1998). Knowing which factors influence the growth curve may help management and improvement programmes (McManus *et al*., 2003).

The Segureña sheep breed represents one of the three pillars of the Spanish sheep meat production of autochthonous breeds. Both in the past and present, it has helped establish the rural population by maintaining centenary livestock farming activities where, until now, transhumant practices adapted perfectly to the glens and paths that flow through most of the country (Hernández, 2004). Mainly exploited in extensive and semi-extensive conditions, these animals are one of the components that balance the ecosystem of the regions they inhabit, thereby making them a mainstay of environmental and social sustainability. Despite this difficult and disadvantaged environment, this breed reached the most competitive and highest production returns (León *et al*., 2007). Its general appearance is agile and graceful, with a medium-size body (males reach 90 kg and females 60 kg) and a proportional head. Their profile is slightly convex and presents overall elongated shapes. One of the characteristics of the Segureña breed is its good sexual precocity where, in a well-fed group, the first delivery can occur at between twelve and fourteen months. Ewe prolificacy is generally high, with some selected herds reaching 175 animals born from 100 parturitions, although the usual numbers are around 135 or 140 animals per 100 parturitions (Hernández, 2004).

Lambs are suckled by the dams during their first weeks of life. Currently, reproduction remains closely tied to commercialisation and lambs are weaned early, with an interval between births of about eight months, *i.e.* three parturitions every two years. The lifespan of a breeding ewe is approximately 7 years, during which it can have approximately 10 parturitions.

The lambs of this breed are of high quality for human consumption and are slaughtered when their weight is between 24 and 30 kg. The slaughterhouse return rate is about 51% of harvested meat, owing to a lightweight lambskin that represents 8% of the total live lamb.

In 1997, after the implementation and development of weight control in lambs and the morphological assessment programme, the National Association of Segureño Sheep Breeders (ANCOS) received official support from the Regional Autonomous Governments

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Key words: Growth, Interactions, Multifactorial analysis, Sex.

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Contributions: JVC, negotiations with the Association for implementation of actions to be undertaken, experimental design, genetic evaluations (animal model applied, fixed effects) as well as yielding of mathematical model to apply for settings of the field data, general supervision of work; SN, performing fieldwork, weighing, genealogical control and transfer data to the database, liaison with ANCOS association, support in research, statistical analysis and interpretation of results; JML, support in statistical analysis and interpretation of results.

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of Andalucia and Murcia to initiate the corresponding selection and genetic improvement scheme for this breed, with the assistance of the University of Córdoba.

Several authors (Strizke and Whiteman, 1982; Dimsoski *et al.*, 1999; Macedo and Arredondo, 2008; Gbangboche *et al*., 2011; Momoh *et al.*, 2013) have identified sex and birth type as two factors that have major influence on the growth of sheep, variables that significantly affect the performance of production systems, whose purpose is to obtain the greatest economic profit in the shortest time possible (Tron *et al.*, 2003). Due to market demands, lambs are born year-round, leading several researchers (Strizke and Whiteman, 1982; Souza and Bianchini Sobrinho, 1994; Tron *et al.*, 2003; Hinojosa-Cuéllar *et al.*, 2012) to study the effect of birth season on lamb weights in order to determine if there is in fact any season with better results for lamb weight.

The herd has an effect on lamb growth that is caused by a range of components with overlapping influences, resulting in direct and indirect effects on the animals' development. Indirect effects are usually the most important for ruminant, such as ambient temperature and factors that control the moisture level in soil which, by affecting plant growth, ultimately influence the quantity and quality of available nutrients. A large part of the same variety of factors determine the microclimate of many microorganisms and vectors, which play an important role in the dynamics of parasitic organisms and therefore in disease levels. Cold, wet and windy conditions, which are most extreme in high altitude areas, cause acute stress and lead to hypothermia in neonates, or pneumonia in suckling and immature lambs. These factors generally do not persist long enough to affect growth in the long term (Charles, 1985).

Due to the lack of information on growth patterns in Segureño lambs, the aim of this study was to characterise and evaluate the effects of the main non-genetic factors, such as sex, birth season, herd, birth year and birth type, on the growth of Segureño lambs, and their interactions on weight and growth parameters in the Segureño sheep breed. This knowledge is crucial when designing the best models for genetic analysis with a minimal computational cost (Lambe *et al.*, 2006).

Materials and methods

The growth data used in this study belongs to historical data from ANCOS collected over the past 11 years in 41 herds. Values where the average weight data was±2*standard deviation in each age were excluded, resulting in a total of 59,704 lambs with 129,377 body weight.

The animals are raised during the day in natural pasture, depending on the hours of daylight and therefore the time of year and weather conditions; sheep are supplemented in the last month of gestation and during lactation (usually cereals such as barley) and during the dry season all animals are supplemented. Usually animals are sheltered overnight. Births occur year-round, but mainly in three seasons: January (replacement), May (replacement/sale) and August (sale). Lambs are left with dams until aged 45 days, from this age they are sent progressively for fattening aged around 60 days until reaching slaughter age.

Information considered age and weight at three developmental stages: P1) early weaning (stage considered between 16 and 35 days), with 20,851 observations; P2) late weaning (stage considered between 36 and 55 days), with 17,872 observations; and P3) final weight (stage considered between 56 and 80 days), with 14,216 observations.

Lambs from triple or higher birth type were clustered on one level denominated triple or higher, due to their low frequency, thus the birth type classification was established on three levels: single, double and triple or higher.

Birth dates were grouped into four seasons: from March 21 to June 20 (spring); from 21 June to 22 September (summer); from September 23 to December 20 (autumn); from December 21 through March 20 (winter).

As a preliminary study, a statistical analysis using the univariate general linear model from the statistical package IBM SPSS Statistics v.19 was performed to analyse the volume of variance explained by the pure effect of the isolated factors on each variable (P1, P2 and P3). Statistic model, using the non-linear regression from IBM SPSS Statistics v. 19, included 5 fixed effect factors: sex (2 levels), birth season (4 levels), herd (38 levels for P1, 35 levels for P2 and 24 levels for P3), year (11 levels) and birth type (3 levels) and 2 covariates: lamb's age at weighing and age of dam at lambing. The model fitted was:

$$Y=\mu+S+N+H+A+P+SN+SH+SA+SP+NH+NA+NP+HA+HP+AP+SNH+SNA+SNP+SHA+SHP+SAP+NHA+NHP+NAP+HAP+SNHA+SNHP+SHAP+SNHAP+E+M+\varepsilon$$

where Y=weight of a lamb at age A;

μ=mean;

S=sex (1,2);

N=birth season (1..4);

H=herd (1..38);

A=year (1..11);

P=birth type (1..3);

E=lamb's age (days);

M=dam's age at lambing (year);

SN, SH, SA, SP, NH, NA, NP, HA, HP, AP, SNH, SNA, SNP, SHA, SHP, SAP, NHA, NHP, NAP, HAP, SNHA, SNHP, SHAP, NHAP, SNHAP=interactions between factors; ε=residual error.

The dam's age at lambing, in years, and the lamb's age at weighing, in days, were used as covariates to correct the phenotype observation of weaning weight. This is because lambs are not all born on the same day but are weighed together, which means they are weighed at different ages. Comparison of means was performed *a posteriori* by Tukey test, setting $P<0.05$ to identify significant differences between treatments.

Non-significant interactions ($P>0.05$) were removed from the model in each developmental phase, and the data were re-analysed with a model including only the main factors, covariates, and significant interactions.

Results and discussion

Weight recording is essential in meat breeding, because these traits constitute important selection criteria in the improvement programmes. These data are not only useful in genetic purposes, they are also important to develop economic prognostics and evaluations, and to make prevision on feeding, reproduction and other farming activities. Weight recording is expensive and complex and for this reason some successful alternative has been proposed in meat sheep by using simple characters highly related to the lamb growth (Sarti *et al*., 2003).

In the present study an important amount of data belonging to the meat recording programme of the Segureña sheep breed has been used to develop a deep study of the physiological growing performance of the breed, taking into account the most important non genetic sources of variation.

As shown in Table 1, the sex effect on lambs weight increases as the animal develops (1.4, 2.8 and 5.2% for P1, P2 and P3 respectively), showing the impact of sexual dimorphism, as found in the study in Navajo sheep performed by Eltawill *et al.* (1970) and in contrast to the finding from Sarti *et al.* (2003), in Appenninica and Merinizzata sheep breeds; regarding birth type, the effect decreases as the lamb develops (9.8, 7.4 and 7.3% for P1, P2 and P3 respectively) (Table 1).

The analysis of variance was used to evaluate the influence of several non-genetic sources of variation and interactions between these factors on weight at different developmental stages, with a view to accesses to the physiological growth of the Segureña lambs under the influence of different non genetic factors and their interactions. General results of the ANOVAs are shown in Table 2. The main effect of the factor year and age of dam at lambing covariable are non-significant at P3 (P>0.05). The interaction between all five factors is non-significant (P>0.05) for all developmental stages while some of double, triple and quadruple interactions are significant (P<0.05) for the three variables under study. The reduced determinative coefficient of the model that includes only the significant main effects, covariables and interactions, ranges between 44.3 and 48.9%.

Sex

Sexual dimorphism was evident in the breed: lamb weights significantly different between males and females (P<0.001) as has been pointed out in Table 2. This fact has been also reported by Macedo and Arredondo (2008), Baneh and Hafezian (2009), among other authors. As shown by numerous authors (Strizke and Whiteman, 1982; Dimsoski *et al.*, 1999; Rodríguez *et al*., 1999; González *et al*., 2002; McManus *et al.*, 2003; Ulutas *et al*., 2010; Gbangboche *et al.*, 2011) males presented a higher average weight compared to females. All the literature consulted reflected a significant effect of the sex, with higher weight recorded for males when compared to females. However, other studies performed in different races and under different production systems indicated no differences attributed to sex for preweaning growth (González *et al*., 2002) and some authors even found higher growth rates at 30 and 60 days in females, with no difference in weaning weight for lambs of both sexes (Gbangboche *et al*., 2006b).

This tendency in body weight may be attributable to different physiological functions in both sexes, mainly of hormonal nature, which tend to become more pronounced as the animals approach maturity. This effect of sex on postnatal growth is related to testosterone production, a steroid hormone whose anabolic effects act as growth promoter (Macedo and Arredondo, 2008). Regarding the influence of sex on lamb weight at different developmental stages, in general terms, it is estimated that in male lambs this is 5.07, 6.60 and 8.33% higher than in females, at P1, P2 and P3, respectively. Similar values were found by Macedo and Arredondo (2008).

The effect of double interactions between sex and other factors was only significant with the herd factor in variable P3 (P≤0.001) and with the birth type factor in variables P1 and P3 (P<0.05), an interaction that was also identified by other authors (Assan and Mazuka, 2005; Akhtar *et al.,* 2012) (Table 2).

Birth season

Birth season is another factor that must be considered in the development of animals and, consequently, in their reproductive management (Hernández, 2004; Quesada *et al.,* 2002). Because there are four seasons, food production suffers large variations throughout the year, affecting both the quantity and quality of food, which influences lamb lactation by altering their physical condition, a situation evidenced by several studies (Baneh and Hafezian, 2009; Momoh *et al.*, 2013).

The birth season effect was significant (P<0.001) for all developmental stages (Table 2), according to others authors (Akhtar *et al.*, 2012; Hinojosa-Cuéllar *et al*., 2012). The lowest average weights were reached by lambs born in summer (8.73±1.77 kg), and the highest values were presented by lambs born in winter (9.10±1.77 kg) (Appendix), in agreement with

Table 1. Determinative coefficient of the effect of each factor on weight of Segureña breed lambs, at three developmental stages, obtained with the univariate general linear model.

Factor	Developmental stage		
	P1	P2	P3
Sex	1.4	2.8	5.2
Birth season	1.0	1.3	0.8
Herd	9.2	6.8	7.0
Year	2.2	3.1	1.8
Birth type	9.8	7.4	7.3

P1, early weaning between 16 and 35 days; P2, late weaning between 36 and 55 days; P3, final weight between 56 and 80 days. Values are expressed as percentage.

Table 2. Determinative coefficients of significant level of factors, interactions, covariates and models obtained with ANalysis Of VAriance for weight at the three developmental stages.

Source	Developmental stage		
	P1	P2	P3
SEX	<0.001	<0.001	<0.001
B_SEASON	0.002	<0.001	<0.001
HERD	<0.001	<0.001	<0.001
YEAR	0.001	<0.001	-
B_TYPE	<0.001	<0.001	<0.001
AGE	<0.001	<0.001	<0.001
AGEDAM	<0.001	0.006	-
HERD * YEAR	<0.001	<0.001	<0.001
HERD * SEX	-	-	0.001
HERD * B_TYPE	<0.001	<0.001	<0.001
HERD * B_SEASON	<0.001	<0.001	<0.001
B_SEASON * YEAR	<0.001	-	0.003
YEAR * B_TYPE	<0.001	-	0.002
SEX * B_TYPE	0.012	-	0.015
HERD * YEAR * B_TYPE	<0.001	<0.001	<0.001
HERD * B_SEASON * YEAR	<0.001	0.003	<0.001
HERD * B_SEASON * B_TYPE	0.002	0.033	0.003
B_SEASON * YEAR * B_TYPE	-	-	0.015
HERD * B_SEASON * YEAR * SEX	-	-	0.031
HERD * B_SEASON * SEX * B_TYPE	0.031	0.016	-
B_SEASON * YEAR * SEX * B_TYPE	-	0.049	0.032
$R^2_{reduced}$	0.489	0.456	0.443

P1, early weaning between 16 and 35 days; P2, late weaning between 36 and 55 days; P3, final weight between 56 and 80 days.

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Table 3. Average weights and number of observations by birth type and sex at three developmental stages of Segureña breed lambs.

		P			Sex		P×Sex					
							S		D		T	
		S	D	T	M	F	M	F	M	F	M	F
P1	N	10042	9925	884	10464	10387	4909	5133	5089	4836	466	418
	Average weight	9.50[a]	8.04[b]	7.89[c]	9.12[a]	8.68[b]	9.82[d]	9.19[a]	8.55[e]	8.22[c]	8.00[c]	7.77[c]
P2	N	8415	8645	812	8925	8947	4152	4263	4375	4270	398	414
	Average weight	14.51[a]	13.18[b]	12.37[c]	14.21[a]	13.33[b]	15.06	13.97	13.53	12.81	12.71	12.05
P3	N	5754	7625	837	6910	7306	3018	2736	3856	3769	432	405
	Average weight	20.12[a]	18.56[b]	17.12[c]	19.89[a]	18.36[b]	19.30[a]	21.03[c]	17.85[b]	19.28[d]	16.48[d]	17.81[e]

P, birth type; S, single birth type; D, double birth type; T, triple or higher birth type; M, male; F, female; P1, early weaning between 16 and 35 days; P2, late weaning between 36 and 55 days; P3, final weight between 56 and 80 days; N, number of observations. [a-e]Means with different letters within each factor or interaction are statistically different (P≤0.05).

the results found by Rodríguez *et al*. (1999), Quesada *et al*. (2002), Hernández (2004) and Momoh *et al.* (2013).

Interaction between birth season and herd was significant (P<0.001) in all variables and the interaction between birth season and birth year was significant (P<0.05) in variables P1 and P3 (Table 2).

Herd

One important performance factor on lambs is the physical environment and climate, as was also observed by Charles (1985), Sarti *et al.* (2003), Kittelsen (2008) and Lavvaf and Noshary (2008). In his study on the effect of herd and management in the Ancient Norse breed, Kittelsen (2008) found significant differences among animal weights in different locations, although found no differences among the weights due to different types of management. The herd can have significant effect due to differences in management and environmental conditions (Baneh and Hafezian, 2009).

The effect of the herd factor was significant (P<0.001) on lamb weights at different developmental stages. The double interactions effect between herd and birth season, birth year and birth type were significant (P<0.001), while the double interaction between herd and sex was only significant (P≤0,001) for older lambs (Table 2).

Using the Tukey test, and under the herd effect, average weights were grouped into 18 homogeneous subsets at P1. This number dropped to 14 at P2 and the most developed lambs were grouped together into 11 homogeneous subsets; this can be due to a smaller number of herds being observed. There are herds that stand out due to the superiority of their average weight at all developmental stages (*e.g.* herd B with mean weights of 10.43, 15.29 and 20.54 kg for P1, P2 and P3, respectively), while others stand out due to the inferiority of these values (*e.g.* herd HS with mean weights of 7.76 , 12.41 and 17.53 kg for P1, P2 and P3, respectively) (Appendix). Bela and Haile (2009) also found variations in the growth characteristics of lambs reared in different locations. The pronounced differences between the herds studied show that diversity in management (health and nutrition) has a great influence on lamb weights. The same results were achieved by Baneh and Hafezian (2009).

Birth year

The birth year can cause variations in lamb weights at different ages due to the effect of climate conditions (precipitation, humidity and temperature), environmental conditions and management. Climate and environmental changes affect the quality and quantity of pasture forages, which also affects the provision of food and other animal needs (Momoh *et al.*, 2013). Differences in nutrition (especially during pregnancy), management and hygiene in the various years, are some reasons for the effect of birth year on body weight in different ages (Baneh and Hafezian, 2009).

Birth year affected (P<0.001) body weight at weaning but was not significant (P>0.05) on the body weight of older lambs, unlike Akhtar *et al.* (2012) who, in their study on Buchi sheep, concluded that the effect of birth year was only significant on more developed animals. Double interactions were significant (P<0.001) between birth year and herd, in agreement with Baneh and Hafezian (2009). The effect of the interactions between birth year and birth season and between birth year and birth type were significant (P<0.05) for P1 and P3 variables (Table 2). Unlike the results found by Akhtar *et al.* (2012), the interaction effect was not significant (P>0.05) between birth year and sex in all three variables (Table 2), indicating that these factors are independent. The interaction between birth year and birth season demonstrates that seasons are not equal throughout the years, and different effects were obtained with different combinations of birth year and seasons. The average body weight for birth year and birth season ranged between 7.67±1.19 kg (spring year 4) and 10.23±1.81 kg (autumn year 6) at P1 and between 18.07±3.35 kg (summer year 11) and 21.32±3.26 kg (spring year 2) in more developed lambs.

Using the Tukey test, under the birth year effect, average weights were grouped into 6 homogeneous subsets at P1 and into 5 at P2 (Appendix).

Birth type

Although Quesada *et al.* (2002) found no differences in weaning weights among lambs from different birth types, and other authors (González *et al.*, 2002) concluded that after weaning, lambs from multiple births reach daily weight gains that are higher than those of single birth lambs, several studies in different breeds (Eltawil *et al.*, 1970; Robinson *et al.*, 1977; Dimsoski *et al*., 1999; Rodríguez *et al*., 1999; Hernández, 2004; Hinojosa-Cuéllar *et al*., 2012, Momoh *et al*., 2013) show that birth type affects the birth weight of lambs from birth to 80 days, with single born lambs reaching the highest weights. Thus, although in general terms birth type does affect ovine growth, there may be particular variations for each breed and each production system.

Birth type had significant effect on weight (P<0.001) at every developmental stage (Appendix). The double interaction effect between birth type and herd was significant (P<0.001) at all developmental stages (Table 2), in agreement with the results found by Baneh and Hafezian (2009). Interaction effects were significant (P<0.05) between birth type and birth year and between birth type and sex for P1 and P3 variables (Table 3). In their studies on ovine, Hussain *et al.* (2013)

and Akhtar *et al.* (2012) obtained a non-significant interaction between birth type and sex, unlike the findings in this study. The effect of interactions between birth type and birth season was non-significant (P>0.05) for any of the variables (Table 2).

Single birth lambs were heavier by 18.16, 10.09 and 8.41% when compared with twins at P1, P2 and P3, respectively. Differences became more pronounced when comparing single birth lambs with triple or higher birth, with percentage values of 20.41, 17.30 and 17.52% (Appendix). Most studies confirm the superiority of the body weight of single birth lambs over multiple birth lambs (Dickson-Urdaneta *et al.*, 2004; Gbangboche *et al.*, 2006a; Hinojosa-Cuéllar *et al.*, 2012; Ramirez-Tello *et al.*, 2013). This also occurs in the study by Bela and Haile (2009), where the effect of birth type on growth decreases with the lamb's age.

Conclusions

Applying univariate models to isolated variation factors, the determinative coefficient for each is an indicator of the variation explained by each factor. Gathering with the significance inferred for the several factors with the multifactorial models, we can appreciate how sexual dimorphism is evident at the earliest weights but is extreme at the final weight. Therefore, the decision for consignment to the slaughterhouse in either sex should be based on weight and never age.

The most important effects were herd and birth type: the first is justified by great differences in the management of herds; the second case is due to the difference between the dam's lactogenesis capacity, meaning that this factor's influence is greater when the lamb is more dependent and decreases when the lamb reaches late weaning age.

In most meat sheep breeding programmes the genetic models enclose the interactive effects of the combined herd-year-season factors. In the present study these factors are also studied isolated, in order to access to their direct effects upon the traits. The influence of the birth year was relatively small and uncontrolled, like the birth season.

The variance explained by the multifactorial model ranged between 44 and 49%, therefore we consider it very efficient for the three variables in study and find that it provides very important information for the design of genetic analysis models in order to obtain maximum orthogonality at a lower computational cost.

The herd factor proved highly interactive: both double and triple interactions, in which this factor was involved were, in the most part, clearly significant. This derives, mainly, from its great responsibility in explaining the variance. The opposite occurred with the birth season factor: this is why, despite being polioestrus animals, the concentration of births in certain times is due to commercial reasons of market demand and not to a better response to growth in certain seasons.

Birth type significantly interacted with other factors, due to the large volume of variance that it explains. The influence of this factor on variation decreases with age but, contrary to what is described in the literature, in this case compensatory growth does not neutralise the weight differences found in single births when compared with multiple births. This leads us to question genetic improvement based solely on prolificacy, as multiple birth lambs grow significantly less and thus reach market weight later. The situation is most extreme among female lambs from triple or higher births, compared with single birth males.

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APPENDIX

Appendix Table 1. Basic statistical information of each factor that affects weight at the three developmental stages of Segureña breed lambs.

Fªctor	P1				P2				P3			
	N	MW, kg	SD	CV	N	MW, kg	SD	CV	N	MW, kg	SD	CV
Sex		***				***				***		
Mªle	10,464	9.12^{a}	1.89	20.72	8925	14.21^{a}	2.79	19.62	6910	19.89^{a}	3.5	17.7
Female	10,387	8.68^{b}	1.7	19.55	8947	13.33^{b}	2.42	18.13	7306	18.36^{b}	2.9	16
Birth season		**				***				***		
Spring	3540	9.05^{a}	1.8	19.92	2614	13.94^{a}	2.63	18.86	2220	18.96^{a}	3.3	17.2
Summer	10,186	8.73^{b}	1.77	20.24	9140	13.51^{b}	2.61	19.33	6821	18.87^{a}	3.3	17.6
Autumn	2919	9.03^{a}	1.96	21.74	2342	13.77^{c}	2.71	19.67	2144	19.23^{b}	3.4	17.6
Winter	4206	9.10^{a}	1.77	19.43	3776	14.26^{d}	2.62	18.4	3031	19.64^{c}	3.3	16.6
Herd		***				***				***		
AF	231	8.54^{cdef}	1.9	22.3	-	-	-	-	-	-	-	-
AN	234	$9.26^{klmnopq}$	1.88	20.3	269	14.21^{hijkl}	2.51	17.67	-	-	-	-
AT	2301	8.42^{cde}	1.6	18.97	1802	13.33^{cde}	2.51	18.84	1957	18.51^{bcd}	3.3	17.6
B	393	10.43^{r}	1.98	18.97	433	15.29^{m}	2.7	17.64	332	20.54^{ik}	2.8	13.8
CO	318	$8.98^{fghijklmno}$	1.73	19.28	297	14.09^{ghijk}	2.31	16.38	-	-	-	-
DR	556	$9.21^{jklmnopq}$	1.68	18.2	506	13.68^{defghi}	2.25	16.46	375	18.33^{abc}	2.8	15.4
FP	446	9.29^{lmnopq}	1.72	18.56	368	14.83^{lm}	2.75	18.56	315	19.73^{ghi}	3.2	16
FR	-	-	-	-	402	13.71^{defghi}	2.76	20.11	364	20.56^{k}	3.4	16.7
FV	496	$9.14^{ijklmnopq}$	1.97	21.55	322	14.32^{ijkl}	2.81	19.64	-	-	-	-
GH	661	$9.01^{ghijklmno}$	1.79	19.82	527	13.33^{cde}	2.45	18.41	554	17.66^{a}	3	17
GI	360	8.68^{defghi}	1.7	19.57	290	13.00^{abc}	2.65	20.4	233	18.87^{bcdef}	3.4	17.8
GO	280	$8.98^{fghijklmno}$	1.66	18.5	260	13.39^{cdef}	2.43	18.13	319	18.89^{bcdef}	3.3	17.4
GT	1340	$9.04^{hijklmnopq}$	1.71	18.86	1037	13.78^{efghij}	2.42	17.56	810	20.66^{k}	3.2	15.6
HC	189	$8.83^{efghijkl}$	1.53	17.33	-	-	-	-	218	18.19^{ab}	3.5	19.2
HM	-	-	-	-	149	14.10^{ghijk}	2.74	19.41	-	-	-	-
HR	553	8.20^{abc}	1.73	21.16	527	12.57^{ab}	2.78	22.08	448	17.62^{a}	3.1	17.8
HS	864	7.76^{a}	1.55	20.01	824	12.41^{a}	2.51	20.23	766	17.53^{a}	3.0	17
JF	889	$8.70^{defghij}$	1.63	18.8	699	13.55^{cdefg}	2.51	18.54	805	19.00^{cdefg}	3.2	16.8
JJ	343	$8.80^{efghijk}$	1.51	17.15	304	13.77^{efghij}	2.45	17.8	-	-	-	-
JR	430	$9.10^{jklmnop}$	1.76	19.37	372	14.39^{jkl}	2.57	17.84	-	-	-	-
LH	237	9.64^{q}	1.67	17.34	351	14.27^{ijkl}	2.69	18.83	-	-	-	-
LM	1438	$9.06^{hijklmnop}$	1.76	19.4	1077	13.83^{efghij}	2.61	18.88	1154	19.25^{defgh}	3.3	17
MM	390	$8.99^{fghijklmno}$	1.7	18.94	346	14.13^{ghijk}	2.52	17.81	-	-	-	-
NA	745	10.18^{r}	1.92	18.86	426	16.16^{n}	2.75	17.03	-	-	-	-
NI	260	9.39^{opq}	1.6	17.04	250	13.84^{efghij}	2.4	17.32	-	-	-	-
NN	344	$9.01^{ghijklmno}$	1.66	18.47	360	$13.74^{defghij}$	2.31	16.84	-	-	-	-
PV	372	8.58^{cdefgh}	1.69	19.65	370	13.29^{cde}	2.44	18.37	-	-	-	-
R	269	$8.84^{efghijkl}$	1.75	19.77	267	14.06^{ghijk}	2.62	18.61	-	-	-	-
RJ	200	$9.10^{jklmnop}$	1.89	20.8	-	-	-	-	-	-	-	-
RM	375	10.08^{r}	1.78	17.67	-	-	-	-	198	18.93^{bcdef}	3.0	16
RR	585	8.57^{cdefg}	1.94	22.58	794	13.81^{efghij}	2.78	20.1	959	19.61^{fgh}	3.7	19
SB	281	8.68^{defghi}	1.84	21.2	235	13.52^{cdefg}	2.6	19.21	207	19.76^{ghij}	3.2	16.4
SC	414	$8.83^{efghijkl}$	1.95	22.09	336	13.48^{cdefg}	2.7	20	440	18.74^{bcde}	3.2	16.8
TO	-	-	-	-	180	13.10^{bcd}	2.43	18.56	283	19.04^{cdefg}	3.3	17.1
VC	845	8.45^{cde}	1.63	19.25	870	13.37^{cdef}	2.42	18.13	866	19.00^{cdefg}	2.9	15.3
VJ	1004	$9.07^{hijklmnop}$	1.66	18.34	809	14.02^{fghij}	2.6	18.55	800	19.19^{defgh}	3.1	16.3
VS	194	7.83^{a}b	1.61	20.59	-	-	-	-	-	-	-	-
XP	204	9.34^{mnopq}	2.03	21.79	-	-	-	-	-	-	-	-
Z	921	9.37^{nopq}	1.78	18.95	860	14.69^{klm}	2.53	17.19	719	20.51^{ijk}	3.1	15
ZA	167	9.56^{pq}	1.78	18.59	187	13.78^{efghij}	2.35	17.05	403	19.96^{hijk}	3.3	16.5
ZF	722	8.26^{bcd}	1.61	19.45	766	13.56^{cdefgh}	2.61	19.26	691	19.33^{efgh}	3.3	17.1

Appendix Table 1. Basic statistical information of each factor that affects weight at the three developmental stages of Segureña breed lambs.

Factor	P1				P2				P3			
	N	MW, kg	SD	CV	N	MW, kg	SD	CV	N	MW, kg	SD	CV
Year		***				***				ns		
1	1331	8.74^{b}	1.77	20.28	963	12.93^{a}	2.43	18.78	625	19.44	3.2	16.5
2	1118	9.08^{e}	1.71	18.78	972	14.20^{d}	2.5	17.62	785	20.36	3.5	17
3	1871	9.03^{de}	1.74	19.25	664	14.89^{e}	2.76	18.52	216	19.38	3.2	16.7
4	1037	9.00^{bcde}	1.84	20.46	813	13.95^{cd}	2.61	18.67	589	19.33	3.3	16.8
5	1911	8.89^{bcd}	1.72	19.35	1699	13.58^{b}	2.59	19.09	1310	18.46	3.3	17.7
6	2485	9.39^{f}	1.86	19.83	2275	14.12^{cd}	2.64	18.72	1991	19.42	3.2	16.2
7	2316	9.00^{cde}	1.78	19.74	2279	14.16^{d}	2.59	18.27	2176	19.05	3.3	17.5
8	1870	8.81^{bc}	1.74	19.81	1739	13.84b^{c}	2.5	18.07	1391	19.30	3.0	15.7
9	1440	8.83^{b}	1.84	20.87	1620	13.99^{cd}	2.76	19.74	1246	19.20	3.4	17.8
10	1596	9.00^{bcde}	1.76	19.57	1467	13.60^{b}	2.49	18.29	1741	18.93	3.4	17.9
11	3876	8.49^{a}	1.84	21.73	3381	13.14^{a}	2.67	20.32	2146	18.57	3.4	18.3
Birth type		***				***				***		
Simple	10,042	9.50^{a}	1.86	19.55	8415	14.51^{a}	2.65	18.29	5754	20.12^{a}	3.32	16.50
Double	9925	8.04^{b}	1.58	18.88	8645	13.18^{b}	2.47	18.71	7625	18.56^{b}	3.14	16.91
Triple or higher	884	7.89^{c}	1.38	17.49	812	12.37^{c}	2.24	18.09	837	17.12^{c}	2.88	16.84

P1, early weaning between 16 and 35 days; P2, late weaning between 36 and 55 days; P3, final weight between 56 and 80 days; N, number of observations; MW, mean weight; SD, standard deviation; CV, coefficient of variation (%). $^{a-f}$Means with different letters within each column and within each factor are statistically different. **P≤0.05; ***P≤0.001; ns, not significant.

Animal

Genetic parameters of traits associated with the growth curve in Segureña sheep

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Genetic parameters of traits associated with the growth curve in Segureña sheep

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This paper studies the genetic importance of growth curve parameters and their relevance as selection criteria in breeding programmes of Segureño sheep. Logistic and Verhulst growth functions were chosen for their best fit to BW/age in this breed; the first showed the best general fit and the second the best individual fit. Live weights of 41 330 individuals from the historical archives of the National Association of Segureña Sheep Breeders were used in the analysis. The progeny of 1464 rams and 27 048 ewes were used to study the genetic and phenotypic parameters of growth curve parameters and derived traits. Reproductive management in the population consists in controlled natural mating inside every herd, with a minimum of 15% of the females fertilized by artificial insemination with fresh semen; with the purpose being the herd genetic connections, all herd genealogies are screened with DNA markers. Estimates of growth curve parameters from birth to 80 days were obtained for each individual and each function by the non-linear regression procedure using IBM SPSS statistics (version 21) with the Levenberg–Marquart estimation method. (Co)variance components and genetic parameters were estimated by using the REML/Animal model methodology. The heritability of mature weight was estimated as 0.41 ± 0.042 and 0.38 ± 0.021 with the logistic and Verhulst models, respectively, and the heritability of other parameters ranged from 0.41 to 0.62 and 0.37 to 0.61, with the models, respectively. A negative genetic correlation between mature weight and rate of maturing was found.

Keywords: logistic model, Verhulst model, heritability, lambs, Segureña breed

Implications

Genetic and environmental improvements offer an opportunity to increase production from existing animal resources. The genetic characterization of local breeds is of paramount importance, not only for conservation purposes, but also for the definition of breeding objectives and breeding programmes. Genetic improvement could also contribute to increased productivity.

Introduction

The Segureña breed is one of the most important meat sheep breeds in Spain, Europe and the world. Spain is ranked second in Europe for sheep census and production (MAGRAMA, 2013). Furthermore, the Segureña breed helps boost the local economy of the regions in which it is bred, namely the highlands of Granada, Sierra de Segura and Las Villas, which are among the poorest areas of Europe. This breed is therefore the main reason why people settled in the above-mentioned regions. However, live animals with high genetic values are also an important Spanish export. Segureña sheep are mainly exploited in extensive and semi-extensive conditions due to their excellent capacity for adaptation; they are also a component of the balanced ecosystems in the regions they inhabit, thereby making them a mainstay of environmental and social sustainability (Lupi *et al.*, 2015).

There is an urgent need to increase productivity to improve smallholder farm income and to meet the demands of the growing human population for livestock products. Efforts to improve the productivity of local sheep have been part of national research for the last 30 years.

Most studies on local sheep breeding have, so far, concentrated on evaluating breeds based only on growth performance. Very little has been done to assess the genetic attributes of the breeds for economically important traits based on growth curves. For accurate genetic evaluation and selection, estimates of variance/covariance components and other genetic parameters for important traits should be known. In this regard, growth traits linked to curve

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parameters are important, as they significantly influence the profitability of any sheep production enterprises. The main objectives of this study were to estimate the best-fit growth curve parameters of Segureña sheep, the variance and (co)variance components, heritability and genetic correlations. These parameters, and especially their biological meaning, are informative for breeders as they permit the inference of relevant economic information with regard to the inflexion point and maturity that are not accessible from the analysis of simple growth traits such as weights at different key ages (birth, weaning and slaughtering) or daily gains.

Growth functions have been used extensively to represent changes in size with age, so that the genetic potential of animals for growth can be evaluated and nutrition matched to potential growth. In models of animal production systems, growth curves are used to provide estimates of daily feed requirements for growth. An appropriate growth function conveniently summarizes the information provided by observations on an animal into a small set of parameters that can be interpreted biologically and used to derive other relevant growth traits (López *et al*., 2000).

The desired properties of such growth functions are that weight tends towards a final or asymptotic value with time, that growth rate has a maximum at some intermediate weight, and that the relative growth rate decreases monotonically, preferably in some simple way, as weight increases towards maturity. The Verhulst and the logistic forms are examples of functions with such properties that describe growth as a comparatively simple, single equation. They have three parameters, with the important ones being mature size and rate. Importantly, the values of such parameters have clear biological interpretations (Lewis and Brotherstone, 2002).

Slow growth rate, resulting in low market weight, has been identified as a limitation to profitability. Growth rate is related to maturation rate and mature weight, and it has been suggested that these latter traits are related to other female lifetime productivity parameters in goats; the existence of an optimum size to improve productivity has also been suggested for sheep. Therefore, the rate of gain and mature weight need to be considered in selection programmes. Fast early growth on the part of the slaughter generation and smaller mature size on the part of the reproducing females (though it results in a lower culled ewe value) are desirable traits. Growth curve parameters provide potentially useful criteria for altering the relationship between BW and age through selection, and an optimum growth curve can be obtained by selection for desired growth curve parameters (Bathaei and Leroy, 1998; Abegaz *et al*., 2010).

Based on the parameters of the growth models, other indicators can be derived such as the degree of maturity at a specific time as well as the age and weight at the point of inflection (Blasco, 1999; Goyache, 2005), which indicates a change in the growth rate. The parameters and indicators of growth, derived from non-linear models, can be taken into account in the selection criteria within a breed, with the aim of modifying the shape of the growth curve (Blasco, 1999; Goyache, 2005).

Information of genetic parameter estimation for different traits is useful in formulating breeding programmes because these parameters determine the direction and magnitude of genetic improvement (Mekuriaw and Haile, 2014).

The biological importance of some growth curve parameters are well known. They are related to the estimation of the mature weight of the animals, to the age when they reach maturity, and to the inflection point when the growth slows to a stop, among others. This information is used to support breeders' decisions taken over aspects strongly linked to meat productivity, such as reproduction, body condition, timing of slaughtering decision, etc. Therefore, genetic and economic parameters strongly suggest that growth curve parameters should be taken into account in breeding programmes.

Material and methods

The weight–age data for this study were obtained from 41 330 individuals taken from the historical archives of the National Association of Segureña Sheep Breeders. Each individual had four weight observations: between 0 and 15 days old (P_0), between 16 and 35 days (P_1), between 36 and 55 days (P_2) and between 56 and 80 days (P_3). The weight at 80 days of age (slaughter weight) is economically of great importance in the post-weaning growth of Segureño lambs. The data were collected from 2000 to 2014. This archive contained all the information concerning lamb weights at different ages of reference – birth, early weaning, late weaning and slaughter – and information about the origin of each (livestock, date of birth, parentage, etc.).

The process of data depuration was performed in two phases. Before model fitting, all records were removed that presented an average weight data $\pm 2 \times$ SD in each age or differences between weights of $\leqslant 0$. Then, using the non-linear regression procedure from the SPSS version 21 statistical package, individual data were fitted to the Von Bertalanffy, Verhulst, logistic and Gompertz non-linear models (whose mathematical expressions and biological parameters are given in Table 1) to select the model in which there was more convergence for the general data structure. As repeated measurements are generally autocorrelated, the growth models were fitted to individual lambs to remove any possible bias in statistical inference on growth parameters (Daskiran *et al*., 2010). Growth parameters in this study were estimated using unadjusted weights due to the fact that serial measurements were simultaneously considered in the estimation of parameters (Brown *et al*., 1976).

In a previous study of the Segureña breed growth curve, it was concluded that the most suitable function to explain the evolution of weight from birth to slaughter age (80 days) in a general population was the logistic model (Lupi *et al*., 2015). Based on that study, we introduced this function into the present study. In this model, the parameter *k* represents the relative growth rate (rate of exponential growth); high values indicate animals with precocious maturity (i.e. animals attained mature weight quickly) and low values indicate

Table 1 *Mathematical description of growth models, biological parameters and growth evaluators*

	Mathematical expression	Inflexion weight	Inflexion age	Growth rate	Age to maturity ($y = a$)	Maturity degree
Von Bertalanffy	$y = a \times (1 - b \times \exp(-k \times t))**3$	$y_i = \frac{8a}{27}$	$t_i = \frac{\ln(3b)}{k}$	$v_c = 3ky\left[\left(\frac{a}{y}\right)^{1/3} - 1\right]$	$-\frac{\ln\left(\frac{1-\sqrt[3]{\frac{y}{a}}}{b}\right)}{k}$	
Verhulst	$y = a/(1 + b \times \exp(-k \times t))$	$y_i = \frac{a}{2}$	$t_i = \frac{\ln(b)}{k}$	$v_c = ky\left(1 - \frac{y}{a}\right)$	$-\frac{\ln\left(\frac{a-y}{y-b}\right)}{k}$	$u = \frac{y}{a}$
Logistic	$y = a \times (1 + \exp(-k \times t))**(-m)$	$y_i = \frac{a}{2}$	$t_i = \frac{-\ln(2^{1/m} - 1)}{k}$	$v_c = mka\left(\frac{e^{-kt}}{1+e^{-kt}}\right)$	$-\frac{\ln\left[\left(\frac{a}{y}\right)^{1/m} - 1\right]}{k}$	
Gompertz	$y = a \times \exp(-b \times \exp(-k \times t))$	$y_i = \frac{a}{e}$	$t_i = \frac{\ln(b)}{k}$	$v_c = ky\ln\left(\frac{a}{y}\right)$	$-\frac{\ln\left(\frac{\ln\left(\frac{y}{a}\right)}{-b}\right)}{k}$	

y = weight, in kg, at age t; t = age in days; a, b, k and m = parameters.

animals with a delayed maturity or that tend to mature more slowly. The parameter m gives the shape of the growth curve and, consequently, determines the inflection point, which is the beginning of the auto-deceleration stage until the animal reaches adult size (Carolino and Gama, 1993; McManus *et al.*, 2003; Lambe *et al.*, 2006; Echeverri *et al.*, 2013; Tariq *et al.*, 2013).

The Verhulst model presented the best convergence and the highest proportion of individual convergence, so individual logistic and Verhulst curves were fitted for all animals with four records of weight/age. Individual parameters of both curves were recorded and stored in a database. Before genetic analysis, these data were submitted to a last depuration phase when we excluded records where the iterative fit did not converge or where the parameter $a \geqslant 60$ in each model and for each individual. Using these rejection criteria, an 'accepted set of sheep' was defined for each estimation method. After this depuration, we retained data from 19 388 lambs (7305 males and 12 083 females), representing 77 552 weight/age observations for the logistic model, and 30 299 lambs' data (12 690 males and 17 609 females), representing 121 196 weight/age observations, for the Verhulst model.

To support the evaluation of practical efficiency of the fitting of both curve, we calculated the mean deviation between the predicted and observed weight and their correlations.

Variance and (co)variance components and the genetic parameters of the curve parameters were estimated with animal models under the REML methodology using the following general formula:

$$y = X\beta + Za + e$$

where y is a vector of observations (a, m and k parameters for the logistic model; a, b and k for the Verhulst model), β a vector of fixed effects:

- herd (126 levels, min 1, max 1265 and 1958, for logistic and Verhulst models, respectively);
- year of birth (15 levels, 2000 to 2014, min 51 and 67, max 4486 and 6737, for logistic and Verhulst models, respectively);
- month of birth (12 levels, January to December, min 234 and 365, max 6544 and 10 293, for logistic and Verhulst models, respectively);
- lamb sex (two levels, male and female, min 7305 and 12 690, max 12 083 and 17 609, for logistic and Verhulst models, respectively);
- kidding type (three levels, single, twin, triplet or more, min 45 and 80, max 10 835 and 15 925, for logistic and Verhulst models, respectively).

a is a random vector of additive genetic effects, X and Z the incidence matrices relating β and a to y, and e a random vector of error effects.

A bivariate animal model (*A-B*, *A-M*, *M-K* for the logistic model, and *A-B*, *A-K*, *B-K* for the Verhulst model) was employed to estimate (co)variance components as follows (Canaza-Cayo *et al.*, 2015):

$$\begin{pmatrix} y_1 \\ y_2 \end{pmatrix} = \begin{pmatrix} X_1 & 0 \\ 0 & X_2 \end{pmatrix}\begin{pmatrix} \beta_1 \\ \beta_2 \end{pmatrix} + \begin{pmatrix} Z_1 & 0 \\ 0 & Z_2 \end{pmatrix}\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} + \begin{pmatrix} e_1 \\ e_2 \end{pmatrix}$$

where y_1 and y_2 are the vectors of observations for traits 1 (parameter a, b, m and k) and 2 (parameter a, b, m and k), respectively; β_1 and β_2 the vectors of fixed effects (herd, year of birth, month of birth, sex, birth type) for traits 1 and 2, respectively; u_1 and u_2 the vectors of random additive genetic effects, and e_1 and e_2 the residual effects for the traits 1 and 2, respectively; X_1 and X_2, and Z_1 and Z_2 the incidence matrices that associate the elements of β_1 and u_1, and β_2 and u_2, respectively, with y_1 and y_2. The variances and (co)variances of all random vectors are equal to:

$$\mathrm{Var} = \begin{pmatrix} u_1 \\ u_2 \\ e_1 \\ e_2 \end{pmatrix}\begin{pmatrix} A\sigma^2_{a1} & A\sigma_{a1\,a2} & 0 & 0 \\ A\sigma_{a1\,a2} & A\sigma^2_{a2} & 0 & 0 \\ 0 & 0 & I\sigma^2_{e1} & I\sigma_{e1e2} \\ 0 & 0 & I\sigma_{e1e2} & I\sigma^2_{e2} \end{pmatrix}$$

where A is a Wright's numerator relationship matrix, σ^2_{a1} and σ^2_{a2} the variances of the direct additive genetic effect; σ^2_{e1} and σ^2_{e2} the residual variances for traits 1 and 2, respectively; I the identity matrix. The genetic and environmental (co)variance between pairs of traits are $\sigma_{a1\ a2}$ and $\sigma_{e1\ e2}$, respectively.

Table 2 *Performance of models fitting*

	von Bertalanffy (%)	Verhulst (%)	Logistic (%)	Gompertz (%)
Best convergence	11.26	45.74	8.18	8.96
Have converged	23.27	74.06	52.02	40.91

Calculations were carried out using the Multiple Trait Derivate Free Restricted Maximum Likelihood (MTDFREML) program (Boldman *et al*., 1993), a set of programmes employing a simplex procedure to locate the maximum of the log likelihood (*logL).* Convergence was considered to be reached when the variance of function values ($-2logL$) in the simplex was $<10^{-9}$. In the MTDFREML outputs, the population inbreeding average was near to 0, probably due to the large population size and the important number of herds under study.

Results and discussion

The Verhulst model presented the best convergence (45.74%), and the highest proportion of individual convergence (74.06%; Table 2).

The Verhulst model is symmetrical regarding the inflection point; at this point, the function reached 50% from the asymptotic value (parameter *a*). In its first stage, it approaches to an exponential function with a constant relative growth rate. This model considers the growth rate proportional to the achieved growth and that which remains to be achieved (Goyache, 2005). Parameter *b* represents the asymptotic growth proportion that should be reached after birth, established by the initial weight and age values. The parameter *k* represents the relative growth rate; with k^{-1}, we can calculate the time needed to reach maturity (McManus *et al*., 2003). High *k* values indicate animals with precocious maturity.

In general, the logistic model presented a better general efficiency according to the mean deviation between the predicted and observed weight and the correlation between them (Table 3); this was previously shown by Lupi *et al*. (2015). In both cases, the efficiency increased from P0 to P3. These results support both equations as being suitable for the purposes of the present study.

The effectiveness in the predictions is similar on both models, as it is evidenced by the strong correlations between the respective predicted weights at the different ages (Table 4).

The descriptive statistics of the curve parameters for both models are shown in Table 5. The *a* parameter is statistically homogeneous in both models. This parameter for asymptotic weight offered the best opportunity to make direct comparisons among all models as the other parameters measured slightly different phenomena (Brown *et al*., 1976). The values of R^2 indicate that the proportion of variation explained was, in general, high for both models; the average R^2 values across all the growth curves were 0.996 ± 0.02. The R^2 values were, in most cases, close to unity (the variance ratio or *F*-test reached a high level of significance for all the curves and models) and could be used only as an overall measure of fit rather than as a basis for model comparison, as also observed by López *et al*. (2000).

Table 3 *Correlation (r) and mean deviation (md) between observed and predicted weights by both models, separated by age*

	Models			
	Logistic		Verhulst	
Age	*r*	md	*r*	md
P_0	0.817	0.167	0.734	0.220
P_1	0.963	0.356	0.963	0.374
P_2	0.979	0.352	0.984	0.323
P_3	0.998	0.128	0.998	0.113

P_0 = between 0 and 15 days old; P_1 = between 16 and 35 days; P_2 = between 36 and 55 days; P_3 = between 56 and 80 days.

Table 4 *Correlation between the predicted weight with both models (Verhulst and logistic) at 0, 15, 30, 45, 60 and 75 days of live*

	Log_0	*Log_15*	*Log_30*	*Log_45*	*Log_60*	*Log_75*
Ver_0	0.983					
Ver_15	0.752	0.985				
Ver_30	0.487	0.945	0.997			
Ver_45	0.316	0.803	0.950	0.999		
Ver_60	0.191	0.573	0.769	0.929	0.999	
Ver_75	0.109	0.322	0.520	0.750	0.934	0.997

Log_0, Log_15, Log_30, Log_45, Log_60, Log_75 predicted weight with logistic model at 0, 15, 30, 45 60 and 75 days of live. Ver_0, Ver_15, Ver_30, Ver_45, Ver_60, Ver_75 predicted weight with Verhulst model at 0, 15, 30, 45 60 and 75 days of live.

Parallelism between the performance of both models can be graphically observed in Figure 1. Weight averages estimated with both functions were similar and presented similar deviation regarding the observed weight. Unlike what presented by several authors (Brown *et al*., 1976; Lambe *et al*., 2006) weights were underestimated at early ages and overestimated at slaughter age. It could be due to the restricted period of the animal life considered here, which is the commercial life, probably with the enlargement of the tested period to the whole life of the animals these bias could be balanced.

Heritability (h^2) is defined as the proportion of phenotypic variance that is due to genetic additive diversity. Additive genetic correlations quantify the levels of linkage and pleiotropy existing among additive loci determining the performances of two different traits (Mekuriaw and Haile, 2014).

Obviously, heritability and genetic correlations are important information among the factors determining genetic improvement in any trait (Mekuriaw and Haile, 2014). So, the first step for introducing a new selection criteria into a breeding programme is the calculation of the genetic parameters of the trait.

Table 5 *Descriptive statistics of the curve parameters for logistic and Verhulst model for Segureña lambs*

	Logistic				Verhulst			
	a	*m*	*k*	R^2	*a*	*b*	*k*	R^2
Mean	34.993	0.026	3.201	0.996	31.158	0.039	7.684	0.995
SD	11.225	0.008	0.516	0.008	9.793	0.031	3.005	0.012
CV	32.08%	31.58%	16.12%	0.79%	31.43%	78.51%	39.11%	1.18%

CV = coefficient of deviation; *a* = defined as the asymptotic value; *b* = allows calculation of the inflection age; *k* = relative growth; *m* = gives the shape of the growth curve; R^2 = pseudo R^2 (determinative coefficient).

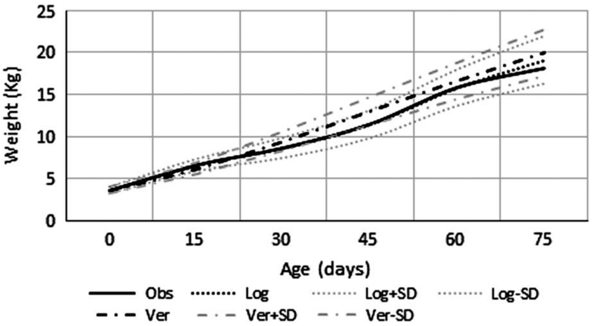

Figure 1 Curves obtained by observed weight average and estimated by logistic and Verhulst models (Supplementary Table S1).

BW and rate of gain are among the most economically important and easily measured traits of sheep; for this reason, weights and daily gains are the most common selection criteria in meat sheep breeding programmes. Knowledge of the particular trait and phase of the animals' growth, which is the basis for selection, is the most important one. The potential for genetic improvement is largely dependent on the genetic parameters of the growth weight trait upon which selection may be applied (Mekuriaw and Haile, 2014).

Results of the (co)variance components and genetic parameters estimation under the two different models are presented in Table 6. The heritability (h^2) estimates for the *a*, *b* and *m* parameters were important, in the range of 0.36 ± 0.020 and 0.49 ± 0.034; similar values for the asymptotic value were found by Hossein-Zadeh (2015) in a study of Guilan sheep and by Lewis *et al.* (2002). For the parameter *k*, the heritability was high (0.60) in both models. These results are similar to those estimated by Bathaei and Leroy (1998) for Mahraban Iranian sheep, but higher than the results presented by other studies (Lewis *et al.*, 2002; Abegaz *et al.*, 2010; Méndez-Gomez *et al.*, 2014). If these results are translated to their biological meaning, we could interpret the asymptotic weight (*a*) and the maturing rate (*k*) showing important levels of additive variability, which implies an interesting suitability for selection. Maturing rate was more additively heritable, so the perspectives for selection over this trait are even more promising in this breed. The important positive additive genetic correlations between asymptotic growth proportion (*b*) and the rate of maturity (*k*) demonstrates the close relationship between the two parameters; a high asymptotic growth proportion implies a high rate of maturity, as expected. Other parameters, such as additive, environmental and phenotypic variance, present higher values in the logistic model for parameter *a* (43.721, 63.461 and 107.182) but lower for parameter *k* (0.00003), as shown in Table 6. This is explained by each models' performance, which produced important differences in the estimation of these parameters. Similar values for maturity rate were found by Hossein-Zadeh (2015) in a study of Guilan sheep.

With regard to the heritability (h^2) estimates for the inflection point, the estimates obtained for weight and age at the inflection point in the current study were moderate (0.41 for both with the logistic model and 0.38 and 0.46, respectively, with the Verhulst model); for weight inflexion, it was higher than the results presented by Méndez-Gomez *et al.* (2014) in their study of Chiapas lambs, but lower for the inflexion age.

However, an important point in the current study was the similar estimation of the genetic parameters for the four curve traits (*a*, *b*, *m* and *k*). This means that, independently of the volume of the variance components estimated for each model, the ratios between the phenotypic and the additive variance stayed constant. So, both models could supply information for breeding evaluation in the Segureño breeding programme.

Biologically, the most important relationship was between *a* and *k*. The negative additive genetic correlations (-0.82 ± 0.098 and -0.70 ± 0.071 for the logistic and Verhulst models, respectively) and phenotypic (−0.78 and −0.66, respectively) correlations between these two parameters indicated that animals with faster growth rates were less likely to attain as large a mature weight as those that grew more slowly in early life (Tables 7 and 8). In other words, animals that were heavy at maturity tended to have a slower growth rate and be relatively smaller in BW at earlier ages. This finding is in agreement with reports by Fitzhugh and Taylor (1971) and Bathaei and Leroy (1998), and is important information for the transmission of more profitable traits for early lamb growth. Hossein-Zadeh (2015), in a study of Guilan sheep, found lowest values for the phenotypic correlations between *a* and *k*, but these were still negative according to our findings.

The moderate-to-high heritability and correlations among the growth curve parameters make it clear that genetic changes in growth patterns can be accomplished. An increase in mature weight is generally accompanied by a decrease in maturity rate (Bathaei and Leroy, 1998). The genetic correlation between mature weight (*a*) and rate of maturing (*k*) indicated a strong genetic antagonism (−0.82 and −0.70 for the logistic

Table 6 *Estimates of variance components, genetic parameters and genetic correlations of the estimated parameters for logistic and Verhulst models*

Traits	σ^2_a	σ^2_e	σ^2_p	h^2	e^2
Parameter *a*					
Logistic	43.721	63.461	107.182	0.41 ± 0.042	0.59 ± 0.039
Verhulst	31.559	51.135	82.694	0.38 ± 0.021	0.62 ± 0.021
Parameter *m*					
Logistic	0.101	0.100	0.201	0.49 ± 0.034	0.51 ± 0.033
Parameter *b*					
Verhulst	2.560	4.463	7.023	0.36 ± 0.020	0.64 ± 0.020
Parameter *k*					
Logistic	0.00003	0.00002	0.00006	0.60 ± 0.062	0.40 ± 0.059
Verhulst	0.00514	0.00349	0.00863	0.60 ± 0.023	0.40 ± 0.023
Weight at inflection point					
Logistic	10.981	15.813	26.794	0.41 ± 0.028	0.59 ± 0.028
Verhulst	7.887	12.788	20.675	0.38 ± 0.021	0.62 ± 0.021
Age at inflection point					
Logistic	177.225	260.137	437.363	0.41 ± 0.029	0.59 ± 0.029
Verhulst	154.893	180.309	335.203	0.46 ± 0.022	0.54 ± 0.022

σ^2_a = additive variance; σ^2_e = environmental variance; σ^2_p = phenotypic variance; h^2 = heritability; e^2 = environment proportion in the total variance.

Table 7 *Estimates of heritability (diagonal), genetic (above diagonal) and phenotypic (below diagonal) correlations between logistic growth curve parameters in Segureño lambs*

Parameters	*a*	*m*	*k*	Wi	Ai
a	0.41 ± 0.027	0.97 ± 0.022	− 0.82 ± 0.098		
m	0.94***	0.51 ± 0.028	− 0.81 ± 0.099		
k	− 0.78***	− 0.79***	0.62 ± 0.031		
Wi				0.41 ± 0.028	0.91 ± 0.138
Ai				0.92***	0.41 ± 0.029

Wi = weight at inflection point; Ai = age at inflection point.
***$P < 0.001$.

Table 8 *Estimates of heritability (diagonal), genetic (above diagonal) and phenotypic (below diagonal) correlations between Verhulst growth curve parameters in Segureño lambs*

Parameters	*a*	*b*	*k*	Wi	Ai
a	0.39 ± 0.021	0.95 ± 0.112	− 0.70 ± 0.071		
b	0.92***	0.37 ± 0.020	− 0.67 ± 0.068		
k	− 0.66***	− 0.59***	0.61 ± 0.023		
Wi				0.38 ± 0.021	0.88 ± 0.099
Ai				0.89***	0.46 ± 0.022

Wi = weight at inflection point; Ai = age at inflection point.
***$P < 0.001$.

and the Verhulst model, respectively) between the two growth characteristics, suggesting that selection for early maturity would lead to lower mature weights. Lewis *et al*. (2002) and Abegaz *et al*. (2010) presented a lower value for this genetic relationship in their studies. In other words, selection for increased growth or maturing rate tends to decrease mature weight (Bathaei and Leroy, 1998).

A model comparison based on the analysis of the estimates of growth parameters was performed to check whether the models gave similar or different estimates of these parameters. In the case of discrepancies among models of important biological significance, the function giving the most reliable estimates of the analysed growth traits should be chosen. Taking into account the similarity of the heritability and additive genetic correlations between both models, their capacities could be considered to be similar, but the data regarding the individual fit to each model recommend the Verhulst model because it maximizes the number of lambs reaching a complete fitness offering a more information for the genetic analysis.

Other growth traits can be computed for each animal using the corresponding estimates of the equations parameters, such as the maximum growth rate, average growth rate during postnatal growth or the time to half-final growth. These parameters are used to compare the genetic potential of animals and to understand the effects of genetic factors on growth; it is important to choose a model that provides accurate estimates of these parameters. The comparison between models in terms of estimating growth parameters revealed that, in spite of small differences between the values obtained with each model, ranking of animals according to those parameters was similar with both models, given the highly significant correlations observed between them (López *et al.*, 2000).

Conclusions

According to the results, both equations tested here were suitable for our purposes, but we recommend the Verhulst model because it showed greater versatility, permitting the convergence of a larger number on individual lambs. It supposed a larger amount of information and, consequently, a greater precision in the estimates.

Growth curve parameters and especially their biological meaning are of great interest in Segureño sheep breeding programmes. In the present study, aspects such as asymptotic weight, growth rate, shape of the curve and inflection point have shown important levels of additive genetic variation. Therefore, these aspects have economic importance and offer excellent perspectives for genetic response to selection, so most of them should be introduced into the breeding programme as additional selection criteria. Additive genetic correlations were, in general, large, but diverse. This must be taken into account in the introduction of these new traits into the breeding programme, because desirable or undesirable indirect responses to selection will influence interactions among traits in the new growth curve trait breeding programme.

Focussing on this fact, any selective increase in early weights could be associated with an increase in mature weight, which entails an increase in feed cost in the flock. This is particularly important where supplementary feed costs constitute a relatively large proportion of the total costs. Selection could be made for animals with faster growth rate at an early age and/or that are early maturing. Faster growth rate increases the proportion of feed intake used for tissue synthesis and reduces total inputs/unit of weight gain.

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Supplementary material

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1. Los modelos considerados en la presente investigación - Brody, von Bertalanffy, Verhulst, logístico y Gompertz - son adecuados para describir el crecimiento de la raza ovina Segureña, a excepción del modelo de Brody que no convergió en la curva comercial (del nacimiento al sacrificio).
2. La función más adecuada para explicar el crecimiento biológico de la raza Segureña, desde el nacimiento hasta la madurez, es el modelo de von Bertalanffy, para ambos sexos.
3. Los parámetros de la curva biológica mostraron diferencias importantes entre sexos, lo que nos lleva a reconocer el fuerte impacto de dimorfismo sexual en el crecimiento hasta la madurez. Destacamos el valor más elevado en tasa de crecimiento de las hembras, lo que indica que alcanzan la madurez antes que los machos.
4. Desde el nacimiento hasta el sacrificio, la función más adecuada para explicar la curva de crecimiento comercial de los corderos Segureños es el modelo logístico. Durante este período también se observó un dimorfismo sexual en el crecimiento pero menor que en la curva biológica.
5. Estos resultados muestran su importancia zootécnica para la gestión de ambos sexos en cebo y para la toma de decisiones para el sacrificio, pudiendo apoyar también los programas de selección, utilizando algunos parámetros de la curva como criterio de selección para mejorar rasgos comerciales importantes, tales como la precocidad.
6. Pudimos apreciar como el dimorfismo sexual es patente desde los pesos más tempranos, pero se hace extremo en el peso final, de lo que se concluye que la decisión de entrada al matadero en uno y otro sexo debe apoyarse en el peso y nunca en la edad.
7. Los efectos más importantes sobre los pesos y crecimientos fueron el rebaño y el tipo de parto: el primero de ellos se justifica por las grandes diferencias de manejo existentes entre los rebaños; en el segundo caso se debe a la diferencia entre la capacidad de lactogénesis de las madres, por ello, la influencia del factor es grande cuando el cordero es más dependiente y disminuye cuando el cordero alcanza el posdestete.

8. La varianza explicada por el modelo multifactorial estuvo comprendida entre el 44 y 49%, por lo que lo consideramos muy eficiente para los tres pesos estudiados y ofrece una información muy importante a la hora de diseñar los modelos de análisis genéticos de los parámetros de las curvas para obtener la máxima ortogonalidad a un menor coste computacional.
9. El factor rebaño se demostró altamente interactivo lo que se deriva, fundamentalmente, por su gran responsabilidad en la explicación de la varianza.
10. La época de nacimiento mostró pocas interacciones. A pesar de ser animales poliéstricos, la concentración de los partos en unas épocas determinadas obedece a razones comerciales de demanda y no a una respuesta mejor al crecimiento en determinadas épocas.
11. El tipo de parto interactuó significativamente con otros factores, debido al gran volumen de varianza que explica aunque su influencia en la variación disminuye con la edad.
12. El crecimiento compensatorio no neutralizó las diferencias de peso entre los partos simples y los múltiples. Esto hace que nos cuestionemos la mejora genética basada únicamente en la prolificidad, ya que los corderos de partos múltiples crecen significativamente menos y con ello alcanzan el peso comercial más tarde.
13. El modelo de Verhulst mostró una mayor versatilidad, permitiendo la convergencia individual de un número mayor de corderos. Esta mejor bondad de ajuste individual nos hizo elegirlo para la obtención de valores individuales de los parámetros para su uso en los análisis genéticos
14. El peso asintótico, la tasa de crecimiento, la forma de la curva y el punto de inflexión han mostrado importantes niveles de variación genética aditiva. Por importancia económica y excelentes perspectivas de respuesta genética a la selección, puedes utilizarse como criterios de selección adicionales.
15. Las correlaciones genéticas aditivas fueron, en general, de gran volumen pero de signo diverso. Esto debe tenerse en cuenta en la introducción de estos nuevos criterios de selección en el programa genético, por las respuestas indirectas a la selección, deseables o indeseables, que pudieran producirse.
16. Cualquier aumento selectivo en los primeros pesos puede asociarse a un aumento de peso a la madurez, lo que implica un aumento del coste en la alimentación del rebaño. La selección podría hacerse para los animales con la tasa de crecimiento más rápido en una edad precoz y/o que son de maduración precoz.

17. Nuestros resultados han demostrado que la utilización de la curva de mejor ajuste poblacional debe dirigirse a aspectos zootécnicos como la alimentación o la economía; pero la curva de mejor ajuste individual nos ofrece parámetros de alto significado biológico de interés estratégico como criterios de selección para los programas de mejora del ovino de carne.

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				Total Cites	Impact Factor	5-Year Impact Factor	Immediacy Index	Articles	Cited Half-life	*Eigenfactor®* Score	*Article Influence®* Score
☐	1	ANIMAL	1751-7311	3146	1.841	2.040	0.506	253	4.1	0.01107	0.609

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Rank in Category: Animal

Journal Ranking

For **2014**, the journal **Animal** has an Impact Factor of **1.841**.

This table shows the ranking of this journal in its subject categories based on Impact Factor.

Category Name	Total Journals in Category	Journal Rank in Category	Quartile in Category
AGRICULTURE, DAIRY & ANIMAL SCIENCE	57	7	Q1
VETERINARY SCIENCES	133	19	Q1

Italian Journal of Animal Science

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Journal: Italian Journal of Animal Science

Mark	Journal Title	ISSN	Total Cites	Impact Factor	5-Year Impact Factor	Immediacy Index	Citable Items	Cited Half-life	Citing Half-life
☐	ITAL J ANIM SCI	1594-4077	886	0.718	0.641	0.177	124	5.8	>10.0

Cited Journal | Citing Journal | Source Data | Journal Self Cites

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Rank in Category: Italian Journal of Animal Science

Journal Ranking

For **2014**, the journal **Italian Journal of Animal Science** has an Impact Factor of **0.718**.

This table shows the ranking of this journal in its subject categories based on Impact Factor.

Category Name	Total Journals in Category	Journal Rank in Category	Quartile in Category
AGRICULTURE, DAIRY & ANIMAL SCIENCE	57	32	Q3
VETERINARY SCIENCES	133	83	Q3