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MÁSTER EN MEJORA GENÉTICA ANIMAL Y BIOTECNOLOGÍA DE LA REPRODUCCIÓN

Análisis genético de la eficiencia alimentaria de la cerda en lactación y sus componentes

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1. RESUMEN

Como consecuencia de la selección genética y las mejoras en el ambiente y manejo de las granjas, el tamaño de la camada ha aumentado en los últimos años de manera que los requerimientos energéticos de la cerda en lactación son ahora mayores. Por otra parte, la mejora de la eficiencia alimentaria de los cerdos en crecimiento ha conducido a una disminución de la capacidad de ingestión y del apetito, que se prolonga al periodo de lactación, por lo que las hembras no son capaces de obtener la energía y nutrientes necesarios para la producción de leche y movilizan sus reservas energéticas. Si esta movilización es excesiva, se producen problemas reproductivos y de salud que terminan con la eliminación temprana de la hembra. En este contexto, se ha planteado que sería necesario mejorar la eficiencia alimentaria de la cerda en lactación mediante selección genética. El objetivo de este trabajo ha sido conocer el determinismo genético de éste carácter y de los caracteres implícitos en su definición, así como las asociaciones genéticas y ambientales entre los mismos para poder diseñar un programa de selección en una población de cerdos Duroc. Los caracteres estudiados son: la ingesta diaria de pienso (dLFI), el balance diario de peso de la cerda (dSWB), el balance diario de la grasa dorsal (dBFB), la ganancia diaria de peso de la camada (dLWG) y el consumo de pienso residual de la cerda (SRFI) durante la lactación como medida de eficiencia global. Los datos proceden de una población de la empresa Batallé y corresponden a 851 partos de 581 cerdas Duroc. Para el análisis de la relación entre los componentes de la eficiencia alimentaria se realizó un análisis bayesiano mediante gibbs sampling utilizando un modelo tetra-carácter con efectos permanentes. Para el análisis de SRFI se utilizó un modelo unicaracter de repetibilidad. Las heredabilidades obtenidas fueron: media posterior = 0.09 [desviación típica posterior = 0.03] para el dLFI, 0.28 [0.08] para dSWB, 0.13 [0.04] para dBFB, 0.22 [0.05] para dLWG y 0.14 [0.06] para SRFI. La correlación genética entre dLFI y dBFB fue alta y negativa (-0.75 [0.12]) y entre dLFI y dSWB moderada y negativa (-0.44 [0.19]). El resto de correlaciones genéticas fueron bajas y no estadísticamente diferentes de cero. Las correlaciones fenotípicas fueron bajas y positivas entre dLFI y dSWB (0.29 [0.03]), dSWB y dBFB (0.32 [0.04]), y entre dLFI y dLWG (0.17 [0.04]). La correlación fenotípica entre dLWG y los balances de reservas corporales fueron bajas y negativas (-0.26 [0.04] con dSWB y -0.17 [0.04] con dBFB). La correlación entre dLFI y dBFB fue nula. Las correlaciones entre efectos ambientales permanentes debidos a la hembra entre dLWG y los demás caracteres fueron bajas y no significativas. Sin embargo, la correlación entre efectos permanentes de dLFI y dBFB fue muy alta y positiva (0.94 [0.03]), mientras que fueron moderadas y

positivas las correlaciones entre dLFI y dSWB (0.65 [0.13]) y entre dSWB y dBFB (0.55 [0.15]). Por tanto, la mejora de la eficiencia alimentaria en lactación, en la población objeto de estudio, sería posible bien directamente utilizando el carácter SRFI o bien mediante un índice que integre sus componentes más importantes.

2. SUMMARY

As a result of the genetic selection and the improvements in the environment and farms management, litter size has increased in the last few years so that the energy requirements of the lactating sow are greater. On the other hand, feed efficiency in growing pigs has led to an ingestion and appetite decrease that is extended to the lactation period, so the females aren't able to obtain the necessary energy and nutrients for milk production and they mobilize their energetic reserves. Whether this mobilization is excessive, reproductive and health problems occur which ends to an early removal of the sow. In this context, it has been suggested that it would be necessary to improve food efficiency of the sow in lactation through genetic selection. The aim of this study is to know the genetic determinism of this trait and traits involved in its definition, as well as genetic and environmental associations between them in order to design a breeding program in a Duroc population. The studied traits are: the daily lactation feed intake (dLFI), the daily sow weight balance (dSWB), the daily backfat balance (dBFB), the daily litter weight gain (dLWG) and the sow residual feed intake (SRFI) in the lactating period as a global efficiency measure. Data come from a population of Bataille's company and corresponds to 851 parities of 581 Duroc sows. For the analysis of the relation between the components in feed efficiency, a Bayesian analysis was taken through Gibbs sampling using a four-trait animal model with permanent effects. A repeatability model was used in the SRFI analysis. The heritabilities obtained were: posterior mean = 0.09 [posterior standard deviation= 0.03] for dLFI, 0.28 [0.08] for dSWB, 0.13 [0.04] for dBFB, 0.22 [0.05] for dLWG and 0.14 [0.06] for SRFI. The genetic correlation between dLFI and dBFB was high and negative (-0.75 [0.12]) and between dLFI and dSWB was moderate and negative (-0.44 [0.19]). The other genetic correlations were low and not statistically different from zero. The phenotypic correlations were low and positive between dLFI and dSWB (0.29 [0.03], dSWB and dBFB (0.32 [0.04]), and between dLFI and dLWG (0.17 [0.04]). The phenotypic correlation between dLWG and the body reserves balances were low and negative (-0.26 [0.04] with dSWB and -0.17 [0.04] with dBFB). The correlation between

dLFI and dBFB was null. The correlations between permanent environmental effects due to female between dLWG and the other traits were low and not significant. However, correlation between the permanent effects from dLFI and dBFB was very high and positive (0.94 [0.03], whereas the correlations were moderate and positive between dLFI and dSWB (0.65 [0.13]) and between dSWB and dBFB (0.55 [0.15]). Therefore the improvement of the lactation feed efficiency, in the population under study, would be possible either using directly SRFI trait or through an index which integrates its important components.

3. EFICIENCIA ALIMENTARIA DE LA CERDA EN LACTACIÓN

a. Introducción

Uno de los principales objetivos de la selección en el sector porcino ha sido la producción de camadas grandes de elevado peso al destete a lo largo de los sucesivos partos de una hembra. Así, por ejemplo, en el índice por el que se selecciona la población Duroc de la empresa Batallé (Figura 1), de la que se han obtenido los datos para este estudio, la prolificidad tiene el mayor peso (38%) seguida por el peso al destete de los lechones (23%).

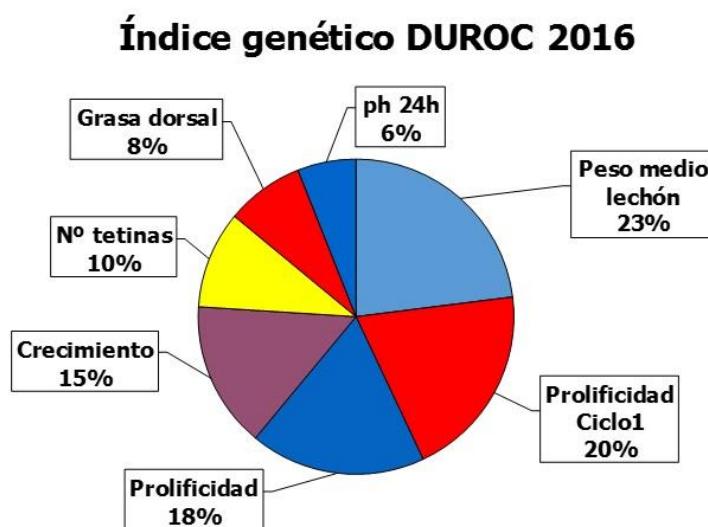


Figura 1: Porcentaje de participación de los diferentes caracteres que componen el índice de selección de la línea Duroc de la empresa Batallé S.A. Datos cedidos por la propia empresa.

En otras empresas de selección porcina, los pesos relativos entre los distintos caracteres son similares a los mostrados para la empresa Batallé.

Como consecuencia de la selección por prolificidad, el tamaño de la camada en las granjas comerciales se ha visto incrementado en los últimos años pasando de 9,26 lechones destetados por camada en 2001 a 11.34 lechones por camada en 2015, según datos de BDporc (Figura 2).

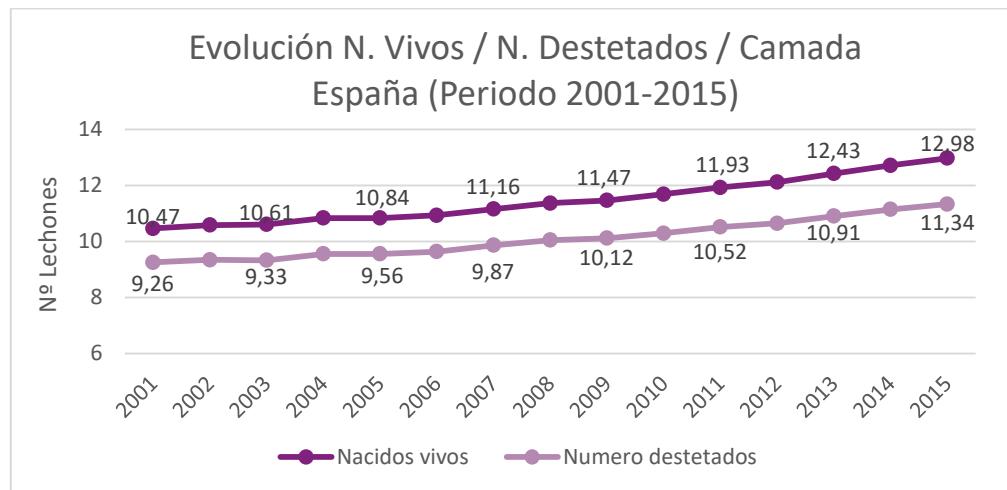


Figura 2: Evolución del tamaño de camada en España entre los años 2001 y 2015. Datos de BDporc.

La producción de camadas grandes y pesadas debe ir acompañada de una elevada producción de leche, para lo que a su vez es necesario que la hembra disponga de suficiente energía y nutrientes procedentes de la ingestión de pienso. En caso contrario, la hembra debe movilizar sus reservas corporales para proporcionar a la camada el alimento que necesita (Kim and Easter, 2001). Las reservas corporales son limitadas y deben satisfacer otros requerimientos de energía tales como los necesarios para el mantenimiento de las funciones biológicas de la propia hembra o su crecimiento, en el caso de hembras jóvenes (Cameron et al., 2002; Eissen et al., 2003).

Los requerimientos de energía y nutrientes, en general, sobrepasan los obtenidos por la hembra a través de la ingestión de pienso, bien porque superan su capacidad de ingestión o por la falta de apetito de éstas como consecuencia de la selección genética. En porcino, además de la prolificidad y el crecimiento de las camadas, se ha puesto un énfasis importante en la obtención de animales magros con bajo índice de transformación de pienso en carne (ver figura 1). Ello ha conducido, en algunos casos a una reducción del apetito e ingestión de pienso de las hembras tanto en su etapa de crecimiento como en la productiva (Kanis, 1990; Cameron et al., 2002; Gilbert et al., 2012) y a una pérdida de peso y depósitos grasos durante la lactación debida a la movilización de reservas corporales

necesaria para satisfacer las necesidades de energía y nutrientes en este último periodo (Cameron et al., 2002; Bergsma et al., 2008). En consecuencia, el rendimiento global de las hembras reproductoras puede verse afectado al aparecer problemas reproductivos y de salud que causan una eliminación temprana de la hembra (Anil et al., 2006; Lundgren et al., 2014; De Bettio et al., 2016).

Diversos autores han señalado la necesidad de incluir en los programas de selección caracteres que tengan una estrecha relación con el comportamiento de las hembras en lactación tales como la ingestión de pienso, capacidad de movilización de reservas corporales o la eficiencia alimentaria en lactación de la propia hembra (Bergsma et al., 2009; Lundgren et al., 2014; Thekkoot et al., 2016; Young et al., 2016). Para optimizar dichos esquemas de selección y también predecir la respuesta esperada es necesario conocer en la población objeto de selección, los parámetros genéticos (heredabilidad y correlaciones genéticas y fenotípicas) de los caracteres que formarían parte del índice con la mayor precisión posible.

b. Caracteres implicados en la definición de eficiencia durante la lactación

La eficiencia alimentaria en lactación puede considerarse como el balance entre la energía y los nutrientes ingeridos por la hembra y el uso que de estos hace la misma. Así pues, está condicionada a una serie de caracteres que podríamos considerar como sus componentes, y que se pueden dividir en 2 grupos:

1. caracteres relacionados con entrada de energía como son aquellos que miden la ingestión de pienso y la movilización de las reservas corporales (es decir, la pérdida de peso corporal y grasa dorsal de la cerda durante la lactación).
2. caracteres relacionados con la producción o uso de energía como son los que miden el crecimiento o ganancia de peso corporal y grasa dorsal de la cerda, el mantenimiento de los procesos biológicos y fisiológicos de la propia cerda, y la producción de leche (cuantificada por el crecimiento y mantenimiento de los lechones).

Otros caracteres que pudieran condicionar la eficiencia alimentaria en lactación son ciertas características de la cerda al inicio de ésta, por ejemplo: el peso y el contenido en grasa de

la cerda al parto y el peso de la camada al nacimiento o al inicio de la lactación tras las adopciones.

Entre los caracteres relacionados con la entrada de energía, la **ingestión de pienso** durante la lactación es el de mayor importancia y más fácil control. Las cerdas empiezan la lactación ingiriendo una pequeña cantidad de pienso hasta que se recuperan del estrés del parto. A partir de entonces, incrementan el consumo rápidamente a medida que la lactación avanza (Hermesch, 2007 ; Kruse et al., 2011). Es importante que la ingestión en lactación sea regular puesto que se ha visto que si el nivel de pienso ingerido por la cerda es inadecuado durante al menos dos días consecutivos en la lactación, el consumo se ve reducido en días posteriores (Koketsu et al., 1996; Bergsma et al., 2009; Schenkel et al., 2010). A largo plazo, sin embargo, tener una ingestión inadecuada durante una lactación no implica que esto también ocurra en las siguientes (Yoder et al., 2013).

El consumo de pienso en lactación se ve afectado por la ingesta en gestación; las cerdas que tienen una ingesta de alimento mayor en gestación, tienen menos apetito durante la lactación que las cerdas que se alimentan en gestación según sus requerimientos energéticos (Dourmad, 1991; Weldon, 1994).

Por otra parte, la condición corporal, es decir, la mayor o menor cantidad de reservas corporales de energía de la cerda al inicio de la lactación, también afecta al consumo durante este periodo (Koketsu et al., 1996). Así, se ha visto, que un mayor espesor de grasa dorsal al parto se traduce en una menor ingestión (Dourmad, 1991).

El tamaño de camada es otro carácter importante que afecta a la ingestión de pienso en lactación. A mayor número de lechones, mayor número de glándulas mamarias funcionales y mayor producción de leche. En consecuencia, también aumenta la energía requerida por la cerda (Kim et al., 1999). Cerdas con camadas entre 10-11 lechones consumen un promedio de .4 kg más de pienso que cerdas con camadas de 3-6 lechones. Sin embargo, a partir de este nivel de prolificidad el consumo no aumenta pues la cerda es incapaz de ingerir más alimento (Koketsu et al., 1996; Hermesch, 2006).

La duración de la lactación también afecta, como cabría esperar, al consumo de pienso. Koketsu et al. (1996) demostraron que cuanto más larga es la lactación más elevado es el consumo medio diario de las cerdas durante este periodo. Así, en lactaciones de 28 días de duración las cerdas consumían diariamente alrededor de 1.4 Kg más que las cerdas con una duración de la lactación de 10 días. Esto se debe principalmente al mayor consumo en el tramo final de la lactación, a partir de la tercera semana. Las cerdas con una lactación

corta, tienden a perder menos peso ya que están menos expuestas a una elevada demanda de nutrientes por parte de los lechones. Sin embargo, a largo plazo, paren más camadas en un mismo lapso de tiempo, lo que puede conllevar a una mayor tasa de eliminación (Anil et al., 2006) debida a problemas asociados con su elevado ritmo reproductivo y productivo.

El nivel de desarrollo de la cerda condiciona el nivel de ingesta durante la lactación. En los 2 primeros partos, la cerda puede llegar a ingerir hasta un 15% menos de energía durante la lactación que en partos posteriores (NRC, 1987, citado por (Koketsu et al., 1996). Según Anil et al. (2006) esto ocurre porque las cerdas jóvenes, aunque tienen una necesidad de energía mayor puesto que aún están en desarrollo, no tienen tanta capacidad intestinal y por lo tanto es muy probable que ingieran una cantidad de pienso por debajo de sus necesidades (Yang, 1989), lo que puede resultar en un fallo reproductivo sobre todo en los primeros partos, antes incluso de que animal se haya llegado a amortizar (Dourmad et al., 1994).

Otros caracteres de tipo ambiental como el estrés o la temperatura también contribuyen a alterar el nivel de ingestión de pienso (Bunter, 2006). Se ha comprobado que temperaturas extremas (por encima de 29°C o por debajo de los 9°) hacen disminuir la ingestión de pienso significativamente y que la temperatura óptima con la que las cerdas ingieren más pienso es de 21-22 °C (Eissen et al., 2003; Bergsma and Hermesch, 2012). En lo referente al estrés por otros factores, la alta densidad de animales dentro de corrales o un elevado número de movimientos del animal (Hyun et al., 1998) pueden afectar negativamente a la ingestión.

La selección para la mejora de la eficiencia de crecimiento magro en el engorde o la disminución del consumo de pienso residual, ha producido animales que consumen menos alimento también en su edad adulta, como es el caso de las cerdas en lactación (Cameron et al., 2002; Hermesch et al., 2008; Gilbert et al., 2012). Hermesch et al. (2008) sugieren incluir en los programas de selección genética el consumo en lactación con objeto de mejorar el rendimiento de la cerda a lo largo de su vida productiva.

La pérdida de peso de la cerda o de condición corporal debida a la **movilización de reservas** energéticas serían las otras fuentes de energía disponibles durante la lactación. Una excesiva pérdida de peso de la cerda durante la lactación debido a una ingestión de pienso insuficiente se ha visto que incrementa el intervalo destete-cubrición, disminuye la tasa de concepción y aumenta la mortalidad embrionaria (Eissen et al., 2000; Yoder et al.,

2013). Por otra parte, produce un deterioro en su rendimiento productivo (menor peso de la camada al destete) (Koketsu et al., 1996; Gilbert et al., 2012; Yoder et al., 2013; De Bettio et al., 2016), lo que puede dar lugar a la eliminación temprana de la hembra (Anil et al., 2006; Yoder et al., 2013).

Similarmente a lo referido para el consumo, la selección por crecimiento magro o eficiencia alimentaria en crecimiento ha tenido como consecuencia, en muchos casos, que las cerdas movilicen más sus reservas corporales (ya de inicio bajas debido a su menor consumo) para alcanzar la cantidad de energía necesaria para la lactación (Cameron et al., 2002; Gilbert et al., 2012).

La mayor parte de la energía disponible durante la lactación se destinará a la producción de leche, que se puede medir de manera indirecta a través de **la ganancia de peso de la camada**. Respecto a la producción de leche, las cerdas que son grasas tienen menor capacidad de secreción de leche (menor número de células secretoras de leche) que las cerdas más magras (Head and Williams, 1991 citado por Eissen et al. (2000)), lo que se traduce en un menor crecimiento de las camadas. Así, se ha visto que la producción de leche era un 15% mayor en cerdas delgadas que en cerdas grasas (Revell et al., 1998). El consumo de la cerda en lactación condiciona, a su vez, el peso al destete. Koketsu et al. (1996) obtienen un incremento de 3kg en el peso al destete de la camada al incrementar de 4 a 7kg el consumo diario de pienso. De la misma forma, Schenkel et al. (2010) encuentran un aumento en el peso al destete de la camada de dos líneas diferentes de cerdos (Yorkshire y Landrace), al aumentar la energía ingerida por la cerda en la lactación.

c. Medidas de eficiencia alimentaria en lactación.

Hasta la fecha se han propuesto tres medidas de eficiencia global de la cerda durante la lactación que son: 1) La eficiencia de la cerda en lactación (en inglés: sow lactation efficiency, SLE) propuesta por Bergsma et al. (2009) como un ratio de energía, 2) el balance de energía de la lactación descrito por Young et al. (2016) y 3) la ingestión de pienso residual de la cerda en lactación (en inglés: Sow Residual Feed Intake, SRFI) propuesta por Gilbert et al. (2012).

1) Eficiencia de la cerda en lactación (SLE)

La medida de eficiencia en lactación se basa en el siguiente esquema de flujo de energía de una cerda en lactación (Figura 3)(Bergsma et al., 2008; Bergsma et al., 2009).

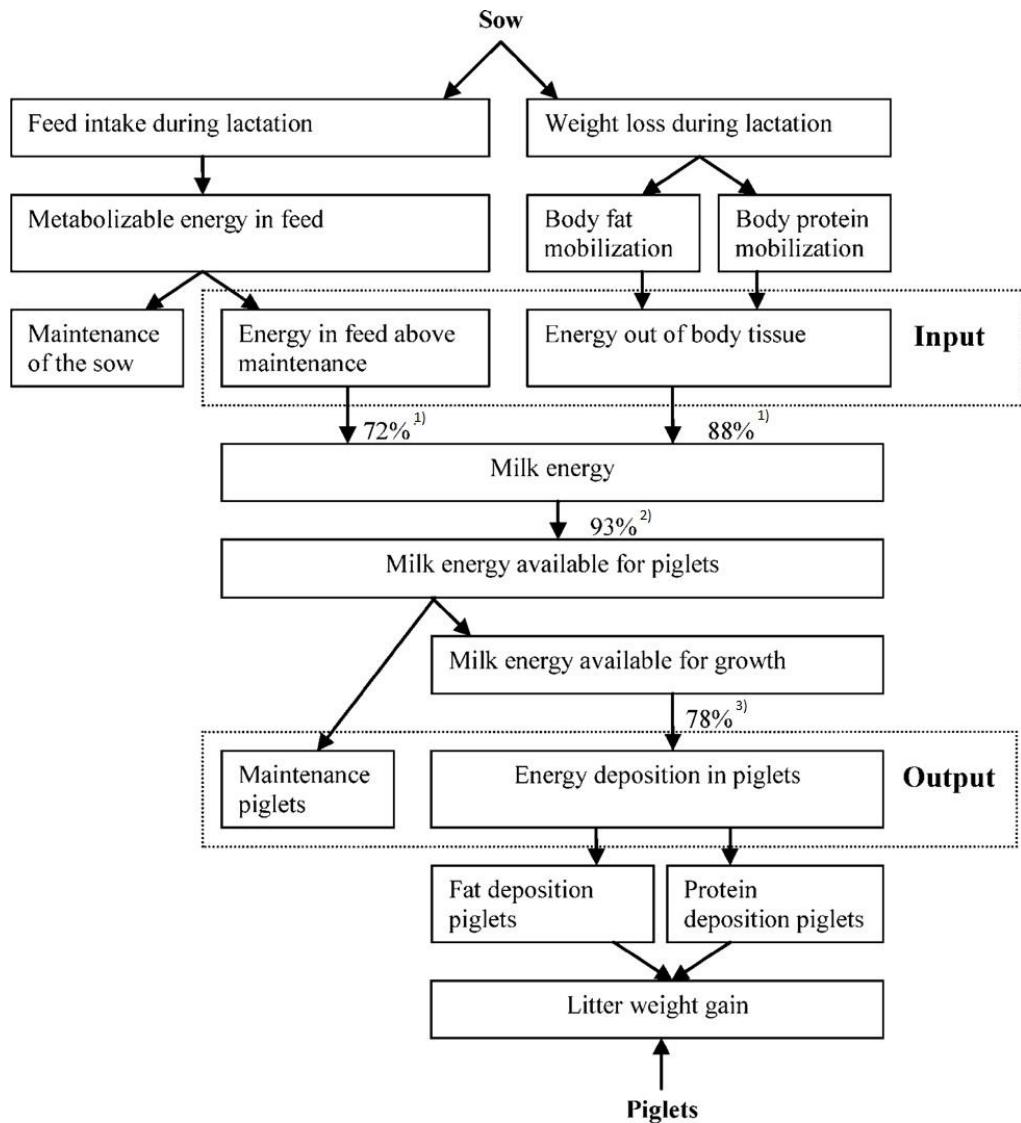


Figura 3: Flujo de energía del Metabolismo de una cerda durante la lactación. (Bergsma et al., 2009; ¹⁾ Noblet et al., 1990, ²⁾ Everts et al., 1995 y ³⁾ Mullan et al., 1993).

En esta figura, la energía que la cerda ingiere por encima de sus necesidades de mantenimiento, junto con la energía procedente de la movilización de tejidos (grasa y proteína), es la que se utiliza para la producción de leche. Los valores de los coeficientes de eficiencia de la transformación de la energía metabólica del pienso ($K_l = 72\%$) o de las reservas corporales ($K_{rl} = 88\%$) en energía de la leche proceden de los estudios que realizó Noblet junto con otros investigadores (Verstegen et al., 1985; Noblet and Etienne, 1987; Beyer et al., 1993)

De la energía de la leche producida, el 93% es la que está disponible para los lechones según Everts et al. (1995). Esta cifra la calcula a partir de la energía digestible de la leche y de la relación entre la energía digestible y metabolizable, resultando un valor de 0.93. La

energía disponible para los lechones se utiliza en el mantenimiento de sus propios procesos biológicos y en su crecimiento. De la energía disponible para su crecimiento se aprovecha un 78% (coeficiente de la eficiencia de utilización de la energía de la leche en crecimiento del lechón; K_g), cifra obtenida de Mullan et al. (1993).

Así pues, se considera como input de energía la suma de los siguientes términos:

$$\text{Input} \left(\frac{\text{MJ ME}}{\text{d}} \right) = (\text{energía total ingerida durante toda la lactación} + \text{energía de la movilización de las reservas de grasa de la cerda} + \text{energía de la movilización de las reservas de proteína de la cerda} - \text{energía necesaria para el mantenimiento de la cerda}) / \text{duración de la lactación}$$

Y el Output es:

$$\text{Output} \left(\frac{\text{MJ ME}}{\text{d}} \right) = (\text{energía en la deposición de grasa de lechones vivos al destete} + \text{energía en la deposición de proteína de lechones vivos al destete} + \text{energía en la deposición de grasa en lechones muertos} + \text{energía en la deposición de proteína en lechones muertos} + \text{energía necesaria para el mantenimiento de lechones destetados} + \text{energía utilizada para el mantenimiento de lechones muertos antes del destete}) / \text{duración de la lactación}$$

A partir de estos valores Bergsma et al. (2008) definen “La eficiencia energética de la cerda durante la lactación” (SLE) que se calcula como un ratio entre el output y el input de energía durante la lactación, ambos en unidades de energía diaria (MJ EM/d).

$$SLE = \frac{\text{Input}}{\text{output}} * 100$$

2) Balance de energía en lactación

Young et al. (2016) y Thekkoot et al. (2016) definieron la eficiencia en lactación de manera alternativa. La eficiencia de Young et al. (2016) es un balance de energía calculado como la diferencia entre la energía retenida por la cerda en el momento del destete y la energía retenida por la cerda al parto. Estas energías se obtienen a partir del contenido de proteína y de grasa en la cerda que se considera que tienen una energía de 23.8 MJ EM/kg

en la proteína y 39.5 MJ EM/kg en la grasa (cifras de Bergsma et al. (2009) obtenidas a su vez de Everts et al. (1995)).

Así pues, la energía que contiene la cerda al parto se obtiene como:

Energía retenida por la cerda al parto(MJ EM)

$$\begin{aligned} &= \text{Contenido de proteína al parto} * 23.8 \\ &+ \text{Contenido de grasa al parto} * 39.5 \end{aligned}$$

La energía que tiene la cerda al destete se obtiene como:

Energía retenida por la cerda al destete(MJ EM)

$$\begin{aligned} &= \text{Contenido de proteína al destete} * 23.8 \\ &+ \text{Contenido de grasa al destete} * 39.5 \end{aligned}$$

Quedando el balance de energía como:

Balance de energía (MJ EM/d)

$$= \frac{(\text{Energía retenida por la cerda al parto} - \text{Energía retenida por la cerda al destete})}{\text{Días en lactación}}$$

Esta medida, a diferencia de otras, no recoge las diferencias en el esfuerzo productivo de las hembras. En cambio el balance de Thekkoot et al. (2016) sí que lo tiene en cuenta. Estos autores proponen una nueva medida de balance energético basándose en el obtenido por Spurlock et al. (2012) para vacuno y con las constantes que reflejan las eficiencias energéticas obtenidas por Noblet et al. (1990), resultando la siguiente ecuación, con todos sus términos expresados en unidades de MJ EM/d:

$EB(MJME/d)$

$= ((\text{Energía proveniente de la ingestión en lactación}$

$- \text{Energía necesaria para el mantenimiento de la cerda}) * 0.72)$

$$- (\frac{\text{Energía necesaria para el mantenimiento de los lechones} + \frac{\text{Energía depositada en lechones}}{0.78}}{0.93} - \frac{0.93}{0.88})$$

- 3) Ingestión de pienso residual de la cerda en lactación (Sow Residual Feed Intake, SRFI)

Basándose en la bien conocida medida de eficiencia alimentaria en crecimiento (residual feed intake, RFI; Kennedy et al. (1993), Rauw et al. (2002) proponen una medida equivalente en lactación, “Sow Residual Feed Intake” (SRFI), que no es más que la cantidad de pienso ingerido por encima o por debajo de las necesidades para mantenimiento y

producción en este periodo, predichas mediante una ecuación de regresión múltiple. Al igual que el RFI, esta medida evita los problemas asociados al uso de ratios, como son el de no tener una distribución normal, y la imposibilidad de saber sobre qué componente (numerador o denominador) se actúa cuando es utilizada para la selección (Kennedy et al., 1993). Por otra parte, evita la realización de transformaciones a unidades energéticas que requieren el uso de coeficientes de cuyo valor no se tiene una absoluta certeza.

Las necesidades de mantenimiento de la hembra se miden a través del peso metabólico ($BW^{0.75}$; (Noblet et al., 1990). Los requerimientos para la producción de leche dependen básicamente del número de lechones nacidos y del crecimiento de la camada durante la lactación (Gilbert et al., 2012). Así pues, la predicción de las necesidades diarias de pienso durante la lactación se hace mediante una regresión múltiple del consumo que utiliza como variable predictoras: la pérdida diaria de peso de la cerda durante la lactación ($d\Delta BW$), la pérdida diaria de grasa dorsal durante la lactación ($d\Delta BFT$), la ganancia diaria de peso de los lechones durante 21 días de lactación ($dLWG_{21}$), el número de lechones vivos al destete (NS), y el peso metabólico de la cerda al destete ($BW^{0.75}$).

Gilbert et al. (2012) señalan que sería interesante seleccionar por este carácter ya que ayuda a encontrar el balance apropiado entre ingestión de pienso y la producción durante la lactación, consiguiendo que las cerdas no movilicen demasiadas reservas, y contribuyendo por tanto a aumentar la longevidad de las mismas.

4. OBJETIVOS

El objetivo de este trabajo es estimar los componentes de varianza de los caracteres implicados en la eficiencia de la cerda en lactación y la asociación entre ellos, con la finalidad última de definir la estrategia de selección para la mejora de este carácter. Específicamente, se han estimado las heredabilidades y otros ratios de variación ambiental sobre la varianza fenotípica, así como las correlaciones genética y ambiental de los siguientes caracteres lactacionales:

- la ingestión de pienso diaria (dLFI),
- el balance diario de peso (dSWB) y de grasa dorsal (dBFB) de la cerda, como medidas de movilización de las reservas corporales
- la ganancia de peso diaria de la camada (dLWG), como medida de la producción

A su vez, se ha estimado el determinismo genético de la ingestión residual del pienso de la cerda en lactación, como medida global de eficiencia alimentaria en este periodo productivo.

5. Genetic parameters of sow feed efficiency during lactation and its underlying traits

a. BACKGROUND

Lactation is one of the most energy demanding processes in the productive life of a sow. Because litter size has increased as a result of genetic selection in the last years (Silalahi et al., 2016) and is still a main objective of the breeding programs, sow energy requirements during lactation are also increasing. On the other hand, most of the pig breeding programs also include among its priority aims the increase of feed efficiency during the growth/finish phase of production. This selection has had as a correlated effects the reduction of appetite and feed intake capacity at this stage of animal's life but also at reproduction stage, during lactation (Gilbert et al., 2012). In this situation, feed consumed at lactation is not enough to sustain milk production and maintenance of other biological functions of the sow leading to a mobilization of body reserves (Noblet et al., 1990). However, excess mobilization of body reserves impairs sow posterior reproductive performance (Lundgren et al., 2014) and lead to early culling, which in turn affects profitability. Recently, Young et al. (2016) has shown that sows selected for low residual feed intake at growing are also more efficient at converting energy from food and body reserves mobilization into piglet growth, which would be additionally improved by a high piglet feed efficiency. Those authors suggest to include in the selection criteria sow feed intake and body condition change at lactation in order to prevent potential negative effects on rebreeding performance due to a negative energy balance (Whittemore and Morgan, 1990; Clowes et al., 2003). In order to include those traits in a selection index, It is essential to have accurate estimates of the genetic parameters of all the traits involved in energy balance of the sow at lactation (Thekkoot et al., 2016) in the population to be selected.

Components of feed efficiency during lactation come from energy metabolism in lactating sows which was defined by Bergsma et al. (2009), based on studies performed by Noblet et al. (1990). Energy inputs are feed intake and mobilized body reserves. This energy is used for growth and maintenance of the sow and for milk production, which in turns is used for piglet growth and maintenance. Lactation feed efficiency results from the combination of all those components. It has been defined as the ratio between the output and the input (Bergsma et

al., 2009), as the difference between the observed daily feed intake of a sow and the predicted daily feed intake required for maintenance and production (Gilbert et al., 2012) or as the body energy balance (Young et al., 2016) of the sow at lactation. Genetic parameters of all those traits have been previously estimated in Yorkshire, Large White or Landrace populations (Bergsma et al., 2008; Gilbert et al., 2012; Thekkoot et al., 2016; Young et al., 2016). However, results could be different in a Duroc population which is characterized for its high content in fat (Sánchez et al., 2017) and probably have a different energy metabolism pattern.

b. OBJECTIVES

The aim of this research was to estimate genetic parameters of traits involved in sow feed efficiency during lactation as well as to know phenotypic and genetic associations between them in a Duroc pig selection line aimed at producing high quality fresh and dry-cured pork products.

c. MATERIAL AND METHODS

Animal Care and Use Committee approval was not obtained for this study because data come from a commercial farm belonging to a private company (Batallé S.A., Spain) which strictly operates in line with the regulations of the Spanish law on animal protection

Animals and Data

Animals belonged to a Duroc pig population which was bred in a commercial farm placed in Riudarenes, Girona. Data from up to two farrowings from 677 sows were recorded from May 2015 to May 2016, distributed in 25 batches.

During gestation sow were housed in groups and fed once a day 2.16 Kg on average of a standard diet containing 2085 Kcal of net energy, a minimum of 125 g of crude protein, 70 g crude fibre, and 6.6 g of total Lysine/kg. On average, a week before parturition sows were transferred to the farrowing house. At that time, they were weighed (SW_E) and backfat thickness (BFT_E) was measured at last rib level using an ultrasound system (PIGLOG 105.MB45). Feed intake was limited to a maximum of 3 Kg before farrowing. Within a maximum of 2 days after farrowing, the number of piglets born alive and stillborn was recorded and adoptions were made to equalize the number of piglets per litter. The number of total born (TB), litter size (i.e. the final number of piglets in the litter; LS_s) and litter weight (LW_s) at the beginning of lactation were recorded and average piglet individual weight (PIW_s) at this time was computed

as $\text{PIW}_s = \text{LW}_s / \text{LS}_s$. Records from litters weighed later than 2 days after farrowing were not included in the analysis. During lactation, sows were fed twice a day a standard food containing 2,325 Kcal of net energy, 166 g of crude protein, 9 g of total lysine, and a minimum of 49.1 g of crude fibre per kilogram. The amount of food supplied was established based on sow feed intake during the previous day. Thus, it was increased when the sow finished the whole food the day before, and was kept constant or reduced otherwise. Daily feed intake was recorded every 3-5 days during lactation. The minimum and maximum amount of feed supplied daily were 2.22 and 9.62 kg/d, respectively. Data from sows with less than 5 daily feed intake records were removed for the analysis. Then, a quadratic function was fitted to the individual daily feed intake data with “lm” function from the “stats” R package (R Core Team). Total feed intake was estimated as the sum of daily predicted feed intake for the period from farrowing to 27 days after that. Finally, daily lactation feed intake (**dLFI**) was calculated dividing total feed intake by lactation length (27 d). Around mid-lactation (12 ± 6 days after birth), litter size (LS_i) and weight (LW_i) were recorded in 2 of the 25 batches. At weaning, litter size (LS_w) and weight (LW_w) were recorded again in all batches. Piglet individual weight at mid-lactation (PIW_i) was obtained as $\text{PIW}_i = \frac{\text{LW}_i}{\text{LS}_i}$. In order to obtain the weight of dead piglets during lactation, mortality rate (**MR**) and piglet average daily gain (**PADG1**) from birth to mid-lactation and, piglet average daily gain (**PADG2**) from mid-lactation to weaning were computed, using information from animals with no missing values for litter size and weight at any time, as:

$\text{MR} = \frac{(\text{LS}_s - \text{LS}_i)}{\text{LS}_s}$, $\text{PADG1} = \frac{\text{PIW}_i - \text{PIW}_s}{\text{date}_i - \text{date}_s}$, and $\text{PADG2} = \frac{\text{PIW}_w - \text{PIW}_i}{\text{date}_w - \text{date}_i}$ in which date_s , date_i and date_w are the dates at start-lactation, mid-lactation and weaning, respectively. Then, those values were used to impute missing values of LS_i as $\text{LS}_i = \text{LS}_s - \text{LS}_s \times \text{MR}$ and of piglet individual weight (PIW_i) as $\text{PIW}_i = \text{PIW}_s + \text{mean}(\text{PADG1}) \times (\text{date}_i - \text{date}_s)$ assuming that mortality rate and growth was the same in all batches.

Estimated weight of dead piglets between start of lactation and mid-lactation (**DPW1**) was computed as $\text{DPW1} = (\text{LS}_s - \text{LS}_i) \times (\text{PIW}_s + (\text{PADG} \times 0.8) \times (\text{date}_i - \text{date}_s))$, and weight of dead piglets between mid-lactation and weaning (**DPW2**) as $\text{DPW2} = (\text{LS}_w - \text{LS}_i) \times (\text{PIW}_i + (\text{PADG2} \times 0.8) \times (\text{date}_w - \text{date}_i))$. In both cases, it was assumed that growth of a piglet that finally died was 80% growth of alive piglets. Finally, daily litter weight gain during lactation was computed as $\text{dLWG} = \frac{\text{LW}_{\text{Total}} - \text{LW}_s}{\text{ND}}$ in which LW_{Total} is the total litter weight at the end of lactation which included the weight of piglets that died before weaning to better account for sow energy output; it was calculated as $\text{LW}_{\text{Total}} = \text{LW}_w + \text{DPW1} + \text{DPW2}$ and ND is the number of days between end and start of lactation.

At weaning, sow body weight (**SW_w**) and backfat thickness (**BFT_w**) were also recorded in the same way as before. Sow weight at farrowing (**SW_f**) was estimated as in Bergsma et al., (2009) (deduced from Noblet et al., 1985):

$$SW_f(\text{kg}) = SW_E(\text{kg}) - LW_S(\text{kg}) \times \frac{TFW_E + PW_E + IUFW_E}{TFW_S}$$

Where, TFW_E is the total foetus weight, PW_E is the placenta weight and IUFW_E is intra-uterine fluid weight, all of them at 109 ± 6 days of pregnancy (i.e time at entrance to farrowing house, when sow weight was recorded), and TFW_S is the total foetus weight at start of lactation. They were estimated as follows;

$$TFW(\text{kg}) = \frac{e^{(8.72962 - (4.07466 \times e^{(-0.03318 \times (\text{dpregn} - 45))}) + 0.000154 \times ENgest \times \text{dpregn} + 0.06774 \times Nf)}}{1000}$$

$$PW(\text{kg}) = \frac{e^{(7.02746 - 0.95164 \times e^{(-0.06879 \times (\text{dpregn} - 45))} + 0.000085 \times ENgest \times \text{dpregn} + 0.09335 \times Nf)}}{1000}$$

$$IUFW(\text{kg}) = \frac{e^{(-0.2636 + 0.18805 \times \text{dpregn} - 0.001189 \times \text{dpregn}^2 + 0.13194 \times Nf)}}{1000}$$

Where, dpregn is the number of days of pregnancy, ENgest is the net energy of total feed intake during gestation (MJ ME/d) and Nf is the number of foetuses estimated here as TB.

Daily balance (gain/loss) of SW and BF were computed as following:

$$\text{Daily sow weight balance (kg)}: dSWB = \frac{SW_w - SW_f}{ND}$$

$$\text{Daily backfat balance (kg)}: dBFB = \frac{BF_w - BF_f}{ND}$$

In which, ND was the number of days between both recordings.

Backfat thickness at farrowing was considered to be the same as BFT_E, assuming that there is no significant change of backfat content during that week (Maes, et. al., 2004).

Sow weight at weaning (**SW_w**) was computed as Bergsma et al. (2009; based on Kim et al., 1999-2000):

$SW_W(\text{kg})$

= $SW_W \text{ recorded}(\text{kg})$

$$= \left(\frac{(NFG - LS_W) \times 73 + (LS_W \times 146.15 + 2.17 \times ADG) \times \left(\frac{1 - DM_w}{100} \right) - NFG \times 431.5 \times \left(\frac{1 - DM_f}{100} \right)}{1000} \right)$$

Where, NFG is the number of functional glands at parturition (NFG = LS_s + 1 (with a maximum of 15)), ADG is the average daily gain of the litter and DM is the percentage of dry tissue (w at weaning and f at farrowing). Components of SW_w were, in turn, calculated as:

$$NFG = LS_s + 1 \text{ (with a maximum of 15)}$$

$$DM(\%) = 31.805 - 0.6027 \times DL + 0.011 \times DL^2 \text{ where, DL is the day of lactation.}$$

$$\text{Sow metabolic weight: } SMW = \left(\frac{SW_f + SW_w}{2} \right)^{0.75} \text{ (Noblet et al., 1990)}$$

$$\text{Litter metabolic weight (kg): } LMW = \left(\frac{LW_E + LW_w}{2} \right)^{0.75}$$

Statistical Analysis

Component traits of feed efficiency (i.e. dLFI, dSWB, dBFB and dLWG) were jointly analysed in a four-trait animal model defined as follows:

$$\begin{aligned} \mathbf{dLFI} &= \mathbf{Xb}_{dLFI} + \beta_{1,1} \mathbf{SW}_f + \beta_{1,2} \mathbf{BF}_f + \beta_{1,3} \mathbf{LW}_s + \mathbf{Za}_{dLFI} + \mathbf{Sp}_{dLFI} + \mathbf{e}_{dLFI} \\ \mathbf{dSWB} &= \mathbf{Xb}_{dSWB} + \beta_{2,1} \mathbf{SW}_f + \beta_{2,3} \mathbf{LW}_s + \mathbf{Za}_{dSWB} + \mathbf{Sp}_{dSWB} + \mathbf{e}_{dSWB} \\ \mathbf{dBFB} &= \mathbf{Xb}_{dBFB} + \beta_{3,1} \mathbf{SW}_f + \beta_{3,2} \mathbf{BF}_f + \beta_{3,3} \mathbf{LW}_s + \mathbf{Za}_{dBFB} + \mathbf{Sp}_{dBFB} + \mathbf{e}_{dBFB} \\ \mathbf{dLWG} &= \mathbf{Xb}_{dLWG} + \beta_{4,1} \mathbf{SW}_f + \beta_{4,3} \mathbf{LW}_s + \mathbf{Za}_{dLWG} + \mathbf{Sp}_{dLWG} + \mathbf{e}_{dLWG} \end{aligned}$$

Where, **dLFI**, **dSWB**, **dBFB**, **dLWG** denotes the vectors of phenotypic records for dLFI, dSWB, dBFG and dLWG, respectively. The systematic effects of batch and parity order were included in the vectors: **b_{dLFI}** for dLFI, **b_{dSWB}** for dSWB, **b_{dBFG}** for dBFG and **b_{dLWG}** for dLWG. Batch effect had 25 levels, with 6 to 45 records each (average equal to 34). Parity order had 6 levels (1, 2, 3, 4, 5, >5 parities) with 116 to 245 records each (average equal to 190). $\beta_{1,1}$, $\beta_{1,2}$ and $\beta_{1,3}$ are partial coefficients of regression of dLFI on SW_f, BF_f and LW_s, respectively. **SW_f**, **BF_f** and **LW_s** are vectors of standardized covariates of SW_f, BF_f and LW_s, respectively. Those pre-farrow traits can have an impact on the corresponding lactation trait. $\beta_{2,1}$ and $\beta_{2,3}$ are partial coefficients of regression of dSWB on SW_f and LW_s, respectively. $\beta_{3,1}$, $\beta_{3,2}$ and $\beta_{3,3}$ are partial coefficients of regression of dBFB on SW_f and LW_s, respectively. $\beta_{4,1}$ and $\beta_{4,3}$ are partial coefficients of regression of dLWG on SW_f and LW_s, respectively.

regression of dBFG on SW_f , BF_f and LW_s , respectively. $B_{4,1}$ and $\beta_{4,3}$ are partial coefficients of regression of dLWG on SW_f and LW_s , respectively. a_{dLFI} , a_{dSWB} , a_{dBFG} and a_{dLWG} are vectors of additive genetic effects for dLFI, dSWB, dBFG and dLWG, respectively. Similarly, p_{dLFI} , p_{dSWB} , p_{dBFG} , p_{dLWG} , and e_{dLFI} , e_{dSWB} , e_{dBFG} , e_{dLWG} are the vectors of permanent effects and residuals for the four traits. X , Z and S are design matrices for systematic, additive genetic and permanent effects, respectively.

Marginal posterior distributions of variance components and all other unknowns were estimated via Gibbs sampling using program gibbs2f90 (Misztal et al., 2002). Prior distributions for all random effects were multivariate normal distributions with a mean of zero and variances:

$$\text{var} \begin{pmatrix} e_{dLFI} \\ e_{dSWB} \\ e_{dBFB} \\ e_{dLWG} \end{pmatrix} = I \otimes R_0, \text{var} \begin{pmatrix} a_{dLFI} \\ a_{dSWB} \\ a_{dBFB} \\ a_{dLWG} \end{pmatrix} = A \otimes G_0 \text{ and } \text{var} \begin{pmatrix} p_{dLFI} \\ p_{dSWB} \\ p_{dBFB} \\ p_{dLWG} \end{pmatrix} = I \otimes P_0$$

being R_0 , G_0 and P_0 4x4 matrices of residual, additive genetic and permanent environmental (co)variances, respectively, and A is the additive genetic relationship matrix. To construct this matrix, the pedigree file comprised 1,659 individuals including up to 3 generations of ancestors.

Random effects e , a and p were considered independent of each other. Prior distributions for the covariance matrices R_0 , G_0 and P_0 were inverse Wishart distributions and priors for systematic effects of the model were assumed to be flat priors.

The analysis of sow residual feed intake (SRFI) was performed using the following model:

$$\begin{aligned} dLFI = Xb + \beta_1 SW_f + \beta_2 BF_f + \beta_3 LW_s + \beta_4 dSWB + \beta_5 dBFB + \beta_6 dLWG + \beta_7 SMW \\ + \beta_8 LMW + \beta_{1b} X_{SW_f} + \beta_{2b} X_{BF_f} + \beta_{3b} X_{LW_s} + \beta_{4b} X_{dSWB} + \beta_{5b} X_{dBFB} \\ + \beta_{6b} X_{dLWG} + \beta_{7b} X_{SMW} + \beta_{8b} X_{LMW} + Za + Sp + e \end{aligned}$$

Where, $dLFI$ is the vector of phenotypic records of dLFI; b is the vector of systematic effects of batch and parity order. Defined as before, β_1 , β_2 , β_3 , β_4 , β_5 , β_6 , β_7 and β_8 are the partial regression coefficients of dLFI on standardized covariates of SW_f , BF_f , LW_s , $dSWB$, $dBFB$, $dLWG$, SMW and LMW respectively. β_{1b} , β_{2b} , β_{3b} , β_{4b} , β_{5b} , β_{6b} , β_{7b} and β_{8b} are vectors of random partial regression coefficients nested to batch of dLFI on SW_f , BF_f , LW_s , $dSWB$, $dBFB$, $dLWG$, SMW and LMW respectively and X_{SW_f} , X_{BF_f} , X_{LW_s} , X_{dSWB} , X_{dBFB} , X_{dLWG} , X_{SMW} , and X_{LMW}

are matrices nesting the respective covariates to the different batches. **X**, **Z** and **S** are design matrices for systematic, additive genetic and permanent effects, respectively. **a**, **p** and **e** are the vectors of additive genetic effects, permanent environmental effects and random residuals of dSRFI as the observed trait (dLFI) was corrected for a number of systematic effects, representing the needs that each sow might have during its lactation.

In this model the prior distribution for the random regression coefficients, permanent, additive genetic and residual effects were independent centred normal distributions with variances:

$$\text{var}(\beta_{ib}) = \mathbf{I} * \sigma_{\beta_{ib}}^2, \text{ for } i=1, 2 \dots 8; \text{var}(e) = \mathbf{I} * \sigma_{e,dSRFI}^2; \text{var}(a) = \mathbf{A} * \sigma_{a,dSRFI}^2 \text{ and } \text{var}(p) = \mathbf{I} * \sigma_{p,dSRFI}^2$$

Prior assumptions of variance components and systematic effects were flat priors.

The gibbs sampler was run for 500,000 rounds with a burn-in of 200,000 rounds. For the posterior analysis, one of each 100 samples was saved. Thus, a total of 3,000 samples from the joint posterior distribution of all location and (co)variance parameters from both models (model 1 and 2) were saved for postgibbs analysis. The “boa” R package (Smith, 2007) was used for convergence diagnostics and to obtain summary statistics of marginal posterior distributions of model parameters.

d. RESULTS

Descriptive statistics

Descriptive statistics of the traits analysed in this study are given in table 1. Sow weighed around 200 Kg at farrowing and had 19 mm of backfat. They consumed 153 kg during lactation (27 days) and lost 2.7 mm of backfat thickness (14% of the initial amount) whereas they gain 1 kg of body weight (0.04 Kg/d) on average, being this amount highly variable (CV=18) with an interquartile range of [-8.6, 12.6] (4.3% to 6.2% of the initial value). Litter weight at farrowing was around 16 Kg on average, growing at a rate of 2.09 Kg/d (0.19 Kg/d per piglet being litter size at the start of lactation 11 piglets).

Table 1: Summary statistics. Phenotypic means, standard deviation (SD) and interquartile range.

Trait	Abbreviation	Units	Mean	SD	Interquartile range
Sow weight at farrowing	SW _f	kg	201.8	22.42	185.8 - 217.1
Backfat at farrowing	BF _f	mm	19.18	3.78	17 - 21
Litter weight at start of lactation	LW _s	kg	15.84	2.84	13.7 - 17.8
Litter size at start of lactation	LS _s	units	10.93	1.02	10 - 12
Litter size at weaning	LS _w	units	9.38	1.35	9 - 10
Daily lactation feed intake	dLFI	kg/day	5.68	0.54	5.32 - 6.03
Daily sow weight balance	dSWB	kg/day	0.04	0.72	-0.41 - 0.51
Daily Back fat balance	dBFB	mm/day	-0.10	0.06	-0.13 - -0.06
Daily litter weight gain	dLWG	kg/day	2.09	0.30	1.8 – 2.3

Impact of pre-farrow traits on feed efficiency during lactation and its component traits

Partial regression coefficients of pre-farrow traits on dLFI, dSWB, dBFB and dLWG are shown in table 2. Body condition at farrowing (BF_f and SW_f) had a significant effect on feed intake during lactation, being BF_f the covariate with the highest effect. Thus, a greater content in BF_f or SW_f resulted in a smaller feed intake (-14.55 g/d per mm of BF_f and -1.8 g/d per Kg of SW_f, respectively. Note that in table 2 regression coefficients are referred to units of sd of the covariates, so the number reported in the text are transformations from those in Table 2, using the variation indicated in table 1. For example, regression coefficient of dLFI on BF_f is -55g/d/unit sd BF_f (table 2). Taking into account that BF_f have an sd of 3.78 (table 1), results in -55g/d/sd * 3.78 mm/sd = -14.55g/d per mm BF_f). Litter weight at the beginning of lactation had the smallest effect. Sows eat 9.5 g/d more per 1 Kg of increment in LW_s.

Sow weight at farrowing also had a significant effect on mobilization of body reserves (i.e. dSWB and dBFB). Heavier sows at farrowing tend to have a greater mobilization of body reserves (i.e. to lose more body weight) than lighter sows (i.e. sow weight increased 13.8 g/d during lactation per Kg of SW_f). In the same way, fatter sows at farrowing tended to mobilize more backfat deposits than leaner sows (they reduce 0.009 mm/d of backfat thickness per 1 mm more in BF_f). Litter weight at the beginning of lactation affects litter growth due mainly to a scale effect but also to body reserves mobilization decreasing the balance of sow weight and

backfat thickness. An increase in 1 Kg in litter weight at the beginning of lactation means a loose of 61.6 g/d in sow weight and 0.004 mm/d of backfat thickness.

Table 2. Regression coefficients (Standard error) of daily lactation feed intake (dLFI), daily sow weight balance (dSWB), daily backfat balance (dBFB) and daily litter weight gain (dLWG) on standardized pre-farrow traits.

Covariate ¹	dLFI	dSWB	dBFB	dLWG
SW_f	- 0.040 (0.023)	- 0.310 (0.023)	0.010 (0.003)	0.006 (0.013)
BF_f	- 0.055 (0.018)	0	- 0.035 (0.002)	0
LW_s	0.027 (0.015)	- 0.175 (0.020)	- 0.012 (0.002)	0.054 (0.010)

¹SW_f = Sow weight at farrowing; BF_f = Back fat at farrowing; LW_s = Litter weight at start of lactation.

Computation of SRFI

Coefficients of the multiple regression used to estimate SRFI are given in table 3. Covariates were standardized and we obtain an estimate of the mean and the variance of the random regression coefficients for each covariate nested to the batch effect. The most variable coefficient was the one corresponding to LMW and the lowest were those related with sow weight (i.e. SW_f and SMW). Because of the high correlation between the variables that define the sow requirements for growth, maintenance and production, it is hard to interpret the value of those regression coefficients.

Table 3: Posterior mean (posterior s.d.) of estimates of regression coefficients on sd units of the covariate (βn) and variance of regression coefficients nested to batch ($\sigma_{\beta nB}^2$) for daily lactation feed intake (dLFI).

Covariate ¹	βn	$\sigma_{\beta nB}^2$
SW_f	- 1.134 (0.379)	0.001 (0.001)
BF_f	- 0.043 (0.022)	0.002 (0.002)
LW_s	- 0.149 (0.032)	0.002 (0.002)
dSWB	0.186 (0.132)	0.008 (0.005)
dBFB	- 0.006 (0.020)	0.003 (0.002)
dLWG	- 0.153 (0.040)	0.003 (0.003)
SMW	1.146 (0.366)	0.001 (0.001)
LMW	0.378 (0.050)	0.057 (0.004)

¹ SW_f = Sow weight at farrowing; BF_f = Back fat at farrowing; LW_s = Litter weight at start of lactation; dSWB = daily sow weight balance; dBFB = daily Backfat balance; dLWG = daily litter weight gain; SMW = Sow metabolic weight; LMW = Litter metabolic weight.

Heritability and proportion of the phenotypic variance due permanent effects

Heritability was low to moderate for feed efficiency during lactation (posterior mean [posterior sd] = 0.14 [0.06]) and its components. The highest values were found for daily changes in body weight of the sow (0.28[0.08]) and the litter (0.22 [0.05]). Both, dLFI and dBFB had a low heritability. The proportion of the phenotypic variance due permanent effects was moderate for energy inputs (i.e. dLFI, dSWB and dBFB) and low for dLWG and SRFI.

Table 4: Posterior means (posterior s.d.) of variance components and ratios of phenotypic variance.

Parameter ²	dLFI ¹	dSWB ¹	dBFB ¹	dLWG ¹	SRFI ¹
σ_a^2	0.014 (0.005)	0.059 (0.018)	0.0001 (0.0003)	0.015 (0.004)	0.016 (0.007)
σ_p^2	0.027 (0.006)	0.049 (0.016)	0.0001 (0.0003)	0.009 (0.003)	0.012 (0.007)
σ_e^2	0.119 (0.009)	0.102 (0.010)	0.002 (0.0001)	0.045 (0.003)	0.087 (0.007)
h²	0.088 (0.029)	0.279 (0.076)	0.133 (0.042)	0.216 (0.052)	0.141 (0.061)
p²	0.169 (0.035)	0.234 (0.077)	0.155 (0.031)	0.131 (0.049)	0.104 (0.064)

¹ dLFI = daily lactation feed intake; dSWB = daily sow weight balance; dBFB = daily Back fat balance; dLWG = daily litter weight gain; SRFI = Sow residual feed intake.

² σ_a^2 = Additive variance; σ_p^2 = Permanent variance; σ_e^2 = Residual variance; h^2 = heritability; p^2 = permanent environmental variation relative to phenotypic variation.

Genetic and environmental correlations

Phenotypic and environmental correlations are show in table 5. All of them were low to moderate. Residual correlations had the same sign than phenotypic correlations.

Phenotypically (Table 5), dLFI was positively associated with daily balances of energy and nutrient reserves and litter weight gain. Therefore, the more a sow eats the more it increases its body weight, backfat reserves and its litter weight. An increase in dSWB was associated to an increase in dBFB (0.32 [0.04]) but to a decrease in LWG (-0.26 [0.04]). In the same way, an increase in backfat thickness corresponded to a decrease in litter weigh (-0.17 [0.04]). Phenotypic and environmental correlations between dLFI and dBFB were null.

Table 5: Posterior means (posterior s.d.) of phenotypic (r_{ph} , above the diagonal) and residual (r_e , below the diagonal) correlations.

$r_e \setminus r_{ph}$	dLFI	dSWB	dBFB	dLWG
dLFI ¹	1	0.289 (0.034)	0.056 (0.038)	0.171 (0.035)
dSWB ¹	0.187 (0.058)	1	0.324 (0.037)	-0.258 (0.037)
dBFB ¹	-0.019 (0.058)	0.311 (0.058)	1	-0.171 (0.037)
dLWG ¹	0.162 (0.052)	-0.235 (0.057)	-0.192 (0.053)	1

¹ dLFI = daily lactation feed intake. dSWB = daily sow weight balance; dBFB = daily Backfat balance; dLWG = daily litter weight gain

Genetic and permanent environment of the sow correlations between energy input and output related traits are shown in table 6. Daily lactation feed intake was highly correlated with dBFB. This correlation was negative for genetic effects (-0.75 [1.12]) and positive (0.94 [0.03]) for sow permanent environmental effects, resulting in the null phenotypic correlation mentioned before. Genetic correlation between dSWB and dLWG was negative and moderated (-0.44 [0.19]). Permanent environment correlation between dLFI and dSWB and between both energy and nutrients balances (i.e. dSWB and dBFB) were moderate and positives. All other genetic and permanent environment correlations were low and not statistically different from zero.

Table 6: Posterior means (posterior s.d.) of sow permanent environment (r_p , above the diagonal) and additive genetic (r_g , below the diagonal) correlations.

$r_g \setminus r_p$	dLFI	dSWB	dBFB	dLWG
dLFI¹	1	0.647 (0.134)	0.937 (0.028)	0.125 (0.222)
dSWB¹	0.306 (0.197)	1	0.545 (0.148)	- 0.088 (0.299)
dBFB¹	- 0.745 (0.124)	0.192 (0.206)	1	- 0.175 (0.212)
dLWG¹	0.255 (0.199)	- 0.441 (0.192)	- 0.082 (0.197)	1

¹ dLFI = daily lactation feed intake; dSWB = daily sow weight balance; dBFB = daily Backfat balance; dLWG = daily litter weight gain

e. DISCUSSION

Traits involved in feed efficiency can be divided into 2 groups: energy input and energy output related traits. Energy sources for a lactating sow are feed intake and body reserves mobilization during lactation (i.e. sow bodyweight and backfat loss). Available energy is used for growth (sow bodyweight and backfat gain) and maintenance of the sow and for milk production, quantified by piglet growth and maintenance. Therefore, dSWB and dBFB traits are variables that quantify the balance of body reserves during lactation, which is negative whenever sow losses weight and/or fat, and positive otherwise. Other traits involved in the definition of lactation feed efficiency are pre-farrow traits which are those measured before farrowing (i.e. SWf, BFF and LWS) that may have an impact on sow lactation performance and are included as a covariates in the analysis of all other traits.

In this study, all those components of feed efficiency during lactation were analysed to gather relevant information for the design of a breeding program to improve this trait. Data come from a Duroc population selected for prolificacy and backfat thickness at the end of the fattening period. Because of selection for prolificacy sow are required to have an increased milk production, and this performance is expected to be repeated through consecutive parities. Litter size at the start of lactation was around 11 piglets in this population. In order to meet all the energy and nutrient requirements during this period sows ate 5.7 Kg/d of food (2.8 % of their weight at farrowing), mobilize 2.7 mm of backfat, which means a 14% of the initial amount of this tissue, and a negligible part of other body tissues (i.e. sow weight loss was very small). Compared with other populations of pigs, sows in our population eat more and mobilize less energy and nutrient reserves. For example, in the two lines divergently selected for RFI in the growing pigs Gilbert et al. (2012) observed that on average, during lactation (28 d), sows eat daily 1.8 % of its initial weight, and lost 20 % of their initial backfat

reserves and 13% of their initial body weight to produce milk for 11.6 piglets. Similar figures are found by Thekkoot et al. (2016) and Bergsma et al. (2008). Therefore, increasing levels of feed intake during lactation are associated with reduced mobilization of body reserves, as it was found by Dourmad (1991).

The potential for increasing levels of sow feed efficiency during lactation through direct selection has previously been reported in a limited number of studies and populations (Bergsma et al., 2008; Gilbert et al., 2012; Thekkoot et al., 2016; Young et al., 2016). In agreement with those studies, results show that this trait is heritable. In our study, feed efficiency during lactation was measured as SRFI which had a low to moderate value of heritability (posterior mean = 0.14 [posterior sd = 0.06]). Sow residual feed intake during lactation was studied by Gilbert et al. (2012), Young et al. (2016) and Thekkoot et al. (2016). Heritability reported by Gilbert et al. (2012) for this trait was the same as the one found by us (0.14 ± 0.06) despite their multiple regression models was not exactly the same. However, Thekkoot et al. (2016) obtained higher values in a Yorkshire and in a Landrace population (0.26 ± 0.05 and 0.30 ± 0.06 , respectively) as well as Young et al. (2016) (0.32 ± 0.05) in two lines divergently selected for RFI coming from a common Yorkshire population. Bergsma et al. (2008), Young et al. (2016) and Thekkoot et al. (2016), reported estimates of heritability for other measures of feed efficiency during lactation such as: lactation efficiency (Bergsma et al., 2008), defined as the ratio of energy output (measured from piglet growth) to energy input (energy from feed and body tissue mobilization above maintenance requirements of the sow); ii) energy balance (Young et al., 2016), defined as the difference between energy retained by the sow at weaning and at farrowing. Heritability estimates of lactation efficiency were in general low ranging from 0.05 to 0.12 (Bergsma et al., 2008; Thekkoot et al., 2016; Young et al., 2016) whereas energy balance showed low to moderated values of this parameter ranging from 0.12 to 0.36 (Thekkoot et al., 2016; Young et al., 2016). However, lactation energy balance cannot be considered as a feed efficiency trait by itself when it does not directly account for the productive effort of the sow, as it is the case of energy balance obtained by Young et al. (2016).

Regarding feed efficiency components, our heritability estimate for dLFI was low (0.09 [0.03]). Gilbert et al. (2012) found higher values of heritability (0.26 ± 0.07) for this trait in two lines divergently selected for RFI obtained from a unique Large White population. Also, greater heritability estimates (from 0.23 to 0.30) were found for sow feed intake during the whole lactation period by Bergsma et al. (2008), Young et al. (2016) and Thekkoot et al. (2016) in Yorkshire and Landrace pig populations or crossbred sows. The low value found in our study

compared with previously reported values is probably due to the inaccuracy of our measurement conditioned by the way feed was supplied to the sows and data were recorded. In those previous studies a computerized feeding systems was used for feeding and for recording data whereas in our study sows were fed manually on the basis of previous day consumption (i.e. quasi ad libitum) and data were not recorded daily but once or twice per week. In our study, feed intake data were predicted from a nonlinear model fitted to recorded data after removing outliers. Another important difference is that our heritability estimate of SRFI is slightly higher than of dLFI, while in the aforementioned studies the former estimate is clearly lower than the second. Sow residual feed intake can be considered to be as dLFI conditioned on traits defining energy and nutrient needs of the sow. Thus, the variance sources of this conditional trait will depend on the covariance structures between dLFI and the conditioning traits, which in our case were relatively different to those previously reported for other lines and studies.

Feed intake and mobilization of body reserves are important traits to consider for the improvement of sows lactation performance (Eissen et al., 2000; Lundgren et al. 2014; Grandinson et al. 2005). Phenotypically, increasing levels of feed intake during lactation are associated with significantly higher litter weaning weights in agreement with results found by Schinckel et al. Schinckel et al. (2010) and Bergsma et al. (2008). On the other hand, dLFI was positively correlated with dSWB, which means that a high level of dLFI is associated with a positive balance of body tissue reserves (i.e. reduced body weight loss) in agreement with Bergsma et al. (2008) and Lundgren et al.(2014) and Thekkoot et al. (2016). However, in our experiment no significant phenotypic correlation was found between dLFI and dBFB unlike Bergsma et al. (2008) who also found a positive relationship between these two traits (negative relationship between lactation feed intake and back fat losses). The lower backfat losses of sows in our experiment and the inaccuracy of our measurement of dLFI could explain this result. At the genetic level, dLFI was highly and negatively correlated with dBFB (- 0.75) and not correlated with dSWB. This could be explained considering that genes that affect both traits are those involved in mechanisms related with energy gathering for biological processes such as milk production. This result is opposite to results found by Bergsma et al. (2008) and Thekkoot et al. (2016) who found a negative correlation between lactation feed intake and weight and backfat losses. Lundgren et al. (2014) also found that genetic correlations between feed intake in one day of lactation and body condition at weaning (measured by the farmers with a visual nine levels scale) was 0.52, indicating that sows with a higher feed intake were able to maintain a better body condition during lactation. Genetic correlation between dLFI

and LWG was null in our experiment in agreement with Thekoot et al. (2016) but unlike Bergsma et al. (2008) who obtain a low to moderate and positive (0.37) genetic relationship between these two traits.

Traits related with body tissue mobilization seems to be heritable and therefore genetic selection for these traits could be successful especially for dSWB. We found a moderate heritability for dSWB (0.28 [0.08]) and a low heritability for dBFB (0.13 [0.04]). Estimates for dBFB are in agreement with those obtained by Grandinson et al. (2005) and Gilbert et al., 2012 (0.10 and 0.14, respectively) but not with Bergsma et al. (2008) who obtained a null heritability for backfat loss. The low heritability estimates for this trait could be explained by the lack of accuracy in the measurement of the backfat thickness, which is particularly problematic in furry animals, as it is our Duroc population. To overcame this issue sows were shaved in the area where backfat thickness was recorded; nevertheless, the measurement error backfat thickness could be around 1-1.5 mm, which is around 40-60% the average total backfat thickness balance during the whole lactation (from Table 1: 0.1 (mm/day)*27 d =2.7 mm/lactation) . Heritability estimated for dSWB was in agreement with those obtained by Bergsma et al. (2008) and Grandinson et al. (2005). Different values were found by Young et al. (2016) and Gilbert et al. (2012) in their divergently selected lines for RFI of growing pigs: the first one had a lower value (0.13) and the second a higher one (0.39).

Daily sow weight balance and dBFB were phenotypically but not genetically correlated. The precision of our estimates of genetic correlation was low because of the limited amount of records and high variability in dSWB. Bergsma et al. (2008) found strong genetic correlations between sow weight loss and protein loss (0.99) and between sow weight loss and fat loss (0.86), whereas Thekkoot et al. (2016) found a lower but also positive genetic correlation in a Yorkshire population and a null correlation in a Landrace population. Body reserves balances were both phenotypically correlated with dLWG being those correlations low (-0.26 and -0.17 for correlations between dLWG with dSWB and dBFB, respectively). This means that increasing levels of body reserves mobilization led to increasing levels of litter growth. At the genetic level, only dSWB was negatively and moderately correlated with LWG. Bergsma et al. (2008) also found a positive phenotypic correlation of LWG with body weight, backfat and protein losses (negative correlation with balances) but no significant correlations between any of those pairs of traits. Thekoot et al. (2016) obtained moderated positive and significant correlations between LWG and body weight and backfat losses in a Landrace population and null and moderate and positive correlations between LWG and body weight loose and between LWG and backfat losses, respectively in a Yorkshire population. Therefore, the

genetic association between dLWG and backfat mobilizations clearly depends on the genetic origin of the population.

Finally, heritability for daily litter weight gain was moderate (0.22) as the one reported by Young et al. (2016) for their high residual feed intake group, and very similar to the heritabilities estimated in other studies: 0.16 (Grandinson et al., 2005), 0.18 (Bergsma et al., 2008).

f. CONCLUSIONS

This study provides estimates of genetic parameters of traits involved in feed efficiency of the sow during lactation as well as a measurement of this global trait in a Duroc population of pigs with a genetic origin completely different to those previously studied. Those parameters could be used to design a breeding program in this population. In general, heritabilities were low to moderate for all traits; nevertheless, their magnitude could be high enough to guarantee a positive response to selection to improve feed efficiency during lactation. Milk production, quantified by litter weight gain, was found to be genetically uncorrelated with feed intake during lactation but moderately correlated with sow weight mobilization. Unlike results found in other pig breeds like Yorkshire, Large White or Landrace, a negative genetic association was found between feed intake and backfat mobilization of the sow during lactation. Further research using structural equation models to assess the causal relationship between energy input and output traits during lactation are required to better understand the energy metabolism mechanisms in lactating sows.

6. REFERENCIAS BIBLIOGRAFICAS

- Anil, S. S., L. Anil, and J. Deen. 2006. Association of inadequate feed intake during lactation with removal of sows from the breeding herd. JSHAP 14: 296-301.
- Bergsma, R., and S. Hermesch. 2012. Exploring breeding opportunities for reduced thermal sensitivity of feed intake in the lactating sow1. Journal of animal science 90: 85-98.
- Bergsma, R., E. Kanis, M. W. Verstegen, and E. F. Knol. 2008. Genetic parameters and predicted selection results for maternal traits related to lactation efficiency in sows. Journal of animal science 86: 1067-1080.
- Bergsma, R., E. Kanis, M. W. A. Verstegen, C. M. C. van der Peet-Schwering, and E. F. Knol. 2009. Lactation efficiency as a result of body composition dynamics and feed intake in sows. Livestock Science 125: 208-222.
- Beyer, M., W. Jentsch, L. Hoffmann, R. Schiemann, and M. Beyer Et. 1993. UNTERSUCHUNGEN ZUM ENERGIE-UND STICKSTOFF UMSATZ VON GRAVIDEN UND LAKTIERENDEN SAUEN SOWIE VON SAUGFERKELN 2. Mitteilung -Chemische Zusammensetzung und Energiegehalt der Tierkörper von graviden, güsten und laktierenden Sauen STUDIES ON

- ENERGY AND NITROGEN METABOLISM OF PREGNANT AND LACTATING SOWS AND SUCKLING PIGLETS 2. Chemical composition and energy content of the bodies of pregnant, non-pregnant and lactating sows)2.
- Bunter, K. L., Hermesch, S., Luxford, B.G. 2006. Sow feed intake and lifetime reproductive performance. AGBU Pig Genet. Wkshp. .
- Cameron, N. D., J. C. Kerr, G. B. Garth, R. Fenty, and A. Peacock. 2002. Genetic and nutritional effects on lactational performance of gilts selected for components of efficient lean growth. Animal Science 74: 25-38.
- Clowes, E. J., F. X. Aherne, G. R. Foxcroft, and V. E. Baracos. 2003. Selective protein loss in lactating sows is associated with reduced litter growth and ovarian function. Journal of animal science 81: 753-764.
- De Bettio, S., A. Maiorka, L. N. E. Barrilli, R. Bergsma, and B. A. N. Silva. 2016. Impact of feed restriction on the performance of highly prolific lactating sows and its effect on the subsequent lactation. Animal : an international journal of animal bioscience 10: 396-402.
- Dourmad, J. Y. 1991. Effect of feeding level in the gilt during pregnancy on voluntary feed intake during lactation and changes in body composition during gestation and lactation. Livestock Production Science 27: 309-319.
- Dourmad, J. Y., M. Etienne, A. Prunier, and J. Noblet. 1994. The effect of energy and protein intake of sows on their longevity: a review. Livestock Production Science 40: 87-97.
- Eissen, J. J., E. J. Apeldoorn, E. Kanis, M. W. A. Verstegen, and K. H. de Greef. 2003. The importance of a high feed intake during lactation of primiparous sows nursing large litters1. Journal of animal science 81: 594-603.
- Eissen, J. J., E. Kanis, and B. Kemp. 2000. Sow factors affecting voluntary feed intake during lactation. Livestock Production Science 64: 147-165.
- Everts, H., M. C. Blok, B. Kemp, C. M. C. v. d. Peet-Schowering, and C. H. M. Smits. 1995. Normen voor lacterende zeugen, CVB, Lelystad.
- Gilbert, H. et al. 2012. Correlated responses in sow appetite, residual feed intake, body composition, and reproduction after divergent selection for residual feed intake in the growing pig. Journal of animal science 90: 1097-1108.
- Grandinson, K., L. Rydhmer, E. Strandberg, and F. X. Solanes. 2005. Genetic analysis of body condition in the sow during lactation, and its relation to piglet survival and growth. Animal Science 80: 33-40.
- Hermesch, S. 2006. First analysis of factors influencing feed intake of sows during lactation. AGBU Pig Genet. Workshop. : 44-49.
- Hermesch, S. 2007 Genetic analysis of feed intake in lactating sows. Proc. Assoc. Advmt. Anim. Breed. Genet. 17: 61-64.
- Hermesch, S., R. Jones, and K. Bunter. 2008. Feed intake of sows during lactation has genetic relationships with growth and lifetime performance of sows, AGBU Pig Genetics Workshop –October 2008.
- Hyun, Y., M. Ellis, G. Riskowski, and R. W. Johnson. 1998. Growth performance of pigs subjected to multiple concurrent environmental stressors. Journal of animal science 76: 721-727.
- Kanis, E. 1990. Effect of food intake capacity on genotype by feeding regimen interactions in growing pigs. Animal Science 50: 343-351.
- Kennedy, B., J. Van der Werf, and T. Meuwissen. 1993. Genetic and statistical properties of residual feed intake. Journal of animal science 71.
- Kim, S. W., and R. A. Easter. 2001. Nutrient mobilization from body tissues as influenced by litter size in lactating sows1. Journal of animal science 79: 2179-2186.

- Kim, S. W., I. Osaka, W. L. Hurley, and R. A. Easter. 1999. Mammary gland growth as influenced by litter size in lactating sows: impact on lysine requirement1. *Journal of animal science* 77: 3316-3321.
- Koketsu, Y., G. D. Dial, J. E. Pettigrew, W. E. Marsh, and V. L. King. 1996. Characterization of feed intake patterns during lactation in commercial swine herds. *Journal of animal science* 74: 1202-1210.
- Kruse, S., I. Traulsen, and J. Krieter. 2011. Analysis of water, feed intake and performance of lactating sows. *Livestock Science* 135: 177-183.
- Lundgren, H. et al. 2014. Genetic parameters for feed intake, litter weight, body condition and rebreeding success in primiparous Norwegian Landrace sows. *Animal : an international journal of animal bioscience* 8: 175-183.
- Misztal, I. et al. 2002. BLUPF90 and related programs (BGF90). p 1-2. Institut National de la Recherche Agronomique (INRA), Montpellier.
- Mullan, B. P., W. H. Close, and D. J. A. Cole. 1993. Predicting nutrient responses of the lactating sow. In: Cole, D.J.A., Haresign, W., Garnsworthy, P.C. (Eds.), *Recent Developments in Pig Nutrition*, vol. 2. Nottingham University Press, Nottingham UK: 332–346.
- Noblet, J., J. Y. Dourmad, and M. Etienne. 1990. Energy utilization in pregnant and lactating sows: modeling of energy requirements. *Journal of animal science* 68: 562-572.
- Noblet, J., and M. Etienne. 1987. Metabolic utilization of energy and maintenance requirements in lactating sows. *Journal of animal science* 64: 774-781.
- Rauw, W. M., P. W. Knap, M. W. Verstegen, and P. Luiting. 2002. Food resource allocation patterns in lactating females in a long-term selection experiment for litter size in mice. *Genetics, selection, evolution : GSE* 34: 83-104.
- Revell, D. K., I. H. Williams, B. P. Mullan, J. L. Ranford, and R. J. Smits. 1998. Body composition at farrowing and nutrition during lactation affect the performance of primiparous sows: II. Milk composition, milk yield, and pig growth1. *Journal of animal science* 76: 1738-1743.
- Sánchez, J. P., M. Ragab, R. Quintanilla, M. F. Rothschild, and M. Piles. 2017. Genetic parameters and expected responses to selection for components of feed efficiency in a Duroc pig line. *Genetics Selection Evolution* 49: 86.
- Schenkel, A. C., M. L. Bernardi, F. P. Bortolozzo, and I. Wentz. 2010. Body reserve mobilization during lactation in first parity sows and its effect on second litter size. *Livestock Science* 132: 165-172.
- Schinckel, A. P., C. R. Schwab, V. M. Duttlinger, and M. E. Einstein. 2010. Analyses of Feed and Energy Intakes During Lactation for Three Breeds of Sows. *The Professional Animal Scientist* 26: 35-50.
- Silalahi, P. et al. 2016. Estimation of the effects of selection on French Large White reproductive performance using frozen semen. *Journal of animal science* 94: 3655-3662.
- Smith, B. J. 2007. *boa: An R Package for MCMC output convergence assessment and posterior inference*. *J Stat Softw* 21.
- Thekkoot, D. M., R. A. Kemp, M. F. Rothschild, G. S. Plastow, and J. C. Dekkers. 2016. Estimation of genetic parameters for traits associated with reproduction, lactation, and efficiency in sows. *Journal of animal science* 94: 4516-4529.
- Verstegen, M. W., J. Mesu, G. J. van Kempen, and C. Geerse. 1985. Energy balances of lactating sows in relation to feeding level and stage of lactation. *Journal of animal science* 60: 731-740.
- Weldon, W. C., Lewis, A.J., Louis, G.F., Kovar, J.L., Giesemann, M.A., Miller, P.S. 1994. Postpartum hypophagia in primiparous sows: I. Effects of gestation feeding level on feed intake, feeding behavior, and plasma metabolite concentrations during lactation. *J. Anim. Sci.* 72: 387-394.

- Whittemore, C. T., and C. A. Morgan. 1990. Model components for the determination of energy and protein requirements for breeding sows: a review. *Livestock Production Science* 26: 1-37.
- Yang, H., Eastham, P.R., Phillips, P., Whittemore, C.T. 1989. Reproductive performance, body weight and body condition of breeding sows with differing body fatness at parturition, differing nutrition during lactation, and differing litter size *Anim. Prod.* 48: 181–201.
- Yoder, C. L. et al. 2013. Estimation of deviations from predicted lactation feed intake and the effect on reproductive performance. *Livestock Science* 154: 184-192.
- Young, J. M., R. Bergsma, E. F. Knol, J. F. Patience, and J. C. Dekkers. 2016. Effect of selection for residual feed intake during the grow/finish phase of production on sow reproductive performance and lactation efficiency. *Journal of animal science* 94: 4120-4132.