Universitat Autònoma de Barcelona

NUEVOS FENOTIPOS Y MODELOS PARA MEJORAR LA PREDICCIÓN DEL VALOR GENÉTICO PARA EFICIENCIA ALIMENTARIA EN ESQUEMAS DE SELECCIÓN PORCINA

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RESUMEN

El objetivo general de la tesis fue explorar distintos procedimientos directos e indirectos de evaluación genética de la eficiencia alimentaria que permitan reducir las inversiones necesarias en sistemas de registro del consumo individual con una mínima pérdida de la eficacia de la selección. Se realizaron cuatro estudios en los que se utilizó información fenotípica de una línea de selección de cerdos Duroc durante el periodo de engorde. Los caracteres analizados fueron medidas individuales del espesor de grasa dorsal, el peso vivo a distintas edades y el consumo de pienso, registrado mediante el uso de comederos electrónicos. A partir de éstos se calcularon otros, también a nivel individual, como la ganancia de peso diaria, el índice de conversión, el consumo de pienso residual, así como los correspondientes a caracteres de comportamiento alimentario (la velocidad de ingesta, el número e intervalo de tiempo entre visitas al comedero y el tiempo de ocupación de éste).

Mediante la utilización de modelos estadísticos mixtos, los trabajos evalúan la importancia de los siguientes aspectos que pudieran afectar a las evaluaciones genéticas de los candidatos a la selección: i) Qué papel pudieran jugar los caracteres de comportamiento alimentario y qué relevancia tienen los efectos de interacción social tanto para estos caracteres como para los caracteres productivos y de eficiencia alimentaria. ii) Qué información pueden aportar los registros de consumo de grupo en la predicción del consumo individual. iii) Qué grado de variación tiene del determinismo genético de los caracteres productivos y de eficiencia alimentaria con la edad.

Los resultados mostraron que las interacciones sociales son factores importantes de variación de los caracteres de comportamiento alimentario, los productivos y los de eficiencia. A pesar de esto, su consideración en los esquemas de mejora parece complicado. Mediante simulación se observó que, utilizando el modelo animal con interacciones sociales para generar los datos, la respuesta que se obtiene con

distintos índices de selección que combinen efectos directos y sociales no es claramente superior a la que se obtiene utilizando el modelo animal tradicional. Esto se debe a los altos errores de estimación de los parámetros genéticos que este tipo de modelos contiene que se traducen en pequeñas o nulas mejoras en la respuesta a la selección.

Con respecto al estudio realizado para evaluar la aportación de los datos del consumo de grupo en los programas de mejora, los resultados mostraron que independientemente de la distribución de datos individuales o de grupo, la calidad de predicción fue aproximadamente la misma y por tanto en la evaluación multivariante el papel de los registros de consumo medio de los corrales parece poco relevante para predecir el consumo individual.

Por otra parte, el grado de variación que muestra el determinismo genético de los caracteres estudiados con la edad es nulo. Es decir, dentro del intervalo de edad considerado (110 - 200 días) las estimas de heredabilidad de los caracteres estudiados fueron constantes, y las correlaciones genéticas dentro de caracteres entre los distintos días fueron cercanas a uno. Por lo tanto, no tiene sentido plantear, por ejemplo, la medición del espesor de tocino a una edad y el crecimiento o peso vivo a otra.

En general, se puede concluir que el único de los factores estudiados que pudiera tener una repercusión clara en la mejora de la eficiencia alimentaria del porcino es el de las interacciones sociales entre animales que comparten corral. No obstante, su implementación práctica parece complicada, ya que la cantidad de datos coetáneos necesarios para estimar de forma precisa los parámetros de los modelos que los incluyen es muy elevada.

SUMMARY

The general objective of the thesis was to explore different direct and indirect genetic evaluation procedures for feed efficiency that allow reducing the necessary investments in systems for recording individual consumption with a minimum loss of the effectiveness of selection. Four studies were conducted using phenotypic information from a selection line of Duroc pigs during the fattening period. The analyzed traits were individual measurements of backfat thickness, live weight at different ages and feed intake, recorded by using electronic feeders. From these, others were calculated, also at the individual level, such as daily weight gain, the feed conversion ratio, the residual feed intake, as well as those corresponding to feeding behavior traits (the feeding rate, the number and interval time between visits to the trough and the occupation time from this).

Through the use of mixed statistical models, the studies evaluate the importance of the following aspects that could affect the genetic evaluations of the candidates for selection: i) What role could the feeding behavior traits play and what relevance do the interaction effects have both for these traits and for the productive and feed efficiency traits. ii) What information can group feed intake records provide in predicting individual feed intake. iii) What degree of variation has the genetic determinism of productive and feed efficiency traits with age.

The results showed that social interactions are important factors of variation of the feeding behavior traits, the productive ones, and the efficiency ones. Despite this, its consideration in the breeding programs seems complicated. Through simulation, it was observed that, using the animal model with social interactions to generate the data, the response obtained with different selection indexes that combine direct and social effects is not clearly superior to that obtained using the traditional animal model. This is due to the high estimation errors of the genetic parameters that this type of model contains, which translate into little or no improvement in the response to selection.

Regarding the study carried out to evaluate the contribution of group feed intake data to breeding programs, the results showed that regardless of the distribution of individual or group data, the prediction quality was approximately the same and therefore in the multivariate evaluation the role of the average feed intake records of the pens seems of little relevance to predict individual feed intake.

On the other hand, the degree of variation shown by the genetic determinism of the studied traits with age is zero. That is, within the considered age interval (110-200 days) the heritability estimates of the studied traits were constant, and the genetic correlations within traits between the different days were close to one. Therefore, it does not make sense to consider, for example, the measurement of backfat thickness at one age and growth or live weight at another.

In general, it can be concluded that the only one of the studied factors that could have a clear impact on improving pig feed efficiency is the social interactions between animals that share a pen. However, its practical implementation seems complicated, since the amount of contemporary data required to accurately estimate the parameters of the models that include them is quite high.

RESUM

L'objectiu general de la tesi va ser explorar diferents procediments directes i indirectes d'avaluació genètica de l'eficiència alimentària que permetin reduir les inversions necessàries en sistemes de registre del consum individual amb una mínima pèrdua de l'eficàcia de la selecció. Per tal d’assolir aquest objectiu es van realitzar quatre estudis, per als quals es va utilitzar informació fenotípica d'una línia de selecció de porcs Duroc durant el període d'engreix. Els caràcters analitzats van ser mesures individuals del gruix de greix dorsal, el pes viu a diferents edats i el consum de pinso, registrat mitjançant l'ús de menjadores electròniques. A partir d'aquests caràcters se’n van calcular altres, també individuals, com el guany de pes diari, l'índex de conversió i el consum de pinso residual, així com els caràcters corresponents a la mesura del comportament alimentari (la velocitat d'ingesta, el nombre de visites a la menjadora i l’interval de temps entre aquestes visites, i el temps d'ocupació de la menjadora).

Mitjançant la utilització de models estadístics mixtos, els treballs avaluen la importància dels següents aspectes que podrien afectar les avaluacions genètiques dels candidats a la selecció: i) Quin paper podrien tenir els caràcters de comportament alimentari i quina és la rellevància dels efectes de la interacció social tant per a aquests caràcters com per als caràcters de producció i eficiència alimentària. ii) Quina informació poden aportar els registres de consum de grup a la predicció del consum individual. iii) Quin grau de variació té del determinisme genètic dels caràcters productius i d'eficiència alimentària amb l'edat.

Els resultats van mostrar que les interaccions socials són factors importants de variació dels caràcters de comportament alimentari, productius i d'eficiència. Malgrat això, implementar-les en els esquemes de millora genètica sembla complicada. Mitjançant una simulació es va observar que, utilitzant el model animal amb interaccions socials per generar les dades, la resposta que se n'obté amb diferents índexs de selecció que combinin efectes directes i socials no és clarament superior a la que s'obté utilitzant el model animal tradicional. Això es deu al nombre

elevat d’errors d'estimació dels paràmetres genètics que aquest tipus de models conté, que es tradueixen en petites o nul·les millores en la resposta a la selecció.

Pel que fa a l'estudi que es va fer per avaluar la importància de l'aportació de les dades de consum de grup en els programes de millora, els resultats van mostrar que, independentment de la distribució de dades individuals o de grup, la qualitat de predicció era aproximadament la mateixa; per tant, en l’avaluació multivariant, el paper dels registres de consum mitjà del grup per predir el consum individual sembla poc rellevant.

D'altra banda, el grau de variació que mostra el determinisme genètic dels caràcters estudiats amb l'edat és nul. És a dir, dins de l'interval d'edat considerat (110 - 200 dies), les estimacions de l’heretabilitat dels caràcters estudiats van ser constants i les correlacions genètiques dins de caràcters entre els diferents dies van ser properes a u. Per tant, no té sentit plantejar, per exemple, la mesura del gruix de greix a una edat i el creixement o pes viu a una altra.

En general, es pot concloure que l'únic dels factors estudiats que podria tenir una repercussió clara en la millora de l'eficiència alimentària del porcí és el de les interaccions socials entre animals que comparteixen corral. Tanmateix, la seva implementació pràctica sembla complicada, ja que la quantitat de dades d’animals coetanis necessàries per valorar de manera precisa els paràmetres dels models que els inclouen és molt elevada.

1. INTRODUCCIÓN GENERAL

La producción de carne de porcino es una actividad ganadera importante por ser uno de los productos de origen animal que mayor consumo presenta por parte de la población humana a nivel mundial (Ritchie y Roser, 2017; OECD, 2019). Fruto de esta intensa demanda la producción ha experimentado un continuo crecimiento en las últimas décadas. El desarrollo de nuevas tecnologías y herramientas empleadas para incrementar la rentabilidad y la eficiencia de la producción han propiciado este crecimiento. (Martínez *et al*., 2005; Gwyther *et al*., 2011; Afonso *et al*., 2020; Mote y Rothschild, 2020). En este sentido, gran parte del desarrollo se debe a la implementación de los programas de mejora, en los que actualmente se sigue trabajando con el propósito de desarrollar nuevas estrategias que permitan acelerar la respuesta y la explotación de esta en esquemas alternativos de cruzamiento. En los esquemas de selección, las evaluaciones genéticas se llevan a cabo sobre aquellos caracteres relacionados con las aptitudes productivas o reproductivas de los animales en diferentes etapas de su vida. En general, la consideración de unos u otros caracteres va asociada con el tipo de línea con la que se esté trabajando y el papel que esta jugará en el esquema de cruzamiento en el que éstas se encuadren.

Esta tesis se focaliza en el estudio de las evaluaciones genéticas para la mejora de los caracteres productivos relacionados con la eficiencia alimentaria, el consumo, el crecimiento y el espesor del tocino dorsal que son medidos durante el periodo de engorde. Estos caracteres son los que reciben la mayor proporción del peso en los índices de selección de líneas para producir machos finalizadores, que se aparean con hembras cruzadas seleccionadas por índices en los que el mayor peso lo reciben los caracteres reproductivos para finalmente obtener animales cuya canal se comercializa.

El coste del pienso consumido durante la fase de cebo supone la mayor partida de gastos de producción en los esquemas productivos de porcino (Bornett *et al*., 2003), de ahí que el crecimiento, y la eficiencia con que éste se produce, sean caracteres de gran importancia económica en estos esquemas (Merks *et al*., 2012). Cualquier consideración de la eficiencia en el uso de pienso durante el cebo debiera considerar el control del consumo, y en el contexto de los programas de selección, la situación óptima de registro del consumo sería aquella en la que éste se obtiene de forma individual en animales alojados en grupo. En este sentido, se puede indicar que la mayor parte de empresas y entidades implicadas en los programas de mejora de mayor dimensión e impacto de la especie porcina disponen de instalaciones equipadas con dispositivos para el control automático de consumo de animales alojados en corrales colectivos. Esto permite controlar el consumo y la eficiencia alimentaria en un buen número de los candidatos a la selección. No obstante, dado el alto coste que suponen estas infraestructuras, en esquemas de selección de menor dimensión o que se desarrollan para nichos de mercado más reducidos, la mejora de la eficiencia alimentaria se sostiene en procedimientos de selección indirectos en los que no se registra el consumo del pienso a nivel individual en los candidatos. Son precisamente estas situaciones las que suponen el nicho de aplicación de los desarrollos de la presente tesis: I) procedimientos de selección indirectos por eficiencia basados en otros caracteres productivos o incorporando información de comportamiento alimentario, II) estrategias de modelado que contemplen las interacciones sociales que se dan entre los animales criados dentro de un mismo corral, III) aprovechamiento de la información al respecto de eficiencia que se pueda extraer de los registros de consumo de grupo y IV) la consideración longitudinal del crecimiento, el consumo y la deposición de grasa para explorar los momentos óptimos de control con respecto a la maximización de la respuesta en eficiencia alimentaria.

El estudio se llevará a cabo con datos de peso vivo, espesor de tocino dorsal y consumo individual que se recolectaron en hasta 15 lotes de cerdos Duroc de una línea maternal de la empresa Batalle. Los animales se criaron en las instalaciones de la granja experimental del CAP-IRTA (Monells). En estas instalaciones se dispone de equipos para el control individual del consumo y, por tanto, se tienen medidas directas del consumo y de la eficiencia alimentaria. En algunos de los trabajos que se incluyen en la tesis se hace un uso directo de estos registros mientras que en otros se emplean para validar las consecuencias de procedimientos indirectos de selección. Para la contextualización del trabajo se ofrece, en primera instancia, una revisión bibliográfica que por un lado considera la situación actual de la porcicultura, focalizándose en regiones en las que esta producción ganadera está aún en desarrollo, como pudiera ser el caso de Colombia. Y por otro presenta las herramientas de modelado genético-estadístico habituales en esquemas de selección para eficiencia alimentaria, así como aquellas que específicamente se desarrollan en este trabajo.

1.1. Censos y producciones del porcino

La cría del porcino (*Sus scrofa domesticus*) para consumo humano es considerada una actividad tradicional ganadera que se inició con la domesticación del cerdo salvaje (*Sus scrofa*) hace unos 8,500 años en oriente próximo (Frantz *et al*., 2015), pero también se sabe que este proceso de domesticación se dio de forma paralela en China. A mediados del siglo XVIII el porcino asiático (*Sus indicus*) fue introducido en Inglaterra, donde se llevaron a cabo los primeros cruzamientos entre ambos tipos de porcino con el propósito de conseguir animales más aptos para la producción de carne (Giuffra *et al*., 2000). A finales del siglo XVIII y principios del siglo XIX tuvieron lugar una serie de acontecimientos históricos en el reino de Gran Bretaña que impulsaron el desarrollo del sector porcino: la llegada del capitalismo y la revolución industrial. Ambos condujeron a una transformación económica, social y tecnológica que décadas más tarde se extendería hacia Europa y América. Por lo tanto, se puede decir que estos fueron los primeros pasos hacia la industrialización del porcino, que tuvieron lugar en Inglaterra con la introducción del porcino asiático lo que condujo a la aparición de nuevas razas comerciales de porcino que al mismo tiempo hicieron posible la entrada de la carne a diversos mercados (White, 2011). Desde entonces, se fueron desarrollando los esquemas de selección para porcino hasta que a mediados del siglo XX se formaron las líneas maternales y paternales de las que actualmente proceden la mayor parte de las poblaciones comerciales que se emplean en la porcicultura moderna (Mote y Rothschild, 2020).

Desde que se dieron inicio a los esquemas de selección para buscar una mejora en la producción de carne de porcino en el siglo XVIII hasta la actualidad, se han formado alrededor de 300 razas comerciales de porcino, que en algunos casos son las mismas razas, pero criadas en diferentes países. El fruto de estos avances en el sector porcino ha conducido a un mejor aprovechamiento de las aptitudes productivas de los animales porque desde el año 1980 hasta la actualidad, más del 95% de las granjas en el mundo producen carne de porcino para consumo humano a partir del cruzamiento entre dos o más líneas diferentes ya sean del tipo paternales o maternales (Mote y Rothschild, 2020). Sin embargo, es importante reconocer que el desarrollo del sector porcino se ha dado también gracias a importantes avances en otras disciplinas diferentes a la de la mejora genética como la nutrición, el bienestar y la sanidad animal. Dichos avances han conseguido constituir el sistema intensivo de producción del porcino, que consiste en su cría a gran escala y en confinamiento, bajo condiciones ambientales de confort, empleándose dietas balanceadas de pienso para cubrir sus necesidades y promover al mismo tiempo un crecimiento rápido de los animales (van de Weerd *et al*., 2009).

Tabla 1. Niveles de producción, importación y consumo per cápita anual de carne de porcino en Colombia

Año	Producción (t)	Importación (t)	consumo per cápita (kg)
2003	123 886	1 939	3,0
2004	129 866	1 488	3,0
2005	129 152	2 380	3,0
2006	149 519	3 142	3,7
2007	177 389	6 307	4,4
2008	170 488	8 878	4,3
2009	172 229	7 196	4,2
2010	194 585	8 082	4,8
2011	226 056	16 354	5,5
2012	243 038	26 818	6,0
2013	257 378	45 244	6,7
2014	277 996	57 693	7,2
2015	319 283	47 578	7,8
2016	356 354	48 853	8,6
2017	371 347	81 411	9,2
2018	409 789	106 028	10,3

(Tomado de: Registros de producción, importación y consumo de carne de cerdo del año 2003 al 2018. Área económica PorkColombia).

En la actualidad, el 92% del total de carne de porcino producida en el mundo proviene de Asia, Europa y Norte América; donde se encuentran los países industrialmente desarrollados (FAOSTAT, 2020). Mientras que los países con alta demanda de carne y bajo desarrollo del sector son aquellos que se encuentran principalmente en Centro y Sur América. Un indicador de este hecho es el inventario de animales con que cuentan los países, según la información que muestra la FAO para el año 2018, España fue uno de los países con mayor población de porcinos, aproximadamente 30 millones de animales, siendo superado sólo por Brasil (41 millones), Estados Unidos (74 millones) y China (441 millones). Mientras que países en vías de desarrollo, como Colombia, sólo contaba con 5,3 millones de animales vivos para ese mismo periodo de 2018 (FAOSTAT, 2020). Este podría ser un ejemplo de aquellos países que presentan un déficit en la producción para autoabastecer las necesidades de sus habitantes como se puede ver en la Tabla 1, donde se observa para el periodo de 2003 a 2018 un incremento anual en la producción de carne de porcino, los niveles de importación y el consumo per cápita. De acuerdo con la información de la Tabla 1, la tendencia de incremento anual para ese periodo fue de 18,879 toneladas/año, 6,059 toneladas/año y 480 g/año respectivamente para producción, importación y consumo.

El sector porcino ha evolucionado de tal forma que actualmente comprende una parte importante de la economía de aquellos países productores. En España, por ejemplo, la industria del porcino representa el 14% de la producción final agraria, pero dentro de las especies ganaderas que se explotan en las granjas, el porcino se encuentra en primer lugar, siendo esta la especie económicamente más importante porque supone el 39% de la producción final ganadera del país (SG Análisis, Coordinación y Estadística, MAPA, 2019). Esta gran relevancia económica hace que sea un sector dinámico, en constante desarrollo y que implementa de manera bastante rápida mejoras técnicas que le permiten continuar siendo vanguardia en el área de la producción animal. La tendencia en los censos puede informar del grado de expansión que el sector experimenta. En la Figura 1 se presentan estas tendencias para distintos países, entre ellos España y Colombia.

En España, así como en otros países, se viene observando una expansión del sector porcino desde el año 2000 hasta el 2018 (Figura 1). Dentro de este periodo en España se ha observado un aumento en el censo de 22 a más de 30 millones de animales vivos (FAOSTAT, 2020). Según un informe interno del país elaborado por el Ministerio de Agricultura, Pesca y Alimentación de España (SG Análisis, Coordinación y Estadística, MAPA, 2019), desde el año 2017, España ya superaba los 30 millones de animales vivos, siendo este el país con el mayor censo poblacional de la Unión Europea. Obviamente, la expansión experimentada en los censos se acompaña de incrementos en las producciones de carne: en 2017, 2018 y 2019 las producciones fueron de 4,30, 4,53 y 4,63 millones de toneladas de carne, respectivamente. Evidentemente, estos incrementos en la producción se vieron reflejados también en el incremento de otros indicadores económicos del sector, como por ejemplo en el consumo per cápita (0,72 Kg de carne/persona y año) y en la exportación (aumento de 186 mil toneladas/año).

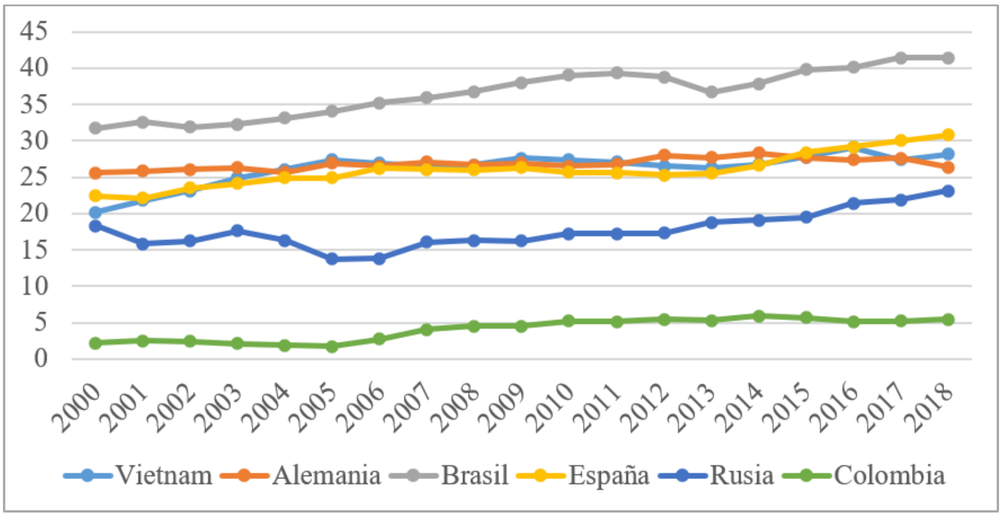

Figura 1. Registro histórico del año 2000 al 2018 del censo poblacional de algunos países desarrollados y otros en vías de desarrollo (expresado en millones) (FAOSTAT, 2020).

En paralelo a esta expansión del sector productor porcino español, y también mundial, se ha de señalar que los productores han tenido que adaptarse a nuevas exigencias y retos que han surgido en torno a la porcicultura, particularmente en lo relativo a la consideración de aspectos como el bienestar de los animales y la sostenibilidad del medio ambiente (Merks *et al*., 2012). En este sentido, los programas de mejora en porcino juegan un papel importante porque a través de estos se busca mejorar las poblaciones para que sean más eficientes para la producción de carne y más resistentes contra enfermedades, pero garantizando unas producciones sostenibles desde el punto de vista social, medioambiental y por supuesto económico. Sin embargo, los resultados de los programas de mejora no serán satisfactorios si no existen condiciones de cría favorables para los animales, así como controles sanitarios, prácticas adecuadas de manejo y una alimentación que les permita expresar su máximo potencial genético. Por esta razón, los criterios de selección utilizados en los programas de mejora deben tener en cuenta, además de los caracteres relacionados con la producción, aquellos que se relacionan con la vitalidad, la longevidad, la supervivencia, la uniformidad en los diferentes niveles productivos, la resistencia a enfermedades, la robustez, la emisión de gases de efecto invernadero, el comportamiento y el bienestar de los animales (Merks *et al*., 2012). Por lo tanto, los porcinos considerados como eficientes para la producción de carne serán aquellos que tengan un rápido crecimiento con la menor utilización de recursos posible. Esto conlleva una producción sostenible desde el punto de vista medio ambiental al reducirse el uso de recursos naturales y los niveles de contaminación.

1.1.1. Esquemas intensivos de producción

La producción intensiva es la alternativa más utilizada para la producción de carne de porcino a nivel mundial. Esta consiste en la cría del porcino en condiciones de confinamiento que se lleva a cabo en las granjas comerciales siguiendo las normas y reglamentos establecidos por cada país. Existen granjas que desarrollan todo el ciclo productivo del cerdo, mientras que otras se encargan de ciertas fases concretas del ciclo productivo: la producción de lechones, la reproducción de los animales o solo a la fase final de engorde. En cualquier caso, el sistema intensivo de producción es una alternativa rentable que además contribuye de forma positiva a un mejor aprovechamiento del espacio disponible en las granjas y de los recursos naturales porque permite tener un mejor control de las enfermedades, la nutrición, el bienestar y el comportamiento de los animales (Maes *et al*., 2020).

La producción intensiva de carne de porcino se realiza mediante el uso de animales cruzados, es decir, animales que provienen del apareamiento entre individuos que pertenecen a líneas paternales y maternales diferentes. Las líneas paternales son aquellas seleccionadas principalmente por caracteres relacionados con la conformación y el crecimiento, y las líneas maternales se seleccionan principalmente por caracteres relacionados con las aptitudes reproductivas de los animales. Se considera que una población de porcinos constituye una línea cuando está sometida a un proceso de selección por determinados caracteres y la reproducción se hace de forma cerrada dentro de la población, es decir, no se producen apareamientos con animales de otras poblaciones (Mote y Rothschild, 2020). La organización de los apareamientos dentro de una misma línea es un tema delicado pues se debe de hacer de forma que se minimice el inexorable incremento de la consanguinidad, igualmente a la hora de seleccionar futuros reproductores la propia selección se deberá ponderar con respecto a la necesaria conservación de la variabilidad. Por el contrario, los apareamientos entre animales de líneas diferentes buscan aprovechar la complementariedad entre los caracteres de las distintas líneas que se cruzan, aprovechar la heterosis que emerge en los cruzados y disipar la consanguinidad acumulada durante el proceso de selección de las respectivas líneas implicadas en el cruce. Es de esta manera que se viene haciendo uso de los animales cruzados en la porcicultura, partiendo de líneas especializadas por determinados caracteres para luego cruzarlas y obtener de este modo animales más eficientes para la producción de carne o para aumentar la prolificidad según sea el caso (Estany *et al*., 1997).

El esquema de cruzamiento comúnmente utilizado para la producción de carne en porcino suele ser el de tres vías (Figura 2), donde unas hembras cruzadas se aparean con machos finalizadores para obtener los animales que serán engordados y llevados a sacrificio para la venta y comercialización de la carne. Con este esquema de cruzamiento se busca principalmente obtener animales más eficientes que alcancen el peso ideal para sacrificio en el menor tiempo posible, para esto se aprovecha la heterosis que emerge del cruce entre líneas diferentes. La heterosis para un determinado carácter es la superioridad del individuo cruzado con respecto al promedio de ese carácter entre las líneas que se cruzan. Esta superioridad es función, por un lado, de la distancia genética entre las líneas que se cruzan, a mayor distancia, se esperaría una mayor magnitud para la heterosis. Y por otro, asumiendo un modelo génico que ignore la epistasis, del grado de dominancia direccional que determina el control génico del carácter. Otra razón para organizar la producción porcina en esquemas de cruzamiento es que mediante estos cruzamientos la consanguinidad acumulada durante los procesos de selección de las distintas líneas se disipará, de manera que los animales sobre los que se sostiene la producción en granjas comerciales no expresarán el efecto de los genes recesivos deletéreos que son los responsables de la depresión por consanguinidad, los animales cruzados son animales con consanguinidad nula. Mediante el cruzamiento también se puede explotar la complementariedad entre líneas implicadas en el cruce, es decir, al animal cruzado cada línea aporta unas determinadas características, de forma que las deficiencias de unas de las líneas implicadas en el cruce quedan compensadas por las virtudes de las otras, por ejemplo las líneas maternales pueden tener una gran prolificidad pero el crecimiento de sus lechones pudiera ser bajo, para complementar este deficiente crecimiento de los lechones de líneas maternales se hace el apareamiento con semen de líneas especializadas en crecimiento, de forma que en los animales finales se está explotando conjuntamente, tanto la mayor prolificidad de las líneas maternales como el mayor crecimiento de las líneas paternales (Blasco y Gou, 1992).

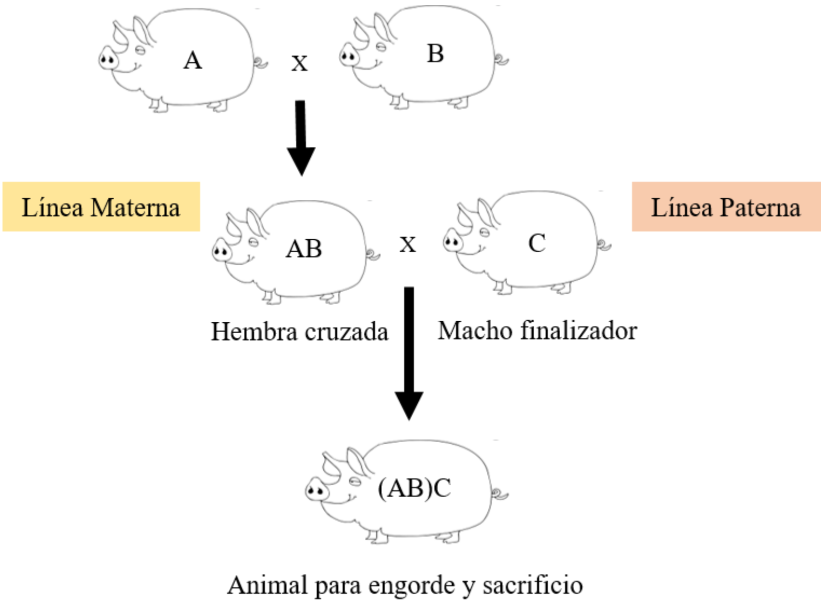

Figure 2. Esquema del cruce a tres vías en porcinos

Las razas generalmente implicadas en las líneas maternales más utilizadas en los esquemas de cruzamiento son Large White, Landrace y Yorkshire. Por otro lado, las líneas paternales que tiene una mayor presencia en el sector son de origen Landrace o Pietrain. La raza Landrace es el origen de líneas tanto maternales como paternales, lo que es claramente un indicador de la irrelevancia del concepto de raza en esquemas de producción intensivos, como es el caso del porcino. En estas producciones el concepto realmente relevante es el de línea, previamente señalado, y es el que puede, de alguna forma, informar sobre las características de las poblaciones implicadas en el cruce, pero no la raza, ya que por ejemplo hay líneas de animales de raza Duroc que manifiestan una conformación y contenido magro similar al de las líneas Pietrain, y otras que tienen niveles de grasa mucho más extremos y que se emplean como machos finalizadores en esquemas de producción de carne de calidad y para fabricación de productos curados de calidad (ANPS, 2011; Gasa y López-Vergé, 2015).

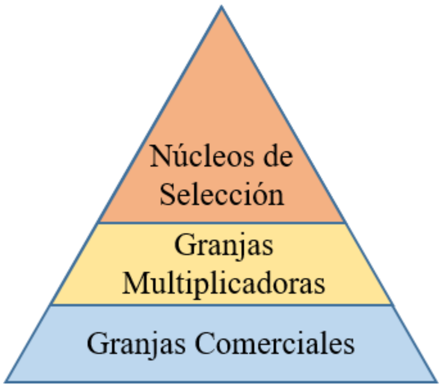

Figure 3. Esquema de producción piramidal en el sector porcino

Dentro de este esquema de producción del porcino, los cruzamientos entre las distintas líneas se llevan a cabo en diferentes fases de acuerdo a los diferentes niveles mostrados en la Figura 3: en los núcleos de selección es donde se evalúa y se selecciona a los mejores individuos que serán los futuros remplazos de los reproductores del núcleo para producir los descendientes de las próximas generaciones, mientras que los individuos que no fueron seleccionados se trasladan a las granjas multiplicadoras. Las granjas multiplicadoras se encargan de diseminar el progreso genético conseguido en los núcleos a través de la producción de hembras cruzadas a partir de dos líneas diferentes (Figura 2) y a través del cruce entre la línea materna y la línea paterna para producir los animales que se llevan a las granjas comerciales para su fase final de engorde. Los centros de inseminación artificial podrían considerarse, en la estructura que se viene describiendo, como granjas multiplicadoras porque en ellos se produce el material seminal de machos finalizadores utilizado para inseminar a las hembras cruzadas y de esta forma se difunde el progreso genético alcanzado en los núcleos de selección (Gasa y López-Vregé, 2015). En algunos casos, la información que se obtiene de los animales cruzados para los parámetros productivos en las granjas multiplicadoras puede ser utilizada en los núcleos de selección para alcanzar mejores resultados en las evaluaciones genéticas de los candidatos a la selección (Tusell *et al*., 2016; Lopes *et al*., 2017; Pocrnic *et al*., 2019) gracias a que se aprovechan las diferentes fuentes de información disponibles para llevar a cabo los programas de mejora en porcino.

La implementación de un programa de mejora en porcino implica una inversión económica importante porque se requiere de una población de animales lo suficientemente grande que permita, por un lado, tener animales disponibles para llevar a cabo los apareamientos y conseguir con estos el progreso genético deseado y, por otro lado, que en estos apareamientos no se incremente demasiado la consanguinidad, algo que, como ya se ha indicado, irremediablemente sucede en poblaciones cerradas reproductivamente. Además de esto, se requiere también de herramientas que permitan la recolección precisa de datos de los animales que luego serán utilizados para las evaluaciones en los núcleos de selección y para esto se necesita personal cualificado tanto para recoger los datos como para su posterior análisis.

1.1.2. Las líneas Duroc en los esquemas de producción

Las líneas porcinas de origen Duroc representan un recurso animal importante para la producción de carne en fresco o productos cárnicos elaborados. En España las poblaciones Duroc se encuentran distribuidas principalmente en las comunidades de Cataluña, Castilla León, Extremadura, Castilla la Mancha y Galicia. Estas líneas llegaron a España procedentes de los Estados Unidos para ser utilizadas como líneas paternas en los esquemas de cruzamiento debido, principalmente, a que son líneas que presentan altos niveles de grasa en la carne, tienen un rápido crecimiento y se adaptan mejor a diversos ambientes comparado con otras líneas de porcino (ANPS, 2017). El uso de estas líneas empezó a ser popular en los esquemas de cruzamiento debido a que la grasa intramuscular es un componente importante que influye sobre la calidad de la carne y por este motivo se sigue utilizando para la producción de productos cárnicos (Blasco y Gou, 1992; Mikule, 2020).

En cuanto a la producción de jamón Ibérico en España, las líneas Duroc juegan un papel importante ya que estas son las únicas líneas que pueden aparearse, según la norma de calidad del Ibérico (Real Decreto 1469/2007, 2 de noviembre), con hembras ibéricas para la producción de jamones, paletas y demás productos curados. Sin embargo, la normativa solo permite que los apareamientos sean entre hembras de Ibérico puras con machos finalizadores Duroc puros o cruzados Ibérico x Duroc. El cruzamiento entre Ibérico y líneas Duroc (I x D) favorece que los productos cárnicos salgan al mercado más rápido que cuando se utilizan líneas puras de Ibérico. Esto se debe principalmente a que el crecimiento de individuos I x D es más rápido que el de los animales Ibéricos, pero esto también se debe a que los sistemas de producción y alimentación implementados para criar a los individuos cruzados suelen ser intensivos, con una alimentación a base de pienso comercial, mientras que los animales ibéricos se suelen criar de forma extensiva y su alimentación suele ser a base de hierba y bellotas que pastorean en la dehesa, dos escenarios distintos que afectan, obviamente a la velocidad de crecimiento de los animales y la duración del periodo de engorde (Bellido *et al*., 2001). De cualquier manera, usando uno u otro sistema de cría y alimentación, en los años 90 se lograba sacar al mercado productos cárnicos con el distintivo de calidad de Ibérico, donde el 75% de la producción de carne para comercialización y consumo provenían de individuos I x D y el restante 25% de líneas puras de Ibérico (Rodrigañez *et al*., 1993). Con respecto a esto último, en la actualidad, el porcentaje de animales puros de Ibérico que salen al mercado es ahora del 17% (Martínez, 2019).

Por otro lado, existe un caso particular en la empresa Batalle de España, donde una línea de origen Duroc se utiliza como hembra maternal en los esquemas de cruzamiento. Esta línea Duroc maternal es la que se utilizó para llevar a cabo los diferentes estudios realizados en la presente tesis. Esta línea fue fundada en el año 1991 (Tibau *et al*., 1999) y desde entonces se ha mantenido en reproducción cerrada, a partir del año 2000 se especializó como línea maternal pues en el índice de selección se consideraban tanto caracteres productivos como el espesor de tocino dorsal y el peso al final del cebo, pero también caracteres reproductivos, como el número de lechones nacidos vivos y el número de pezones funcionales. En el año 2007 esta línea se dividió en dos poblaciones, una se siguió seleccionando por estos mismos caracteres y la otra se enfocó más en caracteres como espesor de tocino dorsal y otros relacionados con la calidad y la infiltración de grasa en la carne (Gol *et al*., 2018).

1.2. Alimentación en porcinos

La alimentación del porcino es punto clave de la producción porque de esta depende que el rendimiento de los animales sea óptimo para producir carne de forma eficiente y rentable. Debido al impacto económico que representa el uso del pienso para la producción de carne, es necesario conocer aquellos factores que pueden afectar al consumo de pienso de los animales para que sea posible implementar sistemas de alimentación apropiados y así garantizar una producción eficiente. Por lo tanto, en esta sección se pretende describir a los aspectos fisiológicos de la alimentación más importantes que tienen lugar en los animales y algunos de los factores que pueden influir en torno esta.

1.2.1. Aspectos fisiológicos de la alimentación de cerdos en crecimiento: Nutrientes, Metabolismo energético, Necesidades para mantenimiento y para crecimiento

La alimentación es una necesidad fisiológica que tienen los animales para satisfacer sus requerimientos nutricionales, pero estos a su vez pueden variar entre animales ya sea por la edad, el sexo o la alimentación como se muestra más adelante. Por lo tanto, es importante comprender que, mediante la alimentación, el porcino aumenta la deposición de tejido magro, tejido graso y cubre las necesidades energéticas mínimas para los procesos metabólicos basales, esto último se refiere a la energía mínima que requieren las células para realizar sus procesos intracelulares y permitir que los animales puedan realizar sus funciones básicas, un ejemplo de estas pudiera ser la respiración (Black *et al*., 2009). La alimentación consiste en activar un mecanismo de diferentes procesos fisiológicos que tienen lugar a lo largo del aparato gastrointestinal que es por donde se desplaza el alimento ingerido, y a medida que el alimento avanza por el tracto digestivo, este sufre transformaciones químicas hasta ser degradado en pequeñas partículas que serán absorbidas por las paredes del tracto. Finalmente, estas pequeñas partículas de nutrientes viajan por el torrente sanguíneo para terminar en los órganos que se encargan de llevar a cabo actividades metabólicas de los tejidos y células (Bondi, 1988a).

Desde los años 90 hasta la actualidad, los requerimientos nutricionales del porcino han ido cambiando, debido a que la respuesta en los programas de mejora ha conducido a animales en los que se han reducido los niveles de grasa y se ha aumentado el tejido magro. Esto ha dado como resultado, animales más eficientes que crecen más rápido y que utilizan menos cantidades de energía. Evidencia de esto es la reducción del consumo de alimento observado en los últimos años que ha sido de 30 g/d por año, aproximadamente y la ganancia de peso ha aumentado 4 g/d anualmente (Knap, 2009). Por lo tanto, se puede decir que se ha conseguido mejorar el rendimiento productivo del porcino actuando desde el campo de la genética durante años de trabajo constante. Sin embargo, existen otras alternativas desde otros campos de estudio como la nutrición para actuar sobre el mismo propósito y donde también se han visto resultados prometedores. En este sentido, es posible alcanzar una reducción cercana al 10% en el consumo de pienso de los animales cuando se administran hormonas de crecimiento, ya que esta hormona estimula la síntesis de proteína, reduce la lipogénesis y por tanto reduce los requerimientos de energía en el cuerpo (Campbell, 1988). Esto indica que la relación que existe entre la ingesta de aminoácidos, la absorción de aminoácidos y los caracteres productivos del porcino como el crecimiento, los niveles de grasa dorsal y la eficiencia alimentaria deben ser conjuntamente explorados desde ambos campos, nutrición y genética, para entender como los unos pueden verse afectados por los otros.

El uso de aminoácidos en la dieta permite la síntesis proteica, fundamental en animales en crecimiento y también clave para la renovación de las estructuras corporales de los animales adultos. Los procesos metabólicos que hacen uso de los aminoácidos pueden verse influenciados por una gran cantidad de factores biológicos; unos asociados directamente al animal, como la genética, el estado fisiológico o el estado de salud; y otros de tipo ambiental que son externos al animal (de Lange *et al*., 2009). Uno de estos factores pudiera ser la composición proteica de la dieta; por ejemplo, se ha comprobado que, si una dieta incluye un 10% más de los aminoácidos requeridos por parte del animal, esto va a modificar los patrones de crecimiento y deposición de tejido graso, reduciéndose el espesor de tocino en un 12% e incrementándose la eficiencia en un 5.5% (NRC, 2012). Más allá de este efecto sobre el crecimiento y la eficiencia se debe señalar que como algunos de los aminoácidos no se pueden sintetizar por parte de los cerdos, éstos deben aportarse con la dieta, son los que se llaman aminoácidos esenciales: lisina, metionina, triptófano y treonina (Blair, 2018). Su control en la dieta es fundamental, pues un déficit en ellos no sólo comprometería el crecimiento y la eficiencia, sino que también daría lugar a problemas patológicos graves.

Además de los aminoácidos existen otros componentes nutricionales que el porcino necesita para sobrevivir como los minerales y las vitaminas. La ausencia o exceso de alguno de estos componentes también puede conducir al detrimento de su rendimiento productivo y reproductivo. El porcino utiliza los minerales para la formación y renovación de los huesos y ayudan también en procesos metabólicos para la utilización eficiente de nutrientes. Entre los minerales más importantes que debe tener una dieta de porcino se encuentran calcio, fosforo, cloro, sodio, hierro, selenio, cobre, manganeso, yodo y zinc. Las vitaminas en la dieta juegan un papel importante porque estas contribuyen al desarrollo de los procesos metabólicos del porcino como la visión, la reproducción, la formación del hueso y la digestión (Blair, 2018).

La energía suministrada en las dietas de porcino permite que todos los componentes nutricionales sean eficientemente utilizados, esta energía proviene principalmente de la ingesta de carbohidratos, pero también de grasas y proteínas . Actualmente se conoce con precisión el rol que tienen estos elementos dentro del organismo de los animales para calcular sus requerimientos nutricionales en las diferentes etapas del ciclo productivo del porcino, sin embargo, existe gran cantidad de factores y situaciones en las que estos requerimientos pueden verse afectados como puede ser el caso de animales enfermos donde resulta difícil cuantificar el cambio de estos requerimientos (de Lange *et al*., 2009).

El aprovechamiento de nutrientes para cubrir las necesidades energéticas de los animales es lo más importante a la hora de suministrar las dietas porque como se ha comentado anteriormente, la energía es necesaria para llevar a cabo las actividades básicas de mantenimiento, como conservar la temperatura corporal, mantener su actividad muscular y por lo tanto es vital para la supervivencia de los animales. Pero, además, en el caso del porcino, es importante para la producción de carne, que sería el resultado de interés productivo relevante derivado del proceso fisiológico que es el crecimiento. La energía que necesitan los animales es capturada a partir de la oxidación de carbohidratos, grasas y proteínas que provienen del alimento, pero también la energía puede ser conseguida a partir del propio animal recurriendo a los depósitos de reservas que en el cuerpo pudiera haber: degradación de glucógeno, grasa o proteína almacenada en el organismo. En vista de la importancia que tiene la energía para los animales, es necesario conocer que la energía en el organismo de los animales sufre una serie de transformaciones como se muestra en la Figura 4 y para entender los diferentes cambios que sufre la energía se deben tener en cuenta las leyes de la termodinámica, donde una primera ley indica que la energía puede cambiar de forma, pero no puede ser creada ni destruida, y la segunda ley indica que toda forma de energía se convierte en calor, es decir, en el contexto nutricional, la energía es liberada en forma de calor. Estas leyes son la base de los nutricionistas para estimar los gastos de energía que los animales tienen en el organismo para llevar a cabo sus actividades metabólicas como se describe a continuación (Gutierrez y Patience, 2012).

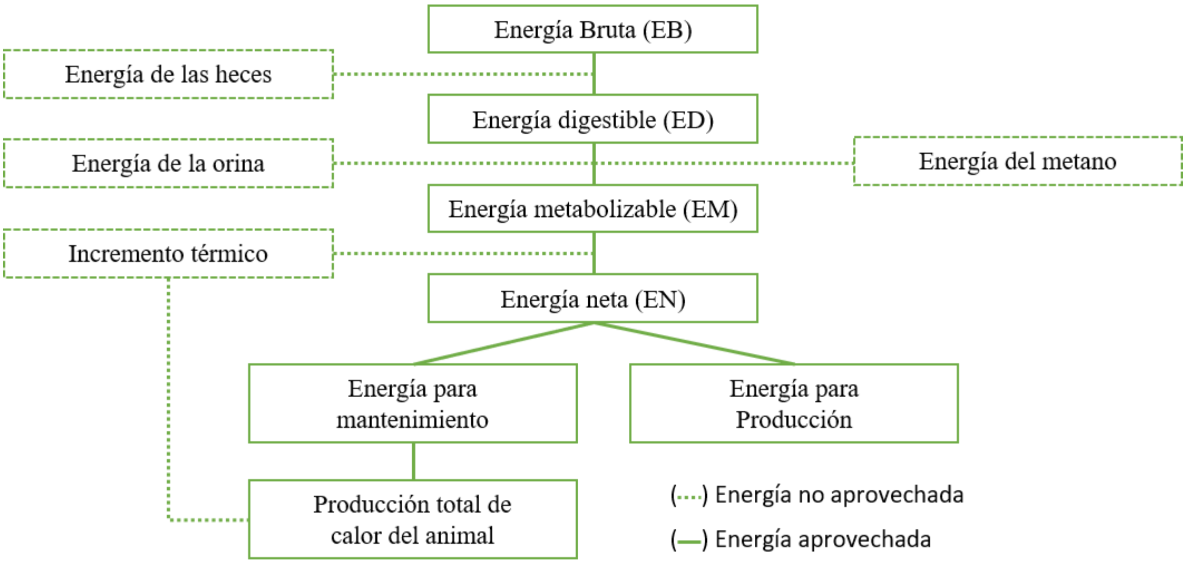

Figure 4. Distribución de la energía de los alimentos en el animal (Tomado de Bondi, 1988b)

La alimentación del porcino empieza por la ingesta de energía bruta (EB), esta es la energía total disponible que tienen los animales a partir de los alimentos. La concentración de EB en los ingredientes del alimento se expresa en kilocalorías por gramo (kcal/g) o mega julios por gramo (MJ/g), para cerdos esta EB asociada a carbohidratos, lípidos o proteínas serían de 4,15 kcal/g, 9,50 kcal/g y 5,65 kcal/g, respectivamente (Ewan, 2001). Esta energía no es completamente aprovechada por el animal, en los propios procesos de digestión y metabolismo se van generando pérdidas que habrá que ir descontando de la EB inicial; en las heces, por ejemplo, se encuentra parte de esta energía del alimento que el animal no pudo digerir, en porcinos, estas pérdidas de energía representan un 20% de la EB.

La energía digestible (ED) es la energía que se queda dentro del organismo y no ha sido expulsada en las heces, por lo tanto, es la energía que el animal pudo digerir y que tiene disponible para sus procesos metabólicos. Cuando esta energía empieza a ser utilizada se vuelven a generar pérdidas, la mayor cantidad de pérdidas se concentran en la orina, aunque también hay una porción de esta energía en gases generados durante el propio proceso de la digestión por parte de las bacterias intestinales, de estos gases el más importante es el metano. Como las mediciones de la energía en los gases son difíciles y en general, en porcino, suponen una proporción pequeña con respecto a la energía excretada por la orina esta porción de las pérdidas se suele ignorar, particularmente en dietas con un porcentaje bajo de fibra (Kil *et al*., 2013). En cualquier caso, se puede señalar que las pérdidas energéticas que en conjunto suponen la orina y la emisión de gases asociados a los procesos fermentativos del tracto intestinal, son de entorno al 4% de la ED ingerida. La porción de energía digestible efectivamente utilizada para llevar a cabo los procesos metabólicos se le conoce como energía metabolizable (EM) (Noblet *et al*., 1994). Tanto la ED como la EM de los animales pueden verse afectadas por factores como el volumen de ingesta. Si se ingieren grandes cantidades de pienso, el alimento tendrá un flujo rápido a través del tracto digestivo y esto evita el buen aprovechamiento de la energía de la dieta. Otro factor que puede alterar la velocidad de tránsito es la composición de la dieta, niveles altos de fibra hacen que el tránsito sea más lento (Varel *et al*., 1984). Por lo tanto, los valores de ED y EM pueden cambiar en función de los ingredientes introducidos en la dieta, por ejemplo, el maíz tiene una ED de 17,3 MJ/kg y una EM de 16.9 MJ/kg, mientras que para la cebada estos valores son de 14,7 MJ/kg y 14,2 MJ/kg (Bondi, 1988b). En este sentido, el interés de la producción se centraría en reducir las pérdidas de energía en heces, orina y calor por fermentación, de esta manera se minimizarían las pérdidas económicas y al mismo tiempo se reducirían las emisiones de óxido nitroso (N_2O), metano (CH_4) y dióxido de carbono (CO_2) en un 2%, 17% y 81%, respectivamente (Philippe y Nicks, 2015).

Con la EM disponible para el organismo de los animales se deben cubrir las necesidades energéticas para el mantenimiento de las funciones básicas del organismo y también para el desarrollo de los distintos procesos fisiológicos por los que los animales domésticos se explotan, en el caso del cerdo de engorde sería su crecimiento. Sin embargo, el acceso a esta energía supone unos gastos que dan lugar a lo que se conoce como incremento térmico (Bondi, 1988b), que sería el calor producido por los procesos químicos y físicos ligados a la digestión y el metabolismo. Dos ejemplos de estos procesos pudieran ser el tránsito intestinal y la energía requerida para llevar a cabo el ciclo de Krebs. La energía neta (EN) será, por tanto, la EM después de haber descontado la energía usada en el incremento térmico, es esta EN la que finalmente queda a disposición del animal para atender sus necesidades de mantenimiento y el resto de sus funciones fisiológicas, como sería el crecimiento o el sostenimiento de la reproducción; es decir, el valor calórico de los productos animales. A modo de conclusión en relación al metabolismo energético se puede señalar que sólo aproximadamente el 25% de la EB queda disponible en forma de EN a disposición del animal (Bondi, 1988b). En el caso del cerdo en engorde las dos funciones básicas que deberá atender son por un lado el mantenimiento y el propio crecimiento. Atender las necesidades de mantenimiento supone disponer de energía y nutrientes para soportar los procesos vitales del animal, como por ejemplo la respiración, la renovación de los tejidos y el mantenimiento de la temperatura corporal. La energía requerida para este mantenimiento no queda retenida en ninguna estructura corporal y por tanto se disipa, sumándose al incremento térmico previamente señalado como necesario para obtener EN a partir de la EM. La medición del calor producido con animales en ayunas es una de las técnicas más precisas para cuantificar las necesidades de mantenimiento. Con respecto al crecimiento o el incremento de peso y tamaño del cuerpo de los animales, se debe señalar que a lo largo de sus distintas fases son distintos los tejidos cuyo crecimiento es el que predomina. En general, en las primeras fases del crecimiento deben crecer los huesos y también los músculos; por lo tanto, en estas fases las necesidades proteicas y de minerales son muy elevadas. En la fase final del cebo la deposición proteica se enlentece, mientras que se acelera la deposición de grasa. El balance del crecimiento de estos dos tipos de tejidos es fundamental ya que el coste energético promedio que tiene la retención de proteína en los animales es de 10,6 Mcal de EM/kg y el coste para la retención de grasa es de 12,5 Mcal de EM/kg (Palomo, 2014). Esto último es así porque 1 kg de tejido muscular contiene entre el 20 y 23% de proteína mientras que 1 kg de tejido graso contiene entre 80 a 95% de grasa. La deposición de tejido muscular supone un menor costo energético comparado con la deposición de tejido graso.

El análisis previo del metabolismo energético y de las necesidades de mantenimiento y crecimiento permite vislumbrar como la eficiencia nutricional y energética de los cerdos en fase de crecimiento va a depender de la variación de ciertos factores nutricionales, ya se ha indicado por ejemplo el papel de la fibra (Stein y Shurson, 2009). Pero también se puede intuir que la existencia de variación individual en las distintas fases del metabolismo energético y de las necesidades de mantenimiento y crecimiento pudiera tener un cierto origen genético que se podría explotarse en los esquemas de selección y mejora, de forma que la media de eficiencia en el uso de energía y nutrientes de una población productiva vaya aumentando. En este sentido se ha demostrado que existe variación genética en la digestibilidad (Déru *et al.*, 2020) y desde hace mucho se tiene constancia de que unas razas basan su crecimiento en la deposición de grasa, por ejemplo, el Ibérico, mientras que otras lo basan en deposición de proteína, por ejemplo, la raza Pietrain, siendo claramente más eficientes la segunda que la primera. Con respecto al mantenimiento igualmente existen evidencias de variación genética entre animales de distinta razas o líneas (Barea *et al.*, 2010) e incluso entre animales de la misma población (Young y Dekkers, 2012).

1.2.2. Control del consumo de alimento

La eficiencia en el uso del pienso es sólo uno de los componentes a tener en cuenta de cara a obtener animales que garanticen una producción rentable de carne magra, los otros serían el crecimiento y la composición corporal de los animales, por un lado, porque ésta puede determinar de forma directa la eficiencia, como se ha indicado previamente, y también porque los distintos mercados pudieran requerir canales más o menos grasas. En cualquier caso, para la consideración directa de la eficiencia en el uso del pienso se necesitan registros del consumo individual. Sin embargo, disponer de esta información implica una inversión considerable en infraestructura para las granjas debido a que el porcino normalmente es criado en grupos y en estos casos los comederos electrónicos son la opción más apropiada. Los comederos electrónicos han demostrado ser una herramienta bastante útil para recoger información del consumo individual del porcino (Eissen *et al*., 1998; McSweeny *et al*., 2001; Casey *et al*., 2005), pero su alto coste los convierte en herramientas de difícil acceso. El precio de una unidad de comedero electrónico del tipo IVOG para recolectar información de porcinos durante el periodo de ceba se encuentra entre los 5000 y 6000 euros (https://hokofarmgroup.com/products/ivog/), esto además implica otros gastos adicionales en torno a este, como el mantenimiento, la instalación, la infraestructura requerida y el personal capacitado para analizar y gestionar la información que estos comederos almacenan.

Como alternativa a la consideración de datos de consumo individuales se ha propuesto el uso de información de consumo del grupo, consumo por corral. En un estudio se sugiere alojar animales en grupos pequeños (Olson *et al*., 2006) porque cuando se aproxima el consumo individual por el promedio de grupo, si el grupo es pequeño, se estará más cerca de la medida real de consumo individual que si el promedio se obtiene con un número de animales grande. Otra alternativa relacionada sería agrupar los animales en corrales por familia (Chu *et al*., 2019), de este modo se pretende reducir la incertidumbre asumiendo que los integrantes del grupo pueden presentar las mismas aptitudes productivas por ser descendientes de los mismos padres, en el fondo el consumo del corral representaría una medida del carácter de los padres. Por lo tanto, la ganancia genética en los caracteres de eficiencia alimentaria que se pudiera alcanzar dependerá de la distribución de los animales de acuerdo con sus relaciones de parentesco y del tamaño de los grupos. En los últimos años se han llevado a cabo diferentes estudios en torno a la consideración del consumo de animales alojados en espacios colectivos en distintas especies de granja: porcinos (Su *et al*., 2018), gallinas ponedoras (Biscarini *et al*., 2008), bovinos (Cooper *et al.*, 2010), conejos (Piles y Sánchez, 2019). En general, en estos trabajos el propósito principal es encontrar una alternativa más rentable al registro directo del consumo individual, pero que permita predecir los valores genéticos para consumo individual a partir de información recolectada a nivel grupal.

1.2.3. El comportamiento alimentario

Los hábitos de alimentación, la preferencia por los alimentos, la cantidad consumida y la velocidad con que estos son adquiridos, es lo que se conoce como el comportamiento alimentario (Morgan *et al*., 2000). Este comportamiento puede verse afectado por factores biológicos como el hambre, el apetito o el sentido del gusto y estos a su vez pueden resultar afectados también por otros de tipo ambiental que son externos a los individuos como la temperatura (Renaudeau *et al*., 2011) o la interacción con otros individuos (Lu *et al*., 2017). Por esta razón, la información que se obtiene del comportamiento de los animales en torno al comedero es importante para identificar aspectos positivos o negativos con respecto al bienestar, la producción y la eficiencia alimentaria. Por un lado, el comportamiento alimentario de los animales pudiera ayudar en la identificación del estado de salud de los individuos, como lo muestra un estudio, donde se observó que existe una relación entre los brotes de neumonía con la duración de las visitas al comedero (Brown-Brandl *et al*., 2013). Por otro lado, el análisis de la información del comportamiento alimentario va a permitir explorar patrones de conducta que pudieran relacionarse con caracteres productivos de interés directo. En cuanto al comportamiento, este ha sido un tema de interés para diferentes campos de estudio durante décadas debido a las consecuencias negativas que pueden traer para la producción que los animales compartan su espacio de alojamiento. En este sentido, se sabe que el porcino es un animal territorial con una tendencia marcada a establecer jerarquías sociales mediante comportamientos agresivos cuando se encuentran en grupo, por lo tanto, en un grupo de porcinos siempre habrá animales dominantes y subordinados o sumisos (Meese y Ewbank, 1972).

En porcinos, la jerarquía de un grupo se establece en los primeros días tras haberse formado el grupo, el establecimiento de esta jerarquía es consecuencia de los resultados de las peleas entre los animales que tienen lugar esos primeros días tras constituirse el grupo y esta jerarquía se mantiene hasta que ingresen o salgan individuos del grupo (Tong *et al*., 2020). El comportamiento alimentario de los animales dominantes de un grupo puede ser identificado a simple vista porque tienden a ser los más agresivos y suelen tener acceso directo y fácil al alimento, mientras que los subordinados tienen un acceso al comedero mucho más limitado (Browns y Edwards, 1994). Es obvio, por tanto, que el desempeño productivo de los animales no sólo va a ser consecuencia de sus aptitudes metabólicas para hacer uso de los nutrientes ingeridos, sino que fruto de las interacciones sociales y la posición de los animales dentro del ranking social, estas aptitudes pueden enmascararse. Por ejemplo, detrás de un animal con gran crecimiento y consumo pudiera haber un individuo que es muy agresivo y que a la larga pudiera penalizar el crecimiento y eficiencia del corral en su conjunto. Por lo tanto, en las evaluaciones genéticas de los candidatos a la selección sería necesario tener presentes estas consideraciones para hacer predicciones del valor genético de los animales lo más libre posible de sesgos debidos a las interacciones sociales (Muir, 2005).

Los comederos electrónicos, como ya se ha indicado, son la herramienta más moderna y precisa para registrar datos de consumo individual en animales alojados en grupo. Pero además también pueden ser de utilidad para recolectar caracteres relacionados con el comportamiento alimentario de los animales. Los caracteres de comportamiento alimentario son aquellos que los animales manifiestan en torno al comedero y ejemplos de ellos son los siguientes: duración de cada visita al comedero, número de visitas diarias al comedero, y a partir de estos se pueden derivar otros caracteres como la velocidad de ingestión o el intervalo entre visitas.

Tabla 2. Heredabilidad (h^2) de los caracteres tasa de alimentación, tiempo de ocupación y número de visitas en porcinos

Carácter	h^2	**Referencia**
Tasa de alimentación (g/min)	0,46	Hall, 1997
	0,50	Young, 2012
	0,56	Do et al., 2013
Tiempo de ocupación (min)	0,45	Hall, 1997
	0,37	Rohrer *et al*., 2013
	0,48	Do *et al*., 2013
Número de visitas (visitas/d)	0,44	Young, 2012
	0,31	Rohrer *et al*., 2013
	0,47	Do *et al*., 2013

La información que estos caracteres ofrecen puede ser de utilidad para mejorar la evaluación de aquellos caracteres considerados dentro de los programas de mejora por eficiencia alimentaria. La razón por la que estos caracteres pueden ser útiles es porque son heredables como se observa en la Tabla 2, y además muestran correlaciones no nulas con los caracteres productivos. Por ejemplo, se han reportado correlaciones genéticas positivas entre la tasa de alimentación y dos caracteres productivos: el espesor de tocino dorsal y la ganancia diaria de peso (Kavlak y Uimari, 2019). Otro estudio ha reportado que existen correlaciones genéticas positivas también entre el tiempo de ocupación en el comedero con los caracteres de ganancia diaria de peso y espesor de tocino dorsal, pero este mismo estudio muestra además que existe una correlación negativa entre los mencionados caracteres productivos con el carácter número de visitas al comedero (Lu *et al*., 2017).

Como se pudo ver en los estudios anteriormente comentados y los que se encuentran citados en la Tabla 2, los caracteres de comportamiento alimentario y los caracteres productivos se encuentran relacionados con los caracteres de eficiencia alimentaria en porcinos. Por este motivo, la información referente a los caracteres de comportamiento alimentario pudiera ser importante para tenerlos en cuenta en las evaluaciones genéticas. Si se incluyen en evaluaciones genéticas de múltiples caracteres a los caracteres productivos y los de eficiencia sería de esperar que mejorase la precisión de la evaluación genética de los caracteres de eficiencia alimentaria fruto de la información adicional que aportarían los caracteres de comportamiento alimentario. Por otro lado, estos caracteres de comportamiento alimentario pueden utilizarse para identificar comportamientos de animales dominantes o subordinados. Conocer el papel social que juegan los distintos animales de un grupo puede ser igualmente relevante para mejorar las predicciones de valor genético de los caracteres productivos y de eficiencia alimentaria (Nielsen *et al*., 1995; Fernandez *et al*., 2011).

1.3. La eficiencia alimentaria en los programas de mejora del porcino

Desde el punto de vista de la producción de carne magra, los animales más eficientes serán aquellos que alcancen el peso de sacrificio en el menor tiempo posible, consumiendo la mínima cantidad posible de pienso, pero manteniéndose en el producto las características deseadas para el mercado al que vaya destinado. Por esta razón los caracteres de importancia económica que se consideran en los programas de mejora de la eficiencia alimentaria son por un lado los relativos al consumo de pienso, la ganancia diaria de peso o el peso al final del cebo y el espesor de tocino dorsal; así como otros que directamente pretenden cuantificar la eficiencia alimentaria y que son funciones de los anteriores: el índice de conversión de alimento y el consumo residual de alimento (Merks *et al*., 2012; Hermesch *et al*., 2015). Todos estos caracteres se deben entender como indicadores de los balances energéticos, de las necesidades de mantenimiento y de crecimiento, y de la composición corporal. En apartados previos se han descrito estos elementos como piezas claves de la fisiología de la nutrición y alimentación de cerdos en crecimiento. La razón por la que a la hora de estudiar la eficiencia consideramos estos indicadores y no directamente en los componentes fisiológicos del crecimiento (uso de energía y nutrientes) es porque estos indicadores son fáciles de medir; mientras que, por ejemplo, determinar las necesidades de mantenimiento de forma experimental, es muy difícil y costoso, y sólo se puede hacer con un número muy reducido (no más de una decena) de animales.

A partir de los caracteres indicadores del párrafo anterior se pueden derivar distintas funciones o índices que pueden interpretarse como medidas directas de la eficiencia alimentaria. Estas medidas se deben entender como índices productivos, que lamentablemente a veces pueden quedar lejos de los procesos biológicos de los que realmente depende la eficiencia y que previamente ya se han revisado. Por lo tanto, muchas veces la consideración de estos índices responde a un aspecto claramente práctico: se trata de caracteres que son relativamente fáciles de medir en grandes grupos de animales alojados colectivamente. El índice de conversión de alimento diario de un individuo se calcula dividiendo el consumo de pienso entre la ganancia de peso diaria y este nos permite medir la cantidad de pienso que un animal necesita para producir un kilogramo de carne (Losinger, 1998). El consumo residual de alimento se obtiene como la diferencia entre el consumo de pienso medido y el consumo que se espera de un animal dadas sus necesidades para mantenimiento, para deposición de grasa y para crecimiento. Estas necesidades en el contexto de los experimentos y programas de selección se aproximan por el peso metabólico en el punto intermedio de la duración del cebo, el espesor de tocino y la ganancia de peso durante el cebo, y se substraen del consumo observado ajustando modelos de regresión múltiple. El consumo residual de pienso cuantifica la cantidad de pienso consumida por encima o por debajo de lo que el animal necesita, por su naturaleza estadística de residuo de una regresión tiene una media de cero (Gilbert *et al*., 2007; Cai *et al*., 2008), y el animal deseable, desde el punto de vista de la eficiencia, sería aquel que tiene valores negativos para esta variable.

Como se ha mencionado anteriormente, la ingesta y también la eficiencia alimentaria dependen de factores intrínsecos y extrínsecos a los animales, y por tanto, los resultados de los programas de mejora por eficiencia alimentaria dependerán, además de los aspectos propiamente vinculados con el determinismo genético de los caracteres (por ejemplo de la heredabilidad o de la intensidad de selección que se pueda aplicar) de cómo esos factores tanto extrínsecos como intrínsecos se han podido controlar en el núcleo. Una falta de control de estos factores va a suponer una mayor relevancia de efectos no genéticos, lo que se traducirá en una menor heredabilidad y por tanto una menor respuesta esperada en los procesos de selección.

En esta revisión, hasta ahora, se ha tratado de transmitir la importancia que los caracteres de eficiencia alimentaria tienen para el sector productor porcino, e igualmente se ha analizado de qué otros caracteres dependen los caracteres de eficiencia, y también se han remarcado algunos de los factores ambientales que sobre ellos influyen. En el presente apartado se van a revisar los procedimientos de selección que se han usado hasta la fecha para mejorar genéticamente los caracteres de eficiencia alimentaria. Se presentan dos grandes grupos de procedimientos de selección, en función de que se puedan tener o no medidas directas de la eficiencia de los animales. Como ya se ha indicado previamente, el limitante para implementar procedimientos de selección directos radica en disponer de medidas de consumo individual de los animales alojados en las condiciones más cercanas posibles a su explotación comercial, i.e. alojados en grupo. De ahí que, en el fondo, disponer de medidas directas de eficiencia alimentaria se pueda asimilar por disponer de datos de consumo individual.

1.3.1. Mejora directa de la eficiencia alimentaria

Obviamente sería el escenario en el que se disponen de medidas de consumo individual y de todos los otros caracteres que puedan intervenir en las definiciones de los índices eficiencia previamente señalados, como por ejemplo el crecimiento o peso final, el espesor de tocino dorsal y el peso metabólico. Englobados en este grupo de procedimientos de selección se incluyen dos procesos de selección divergente por eficiencia alimentaria llevados a cabo de forma experimental en el INRA (Gilbert *et al*., 2007) y en la Universidad de Iowa (Cai *et al*., 2008; Young y Dekkers., 2012). Como se indica, se trata de procesos experimentales que han permitido generar un material de gran valor para el estudio en profundidad de los procesos biológicos que hay detrás de la eficiencia alimentaria. Con estos estudios se ha podido comprobar que la selección por el consumo residual de alimento ha promovido básicamente una reducción de las necesidades de mantenimiento y no tanto un incremento en la eficiencia con la que se lleva a cabo el propio crecimiento (Gilbert *et al*., 2012; Gilbert *et al*., 2017). En este sentido, se ha observado que en dos líneas de porcino seleccionadas por cinco generaciones, una para incrementar el consumo residual y otra para disminuirlo, dio como resultado una reducción de los requerimientos de aminoácidos como la lisina al final del periodo de engorde en ambas líneas, sin embargo, la reducción fue menor para la línea seleccionada para disminuir el consumo residual, donde sus requerimientos fueron de 0.5 g/MJ de energía neta (EN) y 0.6 g/MJ EN para la otra línea (Gilbert *et al*., 2017).

La realidad en los esquemas de mejora comerciales es algo diferente pues en ellos las poblaciones se suelen seleccionar por varios caracteres, en este sentido el planteamiento que parece más adecuado para, de manera conjunta, mejorar la eficiencia a la vez que se incrementan las producciones de carne magra (por ejemplo, incrementando la ganancia diaria y reduciendo el espesor de tocino dorsal) sería la definición de índices lineales que, con los pesos económicos apropiados, ponderen los distintos caracteres de interés: crecimiento o peso final, espesor de tocino dorsal y consumo, de manera que de forma conjunta se van incrementando las producciones sin incrementar el consumo o incluso reduciéndolo (Topigs Norsvin, 2017). Este planteamiento de abordar la mejora de la eficiencia alimentaria mediante indicies lineales se ha estudiado con profundidad en relación con una de las definiciones más habituales de eficiencia alimentaria, el consumo residual de alimento con sus siglas en ingles RFI (residual feed intake). Este carácter se puede considerar como un índice de selección que involucra al consumo y la ganancia u otros caracteres independientes, en el que los pesos de cada uno de estos caracteres son los coeficientes de regresión de los distintos caracteres para explicar el consumo. Es decir, un peso que no tiene en cuenta aspectos económicos sino simplemente la relación biológica entre los caracteres (Kennedy *et al*., 1993).

1.3.2. Mejora indirecta de la eficiencia alimentaria

El principal inconveniente para implementar esquemas de selección directos por eficiencia alimentaria es disponer de datos de consumo individual de animales alojados en las mismas condiciones en las que se explotaran en las granjas comerciales, es decir, alojados en grupo. Es precisamente por esto que el método tradicional de abordar la selección para eficiencia siempre fue la selección indirecta, en general lo que se hacía era seleccionar por índices que daban peso negativo al espesor de tocino dorsal y peso positivo a la ganancia de peso durante el cebo (Merks *et al*., 2012). La justificación fisiológica de este criterio indirecto de selección se ha ofrecido en apartados anteriores: Es más eficiente energéticamente la deposición de magro que la deposición de grasa. La respuesta esperada con este criterio de selección será, en general, menor que la que se obtendría con algún procedimiento directo de selección considerando algún índice de eficiencia, pero en función de los parámetros genéticos de los caracteres implicados con la selección indirecta pudiera incluso alcanzarse respuestas mayores que con la selección directa. Este sería el caso cuando la h^2 del objetivo de selección fuese muy baja, pero su correlación con los caracteres que actúan como criterio fuese alta y éstos a su vez tuviesen unas heredabilidades también altas. En cualquier caso, más allá de la respuesta que se pueda esperar, con los métodos indirectos de selección se evitaba registrar el consumo individual, evitándose así la importante inversión que esto supone. A día de hoy, aunque sigue suponiendo una inversión importante, como ya se ha indicado, casi todas las empresas de selección porcina que participan en el mercado internacional tienen estaciones de control para el consumo de alimento (Briant, 2017; Topigs Norsvin Canada Inc., 2014) que permiten el control de consumo individual y por tanto se puede afirmar que, en los esquemas comerciales de selección en un mayor o menor porcentaje, dependiendo del número de candidatos que pasen por estos sistemas de control de consumo, la selección por eficiencia se aborda de forma directa, es decir considerando información de consumo individual en animales alojados en grupo.

Otra alternativa que se puede clasificar como un método indirecto de selección para mejorar la eficiencia alimentaria pudiera ser la de seleccionar animales a favor de su crecimiento, pero estando alimentados bajo restricción. De esta forma se elimina la variación de consumo que pudiera haber, y toda la variación que se observa en el crecimiento pasa a ser consecuencia directa de la mayor o menor eficiencia que cada animal puede tener. Este procedimiento de selección se usó experimentalmente en trabajos clásicos que han investigado los procesos fisiológicos detrás del uso de los nutrientes y energía del alimento (Cameron *et al*., 1994; Nguyen y McPhee, 2005). No se está al tanto de una implementación práctica y comercial de estos sistemas de selección bajo condiciones de restricción alimentaria. En primer lugar, las condiciones de cría durante estos procesos deben ser diferentes a las que se dan en condiciones comerciales. Para poder realizar una restricción apropiada de tal manera que se garantice que todos los animales tienen el mismo consumo, es preciso alojar a los animales en corrales individuales o al menos en corrales que durante el período de alimentación permita aislarlos unos de otros. Estas diferencias de las condiciones de cría pudieran limitar la respuesta genética debido a la existencia de interacción, es decir que los mejores animales (mejores genes) en las condiciones del núcleo fuesen otros distintos a los mejores animales (mejores genes) en las condiciones comerciales, el grado de penalización dependerá de cómo el ranking cambie en una u otras condiciones. En conejos, cuando se ha evaluado el grado de interacción genotipo con ambiente (GxE) entre animales alimentados bajo restricción y animales alimentados *ad libitum*, se observó una magnitud muy importante de la interacción genotipo ambiente (Piles y Sánchez, 2019). En este estudio, los animales de ambos tratamientos se criaron en grupo, y por lo tanto sin un control individualizado de la ingesta en los racionados, se concluye que parte de esta interacción GxE es atribuible a las fuertes interacciones sociales que se observan entre los animales criados bajo restricción y que no se dan en los criados con alimentación *ad libitum* Piles *et al*. (2017).

Otra alternativa que pudiera considerarse como un método indirecto de selección por eficiencia, pudieran ser aquellas que sin incorporar medidas de consumo individual en las evaluaciones genéticas sí manejan datos de consumo registrados a nivel de grupo, en el caso de los cerdos, estos grupos serían los corrales. Tomar estas mediciones no requiere de grandes infraestructuras ni inversiones, y sí pudieran generar información relevante para mejorar la precisión. Evaluar de forma precisa este punto es uno de los objetivos de la tesis, en cualquier caso, como ya se ha indicado existen estudios en otras especies que presentan modelos y técnicas para considerar esta información de consumo de grupo.

1.3.3. La selección genómica en producción porcina

En los últimos años el uso de información genómica en las evaluaciones genéticas de las poblaciones ganaderas se ha extendido de forma notoria. En el caso del porcino, la mayor parte de las compañías internacionales que venden reproductores implementa de una forma u otra algún procedimiento que considera la información de marcadores densos del ADN (tipo SNP: single nucleotide polymorphism). Las decisiones de selección tomadas en base a estas evaluaciones es lo que se conoce como selección genómica (Meuwissen *et al*., 2001). Los programas de selección que usan la información genotípica y fenotípica de los candidatos a la selección, así como la de los reproductores, podrán beneficiarse en todos los caracteres que se consideren dentro del programa de las ventajas que supone la predicción genómica frente a las predicciones tradicionales de valor genético basadas exclusivamente en información fenotípica y genealógica. Algunos de estos caracteres pudieran ser los relacionados con el consumo y por tanto también los de eficiencia alimentaria.

Los sistemas de evaluaciones genómicas permiten obtener una mayor precisión en la predicción del valor genético de los caracteres implicados en el índice de selección que la que se obtiene cuando se considera exclusivamente información fenotípica y de parentesco (Muir, 2007; Shumbusho, 2013). Otra ventaja importante de la evaluación genómica es que, a edades tempranas de los candidatos, incluso antes de que estos tengan registros fenotípicos, como puede ser el caso de embriones fertilizados *in vitro*, ya se pueden conseguir predicciones de valor genético con precisiones elevadas (König *et al*., 2009; Hayes *et al*., 2013; Shumbusho, 2016). Además, en el caso de los cerdos, así como en otras especies prolíficas, se obtendrán distintos valores de predicción de valor genético para hermanos completos sin registros, lo que ofrece la posibilidad de identificar a los mejores animales con arreglo al criterio dentro de la camada. Cuando se hacen evaluaciones basadas exclusivamente en la información de parentesco y fenotípica no es posible hacer esta distinción, y a todos los animales de la misma camada, antes de que tengan dato, se les asignará la misma predicción de valor genético, el promedio del valor genético de los padres.

La ganancia en precisión de la predicción del valor genético se puede explicar simplemente por el hecho de que en lugar de trabajar con parentesco esperado (los valores de parentesco que se pueden obtener con la información genealógica) se trabaja como parentesco realizado, es decir, se puede distinguir que entre un grupo de hermanos completos, aunque en promedio su parentesco sea 0.5, entre algunas parejas este parentesco será un poco mayor y en entre otras será un poco menor. Esto se consigue porque gracias a la información de los genotipos se tienen las segregaciones mendelianas que se han producido y no es preciso trabajar con los valores esperados de estas segregaciones (Kinghorn *et al*., 1991; Mackinnon y Georges, 1998). Visto de otra forma, como originalmente lo propusieron Meuwissen *et al*. (2001), la ventaja de la selección genómica es que permite incluir el efecto de marcadores moleculares que están ligados a los genes causales en las evaluaciones genéticas. Ambas interpretaciones son equivalentes (Goddard *et al*., 2019).

La posibilidad de anticipar las decisiones de selección a edades más tempranas puede suponer en porcinos una reducción del 25% en el intervalo generacional (Meuwissen et al., 2016). En algunos estudios realizados con diferentes especies domésticas se han encontrado importantes incrementos de ganancia genética con la selección genómica, producto tanto de la reducción en el intervalo generacional, como del aumento en la precisión de la estimación de los valores genéticos. En vacuno lechero cuando la selección genómica se emplea para evaluar toros jóvenes de remplazo se pueden incrementar las respuestas a la selección, con respecto a la que se tenía antes de utilizar las técnicas genómicas, entre un 12% y un 100%, dependiendo del carácter. Estos incrementos son en parte consecuencia de la reducción del intervalo generacional que ha pasado de 5 a 1.5 años (Pryce y Daetwyler, 2012). En otro estudio se observaron también importantes ventajas cuando se evaluaron dos índices de selección con información genómica en ovejas, uno para caracteres productivos y otro para caracteres reproductivos. Los incrementos en las respuestas fueron, con respecto a los índices que sólo emplean información fenotípica y de parentesco, del 8% para el índice productivo y del 72% para el reproductivo (Shumbusho *et al*., 2013). Del mismo modo, en una evaluación realizada para caracteres relacionados con la producción de huevos en gallinas ponedoras se observó que cuando se evalúa a estos caracteres con información genómica, la ganancia genética es un 60% más grande que el valor de ganancia que se obtiene con el método tradicional (Sitzenstock *et al*., 2013). En el caso del porcino, para los caracteres reproductivos como tamaño de camada, peso de la camada y otros relacionados que se miden en el primer parto de las cerdas, que normalmente presentan baja heredabilidad, se observó que considerar información genómica puede dar lugar a ganancias de entre un 23% y un 91% más grandes que las que se observan cuando sólo se considera información fenotípica de los candidatos a la selección (Lillehammer *et al*., 2011), el importante rango de ganancias se debe a que representa distintos escenarios de estructura y cantidad de información genómica disponible. Además de este, en otros estudios realizados con porcino se han reportado importantes incrementos (con respecto a los métodos tradicionales) de precisión en la predicción de los valores genéticos y por tanto también de respuesta para caracteres como el tamaño de camada (Tusell *et al*., 2013), el número de pezones (Lopes *et al*., 2017), la mortalidad al destete (Knol *et al*., 2016), en caracteres relacionados con el contenido graso de la carne (Bergamaschi *et al*., 2019), en caracteres de eficiencia alimentaria como el consumo de alimento (Tribout *et al*., 2012; Nirea y Meuwissen, 2017) o incluso en caracteres de crecimiento donde se usan modelos que incluyen los efectos de interacción social (Hong *et al*., 2019).

Más allá de las predicciones de valor genómico la información molecular permite identificar genes o regiones del genoma implicados en el control de los distintos caracteres productivos y reproductivos. Nuestro interés aquí se centra en diferentes caracteres de eficiencia alimentaria como pudiera ser el caso del consumo de pienso residual, para él se han reportado ocho genes diferentes que pudieran estar implicados en su control (*XIRP2*, *TTC29*, *SOGA1*, *GPCR*, *GRK5*, *PROX1*, *GPR155* y *ZFYVE26*), genes que se encuentran a su vez implicados en diferentes procesos metabólicos (Do *et al*., 2014). En otro estudio con este mismo carácter se han encontrado también otros dos genes (*FTO* y *TCF7L2*) que igualmente parecen controlarlo, en este caso se trata de genes que pudieran tener un efecto pleitrópico sobre caracteres que claramente están vinculados con la eficiencia alimentaria, como es el caso del espesor de grasa dorsal y del crecimiento (Fan *et al*., 2010). También se han reportado dos genes (*HIF1AN* y *LBX1*) que pudieran tener importante influencia sobre el índice de conversión de alimento (Sahana *et al*., 2013). Existen también otros estudios donde se han identificado genes que afectan a diferentes caracteres de eficiencia alimentaria como el consumo de alimento (Davoli *et al*., 2012; Onteru *et al*., 2013; Fu *et al*., 2020; Wang *et al*., 2020), la ganancia media diaria (Fan *et al*., 2010), y los niveles de grasa (Fan *et al*., 2009; Fu *et al*., 2020). Todos estos estudios proveen información muy relevante para entender los mecanismos genéticos que regulan los diferentes procesos fisiológicos relacionados con los caracteres de eficiencia alimentaria.

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2. OBJETIVOS

Esta tesis doctoral se ha realizado dentro del marco de tres proyectos públicos de investigación, uno fue el proyecto Feed-a-Gene que recibió financiación del programa Horizonte 2020 de la Unión Europea con código de referencia 63353, y los otros fueron proyectos del plan nacional de investigación concedidos al IRTA - RTA2014-00015-C02-01 y RTI2018-097610-R-I00 -. La temática general de los tres proyectos de investigación citados es la eficiencia alimentaria en especies monogástricas: Cerdos, Pollos y Conejos. En ellos se abordan distintos aspectos de la eficiencia, en Feed-a-Gene incluyendo cuestiones relativas a otras disciplinas distintas a la mejora genética, como son la nutrición y la fisiología. En el caso de los proyectos del plan nacional todas las actividades desarrollas se afrontan desde la perspectiva de la mejora genética, pero abarcan más aspectos que los estrictamente considerados en esta tesis.

En consonancia con el objetivo global que define la línea de trabajo en la que se encuadran los citados proyectos, el objetivo general de esta tesis fue explorar mecanismos directos e indirectos de selección para proponer en ganado porcino estrategias de mejora de la eficiencia alimentaria que permitan reducir los costes de inversión en sistemas de control de registro de consumo, con respecto a la situación óptima de evaluación y selección que sería la representada por un esquema en el que de forma sistemática se recogen datos individuales de consumo de animales alojados en corrales colectivos.

Los objetivos específicos en que se desarrolla el citado objetivo general son los siguientes:

1) Evaluar la relación que existe entre las medidas de consumo individual, y de otros caracteres productivos, y las medidas de comportamiento alimentario, siendo tanto el consumo como los caracteres de comportamiento alimentario recolectados usando comederos electrónicos.

2) Explorar para las relaciones indicadas en el objetivo uno, qué papel pueden jugar los efectos indirectos de interacción social entre los animales que componen los corrales.

3) Evaluar si la consideración de modelos animales que incluyen los efectos de interacción social da lugar a estructuras de covarianzas que permitan una selección indirecta de la eficiencia alimentaria, mediante la reducción del espesor de tocino dorsal y el incremento del crecimiento diario, que la que se puede conseguir en base a evaluaciones genéticas con el modelo animal tradicional.

4) Con el propósito de evaluar lo que pueda aportar para un programa de mejora genética de la eficiencia alimentaria la información de consumo recogida no a nivel individual, sino a nivel de grupo, se va a determinar la correlación genética entre caracteres productivos y tanto medidas de consumo individual recolectadas con comederos electrónicos como medidas de consumo calculadas como la media de los consumos de los animales de cada corral.

5) Explorar tanto los parámetros genéticos como la predicción fenotípica del consumo individual bajo distintas estructuras de distribución de datos de consumo individuales o colectivos, para identificar la cantidad mínima de datos individuales requeridos para aprovechar la mayor cantidad de datos colectivos.

6) Explorar la variación con la edad en el determinismo genético que tanto los caracteres productivos como de eficiencia pudieran tener, con el fin de definir los momentos óptimos para la recogida de los distintos caracteres de forma que los parámetros genéticos de los mismos sean tales que se maximice la respuesta en la eficiencia alimentaria.

3. ARTÍCULOS Y ESTUDIOS

3.1. Indirect genetic effects on the relationships between production and feeding behaviour traits in growing Duroc pigs

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Abstract

Performance and feeding behaviour traits in growing pigs could be affected by social interaction effects when animals are raised in group. So, properly knowing the genetic correlations between direct and social interaction effects among performance and feeding behaviour traits could improve the accuracy of the genetic evaluations. Our aim was to explore the role of feeding behaviour traits (FBT) and indirect genetic effects (IGEs) in the genetic evaluations of growing pigs. Thus, genetic parameters were estimated for production traits (PT): average daily gain, average daily feed consumption, feed conversion ratio and backfat thickness; as well as for FBT: average daily feeding rate, average daily feeding frequency, average daily occupation time and average daily time between consecutive visits. Traits were recorded in 1144 Duroc pigs during the fattening period. Two bivariate models were fitted: classic animal model and an animal model fitting IGE. Estimations were done following Bayesian procedures. Heritability estimates obtained with classic animal model for all studied traits were medium-high. The additional heritable variation captured by IGE supposed that the ratios of total genetic variance to phenotypic variance (T2) were higher than the heritability estimates obtained with the classic model, except for occupation time trait, when a lower value (0.20 ± 0.19) was estimated. This is due to a high and negative correlation between IGE and direct genetic effects (DGEs) of this particular trait (−0.78 ± 0.27). Results from classic animal model do not evidence a clear role of FBT to improve the accuracy of breeding value predictions for PT; only average daily feeding rate seems to show a positive correlation (around 0.50 to 0.60) with average daily gain, average daily feed consumption and backfat thickness. However, when IGE model was fitted, the number of estimates of genetic correlations between FBT and PT showing a relevant magnitude increased, generally for the correlations between IGE of FBT and DGE of PT; or particularly for the correlations between IGE of average daily feeding frequency, and the IGE of all the PT, except average daily gain. Thus, in evaluations using the animal model with IGE fitted, the inclusion of FBT could aid the improvement of the accuracy of breeding value predictions for PT. This is a consequence of the improved genetic relationships between traits that can be fitted when considering such models.

Implications

The accuracy of breeding value prediction for production traits could be improved if correlated traits are jointly considered in evaluations, and such traits could be feeding behaviour traits. Feeding behaviour traits as well as production traits are recorded in group housed animals; thus, animal models fitting indirect genetic effects could be a tool to account for this fact. Our results show that these models are preferable over the traditional animal model for both production traits and feeding behaviour traits, and particularly when the evaluation is done using animal models fitting indirect genetic effects. The breeding value prediction accuracy for production traits could be increased in such a joint evaluation with feeding behaviour traits, since certain correlations between genetic effects across traits show relevant magnitudes. In addition, these animal models fitting indirect genetic effects offer an improved correlation structure and alternative selection indexes.

Introduction

The relationship between production and behaviour traits is particularly relevant when the animals are reared sharing a common space, as it commonly occurs in swine (Chen et al., 2007; Ellen et al., 2014). Under this housing system, although it could be difficult or costly, obtaining measures of individualized consumption is possible at certain levels of a breeding schema, that is, selection nucleus. This can be done thanks to the availability in the market of feeding devices allowing individual feed intake recording (Eissen et al., 1998). These devices also allow for the recording of individual feeding behaviour traits (FBT; Young, 2012), which might play an important role in any selection programme to improve growth or feed efficiency in pigs as far as they show relevant heritability and moderate genetic correlation with traits of direct economic importance (Labroue et al., 1997; Young et al., 2011). However, these FBT, as they would be recorded in group-housed animals, could be subject to the same issues of interactions between group mates as happen with performance traits (Griffing, 1967; Bijma and Wade, 2008). In this context, animal models fitting indirect genetic effects (AM-IGEs) could be relevant in the exploration of both direct and indirect correlations between PT and FBT. These models assume that the phenotype of an individual is influenced by both genetic effects in the individual itself (direct genetic effect (DGE)) and genetic effects in its pen mates; these are known as indirect genetic effects (IGEs; Bijma and Wade, 2008). The objective of this work was to estimate genetic parameters of PT and FBT during the fattening period in a Duroc line considering either traditional animal models or AM-IGE, with the aim of assessing the role that these FBT might play in a breeding programme for feed efficiency.

Material and Methods

Animal and management

Performances during growing-fattening period (10 – 26 weeks of age) on 1 144 Duroc pigs were recorded in 10 batches from 2007 to 2017 at the Center of Porcine Evaluation (Monells, Girona, Spain) using IVOG feeding stations (Insentec, Markenesse, The Netherland) with a single-space feeder for each pen. Animals represented 430 litters sired by 85 boars and from 399 different sows. The completely known pedigree comprises 5 077 individuals from 671 sires and 3 264 dams. This Duroc line was founded in 1991 (Tibau et al., 1999) and selected as multi-purpose line until the mid 2000's, when the selection index applied changed with the aim of specializing the population as a maternal line, since then most of the weight in the index has been assigned to prolificacy and backfat thickness. For our study, the animals with phenotypic information were housed in 97 different pens having on average (standard deviation) 12.0 (1.5) animals per pen, the size of the pens ranged from 7 to 15 animals. The age at the start of the control was 70 (6) days old and the age at the end of the control was 177(9) days old. In all the batches animals were fed ad libitum on a standard diet satisfying their requirements. As our data covers a long period of time (10 years) certain variation in the diet composition exists across batches. Nevertheless, the average nutrient composition across batches and fattening phases (growing (20-60 Kg) and finishing (60-100/110 Kg)) was the following: 15.0% CP, 4.7% fibre, 4.5% fat, 0.9% lysine and 0.3% methionine, having 3 200 Kcal of metabolic energy per Kg of feed. Variability in the diet across batches will be statistically accounted for by fitting a batch effect in the models. A number of feeding behaviour traits as well as daily feed intake and other production traits were recorded.

Production traits (PT) description

Individual live body weight (BW, kg) and backfat thickness (BF, mm) were recorded during the fattening period, the number of measures performed for both traits on each animal ranged from 4 to 11. BF was measured at 5 cm of the midline between the third and fourth last ribs using ultrasounds (PIGLOG 105, SFK-Technology, Herlev, Denmark). A linear regression model within each animal data set was fitted individually to adjust BF to 180 days of age ($BF_{ij} = \alpha_i + \beta_i * age_{ij} + e_{ij}$). We used this age in spite of the fact that the average age at the end of the fattening period is a few days less (177) because 180 d is the reference age used for the selection of the line, the difference with most of the individual ages at the end of the fattening period is small (no more than 15 days), and around these ages a fairly linear pattern was observed. Average daily gain (ADG, kg/d) was individually computed also using a within-animal linear regression model of live body weight on age, i.e.: $BW_{ij} = \alpha_i + ADG_i * age_{ij} + e_{ij}$. Average daily feed consumption (ADC, kg/d) was computed following Sanchez et al. (2017); missing daily feed intake records were predicted using animal-nested random polynomial regressions and the ADC for a particular animal was defined as the mean of all the available individual daily feed intake records. Feed conversion ratio (FCR) was computed as ADC divided by ADG.

Feeding behaviour traits (FBT) description

The electronic feeders directly report only the duration of each visit to the feeder, from this information, and from the daily occupation pattern, four FBT referring to the completely fattening period were derived. In an initial edition step, hourly blocks were defined, and for each hour and individual, mean feeding rate (g/min), total feed intake (g), number of visits to the trough (number of visits) and total time occupying the trough (s) were calculated. From these hourly basis measurements, daily aggregates for feeding rate, number of visits and time occupying the trough were obtained, for the case of feeding rate the aggregation was only done averaging hours in which feed intake information was recorded, for the case of number of visits and occupation time the aggregation was calculated by summing. In addition, average daily time between consecutive visits to the feeder were computed from hourly records, this was done first by computing the hourly interval between day hours having visits to the feeder and then averaging within animal and day information. Finally, fattening period measurements were obtained as within-animal average across daily aggregates. The resulting traits to be analysed were average daily feeding rate (FR, g/min), average daily feeding frequency (FF, visits), average daily occupation time (OT, min) and average daily time between consecutive visits (FInt, h). Table 1 presents basic statistics of all the aforementioned traits.

Table 1 Descriptive statistics for performance and feeding behaviour traits of growing Duroc pigs

Category	Trait	No. of observations	Minimum	Mean	Maximum	SD
Behaviour	FR, g/min	1 144	15.28	38.60	65.14	7.41
	OT, min	1 144	33.02	60.72	103.49	10.27
	FF, visits	1 144	3.54	10.11	24.88	2.98
	FInt, h	1 144	1.64	3.93	9.89	1.03
Performance	ADG, kg	1 144	0.22	0.82	1.07	0.09
	ADC, kg	1 144	0.86	2.31	3.67	0.37
	FCR	1 144	2.07	2.77	3.89	0.24
	BF, mm	1 144	6.44	18.19	32.74	4.40

FR: average daily feeding rate, OT: average daily occupation time, FF: average daily feeding frequency, FInt: average daily time between consecutive visits, ADG: average daily gain, ADC: average daily consumption, FCR: feed conversion ratio, BF: backfat thickness.

Statistical models

Two bivariate animal models, either considering or not, indirect genetic effects (IGE), were implemented. For all studied traits, the same systematic effects were fitted: Batch (10 levels), age at the end of the control period (covariate) and number of pigs in the pen (covariate). In addition, pen and litter effects were also included, as well as the additive genetic effect. All the previous effects were fitted in the classic animal model (AM) whereas in the AM-IGE, the genetic component was divided into direct and indirect genetic effects (Bijma and Wade, 2008; Duijvesteijn et al., 2012). This last case is the most complex model studied and is represented by the following equation:

$$\begin{bmatrix} \boldsymbol{y_1} \\ \boldsymbol{y_2} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X_1} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{X_2} \end{bmatrix} \begin{bmatrix} \boldsymbol{b_1} \\ \boldsymbol{b_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{p_1}} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{Z_{p_2}} \end{bmatrix} \begin{bmatrix} \boldsymbol{p_1} \\ \boldsymbol{p_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{l_1}} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{Z_{l_2}} \end{bmatrix} \begin{bmatrix} \boldsymbol{l_1} \\ \boldsymbol{l_2} \end{bmatrix} +$$
$$\begin{bmatrix} \boldsymbol{Z_{d_1}} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{Z_{d_2}} \end{bmatrix} \begin{bmatrix} \boldsymbol{d_1} \\ \boldsymbol{d_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{s_1}} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{Z_{s_2}} \end{bmatrix} \begin{bmatrix} \boldsymbol{s_1} \\ \boldsymbol{s_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{e_1} \\ \boldsymbol{e_2} \end{bmatrix}$$

Where $\boldsymbol{y_1}$ and $\boldsymbol{y_2}$ are the vector of observations for the first and second trait, ***b*** is a vector of systematic effects with incidence matrix ***X***; ***p*** is a vector of pen effects with incidence matrix $\boldsymbol{Z_p}$; ***l*** is a vector of litter effects with incidence matrix $\boldsymbol{Z_l}$; $\boldsymbol{d}$ is a vector of direct genetic effects (DGE) with incidence matrix $\boldsymbol{Z_d}$, $\boldsymbol{s}$ is a vector of indirect genetic effects with incidence matrix $\boldsymbol{Z_s}$. The elements of $\boldsymbol{Z}_s$ are 1 for the records from animals sharing the same pen and 0 otherwise; ***e*** is a vector of residuals.

Under AM-IGE model, each individual interacts with *n-1* of its group members where *n* is the group size. Under this model, the total breeding value of an individual i is equal to TBV_i=$d_i + (n-1)s_i$. The total breeding values variation among individuals is σ^2_{TBV}= $\sigma^2_d + 2(n-1)\sigma_{d,s} + (n-1)^2\sigma^2_s$. The ratio between the total breeding value variation and the total phenotypic variance (T^2) might exceed one; because the total phenotypic variation is $\sigma^2_{Phe} = \sigma^2_d + (n-1)\sigma^2_s + r * (n-1) * \left[2\,\sigma_{d,s} + \ (n-2)\sigma^2_s\right] + \sigma^2_p + \sigma^2_l + \sigma^2_e$, where σ^2_d is the direct genetic effects variance, σ^2_s is the indirect genetic effects variance, $\sigma_{d,s}$ is the covariance between direct and indirect genetic effects, σ^2_p is the pen effect variance, σ^2_l is the litter effect variance, σ^2_e is the error variance and r is the mean kinship coefficient between pen members, in our case this coefficient was equal to 0.13. Bijma *et al.* (2007) already presented all these parameter definitions.

Bayesian procedures were used to estimate model parameters, the prior distribution of pen, litter effect and the residuals were: $\boldsymbol{p}|\boldsymbol{P_0}{\sim}N(\boldsymbol{0},\boldsymbol{P_0}\ \otimes \boldsymbol{I})$; $\boldsymbol{l}|\boldsymbol{L_0}{\sim}N(\boldsymbol{0},\boldsymbol{L_0}\ \otimes \boldsymbol{I})$ and $\boldsymbol{e}|\boldsymbol{R_0}{\sim}N(\boldsymbol{0},\boldsymbol{R_0}\ \otimes \boldsymbol{I})$ respectively, where ***I*** are identity matrices of appropriate dimensions, and $\boldsymbol{P_0}$, $\boldsymbol{L_0}$ and $\boldsymbol{R_0}$ are covariance matrices of dimension 2, containing pen, litter and residual (co)variances of the two traits studied at the time and $\otimes$ denotes the kronecker product. All factors were assumed to be independent, except direct and indirect genetic effects. For them the assumed prior distribution was:

$\begin{bmatrix}\boldsymbol{d}\\ \boldsymbol{s}\end{bmatrix}|\boldsymbol{G_0}{\sim}MVN(\boldsymbol{0},\boldsymbol{G_0}\otimes\boldsymbol{A})$, where $\boldsymbol{A}$ is the numerator relationship matrix between individuals, $\boldsymbol{G_0}$ is the covariance matrix, containing the following elements:

$$\boldsymbol{G_0}=\begin{bmatrix}\sigma^2_{d_1} & \sigma_{d_1,d_2} & \sigma_{d_1,s_1} & \sigma_{d_1,s_2}\\ \sigma_{d_1,d_2} & \sigma^2_{d_2} & \sigma_{d_2,s_1} & \sigma_{d_2,s_2}\\ \sigma_{d_1,s_1} & \sigma_{d_2,s_1} & \sigma^2_{s_1} & \sigma_{s_1,s_2}\\ \sigma_{d_1,s_2} & \sigma_{d_2,s_2} & \sigma_{s_1,s_2} & \sigma^2_{s_2}\end{bmatrix}$$

where $\sigma^2_{d_1}$ is the direct genetic variance of first trait, $\sigma^2_{s_2}$ the indirect genetic variance for second trait, σ_{d_1,s_1} and σ_{d_2,s_2} are the covariance between DGE and IGE, for the first and the second trait respectively, σ_{d_1,s_2} is the covariance between DGE of first trait and IGE of second trait, σ_{d_1,d_2} is the covariance between DGE of the two traits and finally σ_{s_1,s_2} is the covariance between IGE of the two traits. In the Bayesian analysis performed, flat priors were assumed for systematic effects ($\boldsymbol{b}$) and for all the variance components previously described: $\boldsymbol{G_0}$, $\boldsymbol{P_0}$, $\boldsymbol{L_0}$ and $\boldsymbol{R_0}$.

The marginal posterior distributions of all unknown parameters were obtained using the Gibbs Sampling algorithm, with the program gibbs2f90 (Misztal et al., 2002). Chains of 1 000 000 samples were run and the first 100 000 iterations were discarded in order to allow the algorithm to reach convergence to the marginal posterior distributions. Then, one sample every 10 iterations was saved, thus the autocorrelation of the chain was reduced. Convergence of the Markov chains was assessed by visual inspection of the trace plots. Finally, Deviance Information Criterion (DIC, Spiegelhalter et al., 2002) was used in order to compare the models based on their fitting quality but penalizing by model complexity.

Results

Heritabilities, ratios of litter and pen variances to phenotypic variance and magnitude of indirect genetic effects

The first remarkable result is that for all considered traits, IGE plays an important role. This is evidenced by the fact that DIC values are always substantially lower

(<18) in the AM-IGE than in the AM (Table 2). In addition to this, the magnitude of T2 was higher than the heritability from the AM for all the studied traits, except for the occupation time in the feeder (posterior mean ± posterior SD) (0.20 ± 0.19). The low value of T2 for the occupation time is related to the fact that a high and negative genetic correlation was estimated between IGE and DGE for this particular trait (−0.78 ± 0.27) with a probability greater than 95% of being lower than zero. This correlation means that individuals with a positive DGE, for animals staying longer in the feeder, tend to have negative IGE, forcing their pen mates to stay for less time. Litter effect variance represented 7% to 14% phenotypic variance for PT and 2% to 6% phenotypic variance for FBT. The ratio of pen variances to phenotypic variances ranged from 4% to 13% for PT and from 6% to 13% for FBT.

Estimated phenotypic and genetic correlations using classic animal model

Although the relevance of IGE is clear, this section presents the genetic and phenotypic correlations between traits obtained with the traditional AM (Table 3). These correlations are presented to describe a putative social structure in the pen, and also to establish a basis for later discussion on the genetic correlations between traits based on the AM-IGE. With regard to the phenotypic correlations nearly all of them can be said to be statistically different from zero. The feeding rate and the occupation time are positively correlated at phenotypic level with all PT, ranging from 0.11 to 0.42. These correlations between the feeding frequency and all the PT are much lower and negative, as high as −0.11. Within FBT, the feeding rate was positively correlated with the time between visits (0.10) and negatively correlated with occupation time (−0.65) and feeding frequency (−0.11). The phenotypic correlation between occupation time and feeding frequency was estimated to be positive (0.20), while negative with the time between visits (−0.28). Finally the estimated phenotypic correlation between feeding frequency and time between visits was −0.60. Regarding the genetic correlations, ADC was positively correlated with the other PT: FCR (0.66 ± 0.22), BF (0.64 ± 0.16) and ADG (0.80 ± 0.13). The genetic correlation between BF and ADG was positive (0.51 ± 0.25).

Table 2 Marginal posterior means (standard deviations) of ratio of variances and DIC of growing Duroc pigs using univariate animal models with and without indirect genetic effects

	AM		AM-IGE						
Trait	h^2	DIC	σ^2_{Phe}	T^2	$\sigma^2_d/\sigma^2_{Phe}$	$\sigma^2_p/\sigma^2_{Phe}$	$\sigma^2_l/\sigma^2_{Phe}$	r(S,D)	DIC
FR	0.30(0.08)	7304.83	48.73(3.38)	0.39(0.29)	0.32(0.08)	0.13(0.04)	0.04(0.03)	-0.19(0.70)	7282.56
OT	0.23(0.10)	8097.19	84.98(4.82)	0.20(0.19)	0.27(0.10)	0.08(0.03)	0.06(0.04)	-0.78(0.27)*	8055.65
FF	0.48(0.09)	4871.82	8.72(0.83)	0.93(0.49)	0.46(0.09)	0.12(0.06)	0.03(0.03)	-0.21(0.41)	4803.53
FInt	0.47(0.08)	2835.14	1.09(0.07)	0.67(0.30)	0.47(0.09)	0.06(0.03)	0.02(0.02)	-0.21(0.47)	2792.88
ADG	0.19(0.08)	2562.15	0.68(0.04)	0.22(0.18)	0.22(0.09)	0.04(0.02)	0.14(0.04)	-0.58(0.42)	2541.09
ADC	0.22(0.08)	5246.81	7.62(0.52)	0.29(0.29)	0.25(0.08)	0.11(0.04)	0.08(0.04)	-0.57(0.47)	5219.54
FCR	0.21(0.09)	4418.22	4.00(0.35)	0.55(0.43)	0.24(0.09)	0.13(0.05)	0.07(0.04)	-0.10(0.70)	4400.04
BF	0.32(0.10)	5579.10	10.75(0.72)	0.51(0.28)	0.35(0.11)	0.05(0.03)	0.09(0.04)	-0.02(0.61)	5553.75

AM: classic animal model, AM-IGE: Animal model including indirect genetic effects. FR: average daily feeding rate, OT: average daily occupation time, FF: average daily feeding frequency, FInt: average daily time between consecutive visits, ADG: average daily gain, ADC: average daily consumption, FCR: feed conversion ratio, BF: backfat thickness. h^2: heritability, DIC: deviance information criterion, σ^2_{Phe}: total phenotypic variance, σ^2_d: direct genetic effect variance, σ^2_p: pen variance, σ^2_l: litter variance, T^2: the ratio between the total breeding value variation and σ^2_{Phe}, $\sigma^2_d/\sigma^2_{Phe}$: portion of phenotypic variance explained by direct genetic effect, $\sigma^2_p/\sigma^2_{Phe}$: portion of phenotypic variance explained by pen effect, $\sigma^2_l/\sigma^2_{Phe}$: portion of phenotypic variance explained by litter effect, r(S,D): genetic correlation between direct and indirect genetic effects of the same trait.

*Probability of being greater than 0>0.95 or <0.05.

Finally, the genetic correlations between FCR and both ADG and BF had large estimation errors; thus, it was not possible to clearly define whether their values are positive or negative, but it seems to be of lower magnitude than the rest of the genetic correlations. Only two genetic correlations out of the six estimated between FBT showed a magnitude statistically different from zero (above diagonal in Table 3). This was the case between feeding rate and occupation time (−0.76 ± 0.16), and between feeding frequency and the time between visits (−0.78 ± 0.09). The other genetic correlations between FBT were low and with undefined signs due to their high estimation errors. The role that FBT might play on the prediction of breeding value for PT was defined by exploring the genetic correlation estimates between PT and FBT (Table 3). Only feeding rate was positively correlated at genetic level with most of the PT (ADG, ADC and BF).

Estimated genetic correlations using animal model fitting indirect genetic effects

Estimated genetic correlations between DGE for PT (above diagonal in Table 4) followed a similar structure to that of the genetic correlations between additive genetic effects obtained with the AM. The only remarkable difference was observed between FCR and BF; in this case the genetic correlation can be declared as positive (0.45 ± 0.19). The estimated genetic correlations between DGE for FBT (above diagonal in Table 4) were similar to the correlation structure between genetic effects from the AM (Table 3). With regard to the estimated genetic correlations between IGE of PT (below diagonal in Table 4), a similar correlations structure, with respect to their directions and also partially to their magnitudes, as that for DGE was observed. However, the estimated genetic correlations between IGE of FBT showed a different pattern (below diagonal in Table 4). The estimate of IGE correlation between the time between visits and occupation time was clearly negative (−0.74 ± 0.19) and the genetic correlation between IGE of feeding rate and the time between visits was also negative (−0.51 ± 0.25). The DGE correlation estimates between these two pairs of traits were not statistically different from zero. Regarding the estimated genetic correlations between DGE for PT and FBT (above diagonal Table 4), the structure was almost the same as that indicated for breeding values from AM; that is, the only FBT related with PT was feeding rate.

Table 3 Genetic (above diagonal) and phenotypic (below diagonal) correlations estimated of growing Duroc pigs using the classic animal model.

	FBT				PT			
Trait	FR	OT	FF	FInt	ADG	ADC	FCR	BF
FR		-0.76(0.16)*	0.22(0.20)	-0.31(0.20)	0.60(0.24)*	0.64(0.22)*	0.40(0.29)	0.53(0.24)*
OT	-0.65(0.02)*		0.27(0.25)	-0.33(0.26)	-0.24(0.38)	-0.30(0.37)	-0.28(0.39)	-0.33(0.36)
FF	-0.11(0.04)*	0.20(0.04)*		-0.78(0.09)*	0.11(0.26)	0.16(0.24)	0.15(0.25)	0.17(0.22)
FInt	0.10(0.04)*	-0.28(0.03)*	-0.60(0.03)*		-0.11(0.28)	-0.09(0.25)	0.04(0.28)	-0.32(0.23)
ADG	0.38(0.03)*	0.16(0.04)*	-0.11(0.04)*	0.10(0.04)*		0.80(0.13)*	0.14(0.41)	0.51(0.25)*
ADC	0.42(0.03)*	0.20(0.04)*	-0.11(0.04)*	0.04(0.04)	0.82(0.01)*		0.66(0.22)*	0.64(0.16)*
FCR	0.16(0.04)*	0.11(0.04)*	-0.03(0.04)	-0.05(0.04)	-0.05(0.04)	0.52(0.03)*		0.41(0.33)
BF	0.29(0.03)*	0.16(0.04)*	-0.09(0.04)*	-0.04(0.04)	0.59(0.03)*	0.68(0.02)*	0.31(0.03)*	

FBT: feeding behaviour traits, PT: production traits, FR: average daily feeding rate, OT: average daily occupation time, FF: average daily feeding frequency, FInt: average daily time between consecutive visits, ADG: average daily gain, ADC: average daily consumption, FCR: feed conversion ratio, BF: backfat thickness. *Probability of being greater than 0>0.95 or <0.05.

Table 4 Genetic correlations estimated among direct genetic effects (above diagonal) and among indirect genetic effects (below diagonal) for production and feeding behaviour traits of growing Duroc pigs using animal model fitting indirect genetic effects

	FBT				PT			
Trait	FR	OT	FF	FInt	ADG	ADC	FCR	BF
FR		-0.71(0.11)*	0.25(0.17)	-0.22(0.17)	0.45(0.19)*	0.47(0.17)*	0.24(0.21)	0.45(0.18)*
OT	-0.90(0.14)*		0.31(0.19)	-0.25(0.18)	-0.01(0.24)	0.02(0.24)	0.06(0.25)	-0.03(0.23)
FF	-0.24(0.29)	0.12(0.32)		-0.72(0.09)*	0.06(0.21)	0.06(0.19)	0.11(0.19)	0.11(0.18)
FInt	-0.51(0.25)*	-0.74(0.19)*	-0.99(0.01)*		-0.09(0.18)	-0.14(0.17)	0.20(0.19)	-0.21(0.18)
ADG	-0.10(0.35)	0.59(0.25)*	-0.82(0.19)*	-0.29(0.30)		0.83(0.08)*	0.13(0.25)	0.55(0.18)*
ADC	-0.14(0.37)	0.10(0.35)	-0.42(0.25)	-0.39(0.29)	0.70(0.21)*		0.61(0.16)*	0.73(0.11)*
FCR	0.61(0.23)*	-0.35(0.29)	-0.74(0.14)*	0.13(0.28)	0.06(0.38)	0.64(0.23)*		0.45(0.19)*
BF	0.16(0.37)	0.28(0.34)	-0.89(0.12)*	-0.97(0.03)*	0.67(0.26)*	0.55(0.26)*	0.75(0.25)*	

FBT: feeding behaviour traits, PT: production traits, FR: average daily feeding rate, OT: average daily occupation time, FF: average daily feeding frequency, FInt: average daily time between consecutive visits, ADG: average daily gain, ADC: average daily consumption, FCR: feed conversion ratio, BF: backfat thickness. *Probability of being greater than 0>0.95 or <0.05.

The image with respect to the relationships between PT and FBT regarding IGE (below diagonal in Table 4) was different; in this case, IGE for feeding frequency was negatively correlated with IGE of all PT, except ADC. Therefore, animals that tend to force their mates into going to the feeder very frequently also produce an effect on their mates that reduces their ADG, BF and FCR. Similarly, animals that tend to increase the time between consecutive visits to the feeder of their mates also produce a reduction in their mates' BF, and the genetic correlation between IGE of the time between visits and BF is close to −1. In addition, the relationships among IGEs show that animals tending to reduce the occupation time of their mates also reduce their ADG, and the estimated genetic correlation between IGE of the occupation time and ADG was 0.59 ± 0.25. Finally, it seems that animals forcing their mates to eat at a higher pace also produce an increase in their mates' FCR. This is because a positive correlation was estimated between IGEs of feeding rate and FCR (0.61 ± 0.23).

In order to have a full picture of the genetic structure between traits when considering AM-IGE for genetic evaluation purposes, it is necessary to study the genetic correlations between traits combining IGE and DGE (Table 5). Among PT the only correlation that was statistically different from zero involved DGE of FCR and IGE of ADG (0.73 ± 0.14). This positive correlation means that animals with a favourable genetic value to induce higher growth rates in their mates also tend to have genetic effects that worsen its own FCR. With regard to FBT, the only correlations between IGE and DGE seeming to be statistically different from zero were that involving DGE of the time between visits and IGE of feeding rate (−0.54 ± 0.20), and those between DGE of feeding frequency and IGE of feeding rate and occupation time (0.68 ± 0.11 and 0.37 ± 0.17, respectively); that is, animals with breeding values that increase their own feeding frequency also have genetic effects that increase feeding rate and occupation time of their mates. With respect to the correlations involving IGE of PT and DGE of FBT, all were relatively weak, and the observed estimation errors do not allow for properly declaring whether they are positive or negative. However, regarding the correlations between IGE of FBT and DGE of PT, many of them were statistically different from zero. For example, DGE of FCR correlates with IGE of all FBT except for feeding rate; as in some cases this correlation was positive (with occupation time and the time between visits), but in another case it was negative (with feeding frequency). Yet another case in which important correlations were detected involved DGE of ADC and IGE of feeding rate feeding frequency and the time between visits. Regarding DGE of BF, it only seemed to be positively correlated with IGE of feeding rate. Finally, it has to be remarked that DGE of ADG was positively correlated with IGE of the time between visits (0.88 ± 0.10) and IGE of feeding rate (0.89 ± 0.11); animals with favourable genetic effects for their own growth tend to carry genetic effects that incline their mates to have longer interval between consecutive visits and to show a high eating speed.

Table 5 Genetic correlations estimated between indirect (IGE) and direct genetic effects (DGE) for different combinations between production and feeding behaviour traits of growing Duroc pigs using animal model fitting indirect genetic effects

	FBT				PT			
Trait	FR$_{DGE}$	OT$_{DGE}$	FF$_{DGE}$	FInt$_{DGE}$	ADG$_{DGE}$	ADC$_{DGE}$	FCR$_{DGE}$	BF$_{DGE}$
FR$_{IGE}$		0.41(0.32)	0.68(0.11)*	-0.54(0.20)*	0.89(0.11)*	-0.82(0.15)*	-0.15(0.34)	0.47(0.18)*
OT$_{IGE}$	0.28(0.31)		0.37(0.17)*	0.33(0.23)	-0.19(0.27)	-0.15(0.23)	0.43(0.21)*	0.01(0.25)
FF$_{IGE}$	-0.15(0.30)	-0.10(0.31)		0.16(0.25)	-0.09(0.36)	-0.53(0.24)*	-0.55(0.23)*	-0.26(0.32)
FInt$_{IGE}$	0.08(0.32)	0.13(0.34)	0.28(0.24)		0.88(0.10)*	0.98(0.02)*	0.57(0.19)*	0.06(0.28)
ADG$_{IGE}$	0.05(0.35)	-0.11(0.34)	-0.06(0.32)	-0.30(0.26)		-0.07(0.26)	0.73(0.14)*	0.29(0.27)
ADC$_{IGE}$	0.11(0.34)	-0.05(0.36)	0.15(0.27)	-0.26(0.28)	-0.42(0.31)		0.24(0.25)	0.07(0.22)
FCR$_{IGE}$	0.13(0.36)	-0.04(0.33)	0.16(0.26)	-0.003(0.26)	-0.27(0.35)	-0.33(0.32)		-0.3(0.34)
BF$_{IGE}$	-0.27(0.32)	-0.03(0.36)	-0.14(0.32)	0.03(0.27)	-0.17(0.37)	-0.29(0.32)	0.06(0.43)	

DGE: direct genetic effect, IGE: indirect genetic effect, FBT: feeding behaviour traits, PT: production traits, FR: average daily feeding rate, OT: average daily occupation time, FF: average daily feeding frequency, FInt: average daily time between consecutive visits, ADG: average daily gain, ADC: average daily consumption, FCR: feed conversion ratio, BF: backfat thickness. *Probability of being greater than 0>0.95 or <0.05

Discussion

Our results clearly address the important role of IGE on the definition of traits recorded in animals raised in groups. This finding was already reported for PT in other pig populations (Bergsma et al., 2008; Chen et al., 2008; Nielsen et al., 2018). Until now, at least to our knowledge, there were no reports on the relevance of the IGE for FBT. These traits have been always considered using AM, and their estimated heritabilities were moderate to high (Young 2012; Do et al., 2013; Lu et al., 2017). When we applied the AM to these traits, we did also find, in general, high heritabilities, ranging from 0.23 to 0.47. Although our model choice criteria favoured the model AM-IGE, the estimation errors of certain parameters, in particular the correlation between IGE and DGE, were high, and only for the case of trough occupation time its negative value can be statistically defined. This indicates that animals with genetic effects to stay longer in the feeder also carry genetic effects that make their mates to shorten their occupation time. The occupation time is a trait with an upper limit (24 h); thus if one animal stays longer in the feeder, its mates consequently have to stay for less time; so, as a result of its definition, a phenotypic correlation would be expected between direct and indirect phenotypic effects. Thus, the estimated genetic correlation could be a consequence of this expected phenotypic relationship.

Hypothesised social hierarchical structure based on correlations between feeding behaviour traits

Indirect genetic effects for a given trait are relevant because of the presence of social interactions between the animals sharing the pen (Bijma, 2014), and these interactions are a direct reflection of the social structure and hierarchy within the group (Meese and Ewbank, 1973). In our study, we have not directly recorded this social structure; however, by inspecting the phenotypic correlations between traits (Table 3, below diagonal), particularly FBT, it could be possible to hypothesise a certain social structure. Therefore, based on the phenotypic correlations between FBT, it can be concluded that animals could be clustered into two groups: (1) Dominants: animals that eat sedately (lower feeding rate), occupying the feeder for a long time (higher occupation time), with a large number of visits (higher feeding frequency) and with shorter intervals between them (lower time between visits). (2) Subordinates: animals that eat more quickly, spending less time in the feeder trough, having a reduced number of visits per day and with longer intervals between visits. This clustering of animals was confirmed using a k-means algorithm on raw phenotypic FBT records; when the clustering was set to just two groups, the following means were defined for each group: Cluster 1 (556 animals) feeding rate = −0.56, occupation time = 0.60, feeding frequency = 0.53 and time between visits = −0.56; and Cluster 2 (588 animals) feeding rate = 0.53, occupation time = −0.56, feeding frequency = −0.50 and time between visits = 0.53, resembling the distribution hypothesised by analysing the phenotypic correlations.

A number of previous studies have researched the relationships between FBT and actual social hierarchy rank. This has been assessed experimentally by exploring the antagonistic interactions between growing pigs. In these studies the relationships are not exactly the same as those we have just hypothesised. Hoy et al. (2012) using crossbreds from Pietrain, Landrace and Duroc breeds showed that dominant animals tend to spend more time at the feeder, but in contrast with our hypothesized social hierarchy those animals had lower feeding frequency. Vargas et al. (1987) in another crossbred population did not find any association between the social rank and feeding frequency; however, they observed that animals with high feeding frequency tend to be those that suffer from a larger number of displacements and aggressions around the trough. Similarly, Nielsen et al. (1995 and 1996) in a LargeWhite×Landrace cross did not find any association between social rank and FBT; nevertheless, in these studies it is stated that this lack of association could be a consequence of the management in their experiments. One example of these management practices could be straw provision. So, apparently, the relationships between FBT and social ranks are far from stable and constant across populations and experiments. A large number of factors have been found to influence either FBT, social ranks or the relationship between them; for example, Baumung et al. (2006) show that differences between breeds have a large effect on FBT. The degree of kinship in a group could also influence the antagonist interactions within that group –which in turn defines the social rank indexes – (Fels et al., 2012), as well as the size of the groups (Nielsen et al., 1996). In addition, variation in certain internal physiological mechanisms, for example, satiety, might play an important role in the relationship between FBT and social rank position (Maselyne et al., 2015). This variety of results is one of the arguments used by Boumans et al. (2018) to propose simulation models as a tool to study the relationships between performances, social rank and FBT.

At a genetic level, given the higher estimation errors, not all the characteristics of the subordinates and dominant animals can be consistently defined. Thus, we could only postulate that dominant animals might carry genetic factors which cause them to eat at a slower pace for longer, and that they carry genetic factors which lead to a larger number of visits to the trough and to a reduced feeding interval. The consideration of AM-IGE will allow further assessment of whether the proposed hierarchy of the population is compatible with the estimated genetic correlations between IGEs within and across FBT. Dominant animals with genes which induce them to stay longer at feeder will also carry genes forcing their mates to play a subordinate role. These subordinates have them a shorter occupation time (negative correlation between DGE and IGE in Table 2), a shorter feeding rate (negative correlation between IGE of occupation time and IGE of feeding rate in Table 4) and lower time between visits (negative correlation between IGE of occupation time and IGE of time between visits in Table 4). Dominant animals will have DGE for increased feeding frequency, and they will induce a genetic effect on their subordinate mates, which supposes a reduction of this trait (negative correlation between IGE and DGE in Table 2). Based on the postulated phenotypic structure we have previously indicated, time between visits of subordinate animals should be increased in parallel to the decline of feeding frequency; this is confirmed by the strong negative (−0.99) correlation between IGE of time between visits and IGE of feeding frequency (Table 4). Dominant animals should have DGEs that reduce their own feeding rate and increase the feeding rate of their mates, and it would be expected that these subordinate animals would have an increased time between visits. Thus, a positive genetic correlation between IGE of feeding rate and IGE of time between visits would be expected, but a negative value has been estimated (−0.51). The available information does not allow us to further explain why this mismatch to our proposed structure happened. However, one simple explanation could be that some of the aforementioned correlations could have been over- or underestimated, and they do not allow for a fully coherent interpretation of the results. Another point, already mentioned, could be that other factors, beyond the social structure, influence the genetic and phenotypic correlations between traits. In spite of these exceptions we believe the overall scenario still applies and is therefore relevant: some animals capitalise the feeder, and others have to adapt to this situation.

Based on the previous discussion, it can be concluded that the parameter estimates of the multivariate models considering IGE are in some cases, but not always, compatible with a hypothesised social hierarchy structure assuming dominant and subordinate animals within pens. A better validation of the estimated model parameters would have been achieved if the actual social hierarchy had been properly assessed. Based, for example, on experiments measuring the degree of antagonistic interactions between pairs of pen mates, in order to define for each animal a social rank index value (one example of such indexes was proposed by Lee et al. (1982)) that could be treated as another trait can be explored for its correlations with PT and FBT.

Is the hypothesised social hierarchical structure evidenced in the relationships between feeding behaviour and production traits?

One of most relevant points in this study was to assess the role that FBT (as proxies of a hypothesised social hierarchy) might play in the genetic evaluation for PT. In this regard, the first assessment we will conduct will be to explore whether the hypothetical social structure defined by the phenotypic correlation among FBT is the major factor responsible for the correlation structure among PT. It can be anticipated that the structure among FBT is not transferred to PT. This can clearly be seen in the phenotypic correlations between feeding rate and all PT, which have the same sign (always positive) as the correlations between occupation time and the PT, when according to the hypothesised social hierarchy structure, correlations of opposite sign would be expected (the phenotypic correlation between feeding rate and occupation time is negative).

One could also expect dominant animals (with low feeding rate according to our hypothesis) to be those having the larger ADC (Hoy et al., 2012), but in light of observed phenotypic correlations this is not the case. These discrepancies, as those previously discussed among FBT, imply that in the definition of the correlations between FBT and PT, other factors beyond the hypothesised social hierarchy have intervened. For those genetic correlations estimated with the AM between FBT and PT being statistically different from zero, the same discrepancy between the postulated social structure and PT was found. Thus, we can only claim, as before, that these positive correlations between ADC, ADG and BF with feeding rate must be connected to some physiological mechanisms, and not only to the fact that the genes involved in defining the position within the social rank are also responsible for greater or lesser growth, intake or backfat depth. Among the processes explaining these positive correlations with feeding rate, we could propose the physical/hormonal satiation mechanism, described in the revision by Maselyne et al. (2015) or further internal mechanism involving other hormonal regulations and nutritional transport processes, previously described as being involved in the feed efficiency of the animals (Reyer et al., 2018).

An overall assessment of the correlations between IGE and DGE across both groups of traits (FBT and PT) seems to show that the predominant direction of this correlation is from IGE of FBT to DGE of PT (Table 5). Only for this group of correlations, values of relevant magnitude were estimated. This implies that IGE of FBT could determine PT, but IGEs of PT do not seem to influence FBT. The interpretation of the observed correlations in light of the postulated social hierarchical structure is extremely complex, and will not be made, given that the proposed social structure is just a hypothesis that has not always shown coherence with the estimated correlations. Nevertheless, the overall relationships between IGE and DGE among PT and FBT can be used to interpret finds in previous studies. Ragab et al. (2018) used FBT as predictors in models fitting IGE of PT, in particular ADG, aiming to improve the prediction performances of the AM-IGE. The limited gain in prediction quality observed in their study (4% to 5 %) can be explained because only IGE of FBT seems to be related to DGE of PT. No relevant correlations have been declared the other way around, that is, between IGE of PT and DGE of

FBT, which would be the relevant parameter to improve accuracy in the model proposed by Ragab et al. (2019).

Until now, our discussion has been driven by a hypothetical social structure, predicted from the phenotypic correlations, and this structure has been used to explain the obtained genetic correlations between traits, and their genetic components of traits (IGE and DGE). We have already indicated that not having the actual social structure in our population is an important limitation for interpreting our results. The other major limitation of our study is associated with the fact that a small dataset has been used to estimate correlation parameters in complex models. Thus, in some cases, large estimation errors have been reported. Nevertheless, when the estimates are precise enough to allow for properly defining the sign of the correlations, in many cases the reported estimates in relation to FBT are compatible with the proposed hypothesis.

Animal model fitting indirect genetic effects enriches the relationship between traits offering further selection index possibilities

Beyond the role that FBT might have played in the definition of PT correlation structure and how this relationship is established, another important result that deserves discussion is the fact that the consideration of multivariate models fitting IGEs would enrich the relationships between traits. This enriched structure could allow for the definition of selection indexes that might better address a given breeding goal. For example, with regard to PT, it was observed from additive genetic correlations obtained using the AM that it could be difficult to envisage selection indexes to indirectly improve FCR by reducing BF while increasing ADG (see genetic correlations in Table 3). However, by considering AM-IGE and differentially weighting IGE and DGE predictions, it could be possible to identify combinations between DGE and IGE (other than the often-used total breeding value prediction (Bijma, 2014)) that might yield a stronger direct response on ADG and BF and an indirect response on FCR. One example could be to select for reducing BF through its IGE, positively correlated with FCR IGE (0.75), while ADG could be improved by selection solely on its DGE, which has a lower correlation with DGE of FCR (0.13).

In this way we would implicitly be considering a selection index accounting both for PT and welfare and FBT (Ellen et al., 2014).

As an overall result we can indicate that the extension of the bivariate model relating PT and FBT to AM-IGE has evidenced that the genetic correlations between these two groups of traits, as well as within type of trait, are more complex than would be expected from the analysis with the AM. To our knowledge, this type of bivariate analysis has not been performed so far, so we cannot contextualise our particular results. However, based on our results we could examine possible benefits of additional selection indexed combining IGE and DGE considering alternatives weighting across traits and effects. These alternative indexes might yield stronger responses in the selection objective than would be expected from indexes based on animal model breeding value predictions or total breeding value predictions from the AM-IGE.

Conclusions

For the two types of traits considered in this study (PT and FBT), models fitting IGEs were statistically preferable over the traditional animal model. The consideration of such models improves the genetic correlation structure between the involved traits; thus opening up the possibility of proposing indexes drives genetic responses for breeding goals which cannot be defined under the traditional animal model. Our results also show that the relationship between FBT can partially be attributed to a social hierarchical structure, but this structure only explains a certain proportion of the genetic relationships between PT and between FBT and PT, particularly those involving IGE of FBT and DGE of PT.

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Declaration of interest

The authors declare no conflict of interest. Ethics statement Animals used in this study came from a commercial population raised under selection nucleus conditions, following all the applicable Spanish and European Union laws with regard to welfare and health control. The fattening period of the animals was conducted at the Institut de Recerca i Tecnologia Agroalimentàries (IRTA) experimental facilities, and for this control period a research protocol was approved by IRTA's Animal Care and Use Committee. Software and data repository resources

The datasets and programmes used in the current study are available from the corresponding author on reasonable request.

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3.2. Selection for feed efficiency using the social effects animal model in growing Duroc pigs: Evaluation by simulation

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Abstract

Background: Traits recorded on animals that are raised in groups can be analysed with the social effects animal model (SAM). For multiple traits, this model specifies the genetic correlation structure more completely than the animal model (AM). Our hypothesis was that by using SAM for genetic evaluation of average daily gain (ADG) and backfat thickness (BF), a large rate of improvement in feed conversion ratio (FCR) might be achieved, since unfavourable genetic correlations between ADG and BF reported in a Duroc pig line could be partially avoided. We estimated genetic and non-genetic correlations between BF, ADG and FCR on 1144 pigs using Bayesian methods considering the SAM; and responses to selection indexes that combine estimates of indirect (IGE) and direct (DGE) genetic effects for ADG and BF by stochastic simulation. **Results:** Estimates of the ratio of the variance of DGE to the phenotypic variance were 0.31, 0.39 and 0.25 for ADG, BF and FCR, respectively. Those of the total genetic variance to the phenotypic variance were 0.63, 0.74 and 0.93. In spite of this, when the SAM was used to generate data and for the genetic evaluations, average economic response was worse than that obtained when BV predictions from AM were considered. The achieved economic response was due to a direct reduction in BF and not due to an improvement in FCR. **Conclusions:** Our results show that although social genetic effects play an important role in the traits studied, their proper consideration in pig breeding programs to indirectly improve FCR is still difficult. The correlations between IGE and DGE that could help to overcome the unfavourable genetic correlations between DGE did not reach sufficiently high magnitudes; also, the genetic parameters estimates from SAM have large errors. These two factors penalize the average response under the SAM compared to the AM.

Background

Since feed represents the largest cost of pig production, improving feed efficiency would result in a high economic benefit (Edwards et al., 1987). For this reason, breeding programs either directly or indirectly focus on improving this trait. Traditionally, indirect improvement in feed efficiency has been achieved by improving growth rate while reducing backfat thickness (BF) (Merks et al., 2012), but reaching such a joint objective can be difficult because these traits are under antagonist genetic control (Steane, 1981; Suzuki et al., 2005). The major challenge in breeding programs that address feed efficiency directly is that individual feed intake needs to be recorded. When animals are raised in group pens, this trait can be measured only by using electronic feeders, which assumes a significant investment and greatly increases the production costs in the breeding program. In this context, when animals are housed in groups, feed efficiency traits, as with any other performance trait, can be affected by social interactions; a concept that was first introduced by Griffing (1976). The social effects animal model (SAM) assumes that a trait is controlled by two genetic effects: the direct genetic effect (DGE) due to genes that have a direct effect on the performance of the animal itself, and indirect genetic effect (IGE) due to genes of its pen mates that act on the animal that is recorded (Bijma et al., 2007). By using the SAM, Nielsen et al. (2018) and Ragab et al. (2019) reported a better predictive ability for growth traits in pigs compared to that of a model without IGE.

In this study, our aim was to explore whether the expected response in feed conversion ratio (FCR) as a result of indirect selection for average daily gain (ADG) and BF when using the SAM for genetic evaluation is improved compared to that achieved when using the traditional animal model (AM). In this analysis, we accounted for the uncertainty regarding the genetic and non-genetic parameters that are required to conduct the evaluation of the selection candidates. For the Duroc population considered in this study, we have already reported genetic correlation estimates between performances (ADG and BF) and feed efficiency traits (FCR) using the AM and SAM (Herrera-Cáceres et al., 2020). Based on these estimates, some advantages for the use of the SAM would be expected for indirect genetic improvement of FCR because it enables different selection pressure to be placed on direct versus indirect genetic effects for traits with unfavourable genetic correlations, thereby partially avoiding the estimated antagonist genetic relationship under the traditional animal model.

Methods

Animals

Performance during the growing period was recorded on 1144 Duroc pigs in 10 batches from 2007 to 2017 at the Center of Porcine Evaluation (Monells, Girona, Spain) using IVOG feeding stations (Insentec, Markenesse, The Netherland) with one single-space electronic feeder per pen. Herrera-Cáceres et al. (2020) described the Duroc line used in this study in detail. The population under study was housed in 97 pens and pen size varied from 7 to 15 animals, with an average pen size of 12.0±1.5 animals. Age of the animals at the beginning and the end of the fattening period was 70±6 days and 177±9 days, respectively.

Description of traits

For this study, average daily gain (ADG, kg), feed conversion ratio (FCR, kg/kg), and backfat thickness (BF, mm) were computed at 180 days of age, as described by Herrera-Cáceres et al. [9]. Basic statistics for these traits are in Table 1.

Table 1 Descriptive statistics for growing Duroc pigs

Trait	Abbreviation	No. of observations	Min	Mean	Max	SD
Average daily gain, kg/day	ADG	1144	0.22	0.82	1.07	0.09
Backfat thickness, mm	BF	1144	6.44	18.19	32.74	4.40
Feed conversion ratio, kg/kg	FCR	1144	2.07	2.77	3.89	0.24

Statistical model

A multi-trait linear model was fitted to ADG, BF, and FCR. The same systematic effects were considered for the three traits: batch, age at the end of the fattening period (covariate), and number of pigs per pen (covariate). In addition, pen, litter, and genetic effects were included. The genetic component of the model was accounted for by separately fitting direct and indirect genetic effects (Bijma et al., 2007), as in the SAM. This three-trait model is represented by the following equation:

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\\ \mathbf{y}_3\end{bmatrix}=\begin{bmatrix}\mathbf{X}_1 & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{X}_2 & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{X}_3\end{bmatrix}\begin{bmatrix}\boldsymbol{b}_1\\ \boldsymbol{b}_2\\ \boldsymbol{b}_3\end{bmatrix}+\begin{bmatrix}\mathbf{Z}_{\mathbf{p}_1} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_{\mathbf{p}_2} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{Z}_{\mathbf{p}_3}\end{bmatrix}\begin{bmatrix}\mathbf{p}_1\\ \mathbf{p}_2\\ \mathbf{p}_3\end{bmatrix}$$

$$+\begin{bmatrix}\mathbf{Z}_{\mathbf{l}_1} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_{\mathbf{l}_2} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{Z}_{\mathbf{l}_3}\end{bmatrix}\begin{bmatrix}\mathbf{l}_1\\ \mathbf{l}_2\\ \mathbf{l}_3\end{bmatrix}+\begin{bmatrix}\mathbf{Z}_{\mathbf{d}_1} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_{\mathbf{d}_2} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{Z}_{\mathbf{d}_3}\end{bmatrix}\begin{bmatrix}\mathbf{d}_1\\ \mathbf{d}_2\\ \mathbf{d}_3\end{bmatrix}$$

$$+\begin{bmatrix}\mathbf{Z}_{\mathbf{s}_1} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_{\mathbf{s}_2} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{Z}_{\mathbf{s}_3}\end{bmatrix}\begin{bmatrix}\mathbf{s}_1\\ \mathbf{s}_2\\ \mathbf{s}_3\end{bmatrix}+\begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\\ \mathbf{e}_3\end{bmatrix}, \qquad (1)$$

where $\mathbf{y_1}$, $\mathbf{y_2}$ and $\mathbf{y_3}$ are the vectors of observations for the first (ADG), second (BF) and third (FCR) trait, respectively, $\mathbf{b}$ is a vector of systematic effects with incidence matrix $\mathbf{X}$; $\mathbf{p}$ is a vector of pen effects with incidence matrix $\mathbf{Z_p}$; $\mathbf{l}$ is a vector of litter effects with incidence matrix $\mathbf{Z_l}$; $\mathbf{d}$ is a vector of direct genetic effects with incidence matrix $\mathbf{Z_d}$, $\mathbf{s}$ is a vector of indirect genetic effects with incidence matrix $\mathbf{Z_s}$. The elements of $\mathbf{Z}_\mathrm{s}$ are 1 for records from animals that share the same pen and 0 otherwise; $\mathbf{e}$ is a vector of residuals.

The prior distributions of pen, litter and residual effects were: $\mathbf{p}|\mathbf{P_0}\sim N\left(\mathbf{0},\mathbf{P_0}\otimes\mathbf{I}_\mathrm{p}\right)$, $\mathbf{l}|\mathbf{L_0}\sim N(\mathbf{0},\mathbf{L_0}\otimes\mathbf{I_l})$, and $\mathbf{e}|\mathbf{R_0}\sim N(\mathbf{0},\mathbf{R_0}\otimes\mathbf{I_r})$, where $\mathbf{I}_\mathrm{p}$, $\mathbf{I_l}$ and $\mathbf{I_r}$ are identity matrices of appropriate dimensions, $\mathbf{P_0}$, $\mathbf{L_0}$ and $\mathbf{R_0}$ are 3x3 covariance matrices for the three traits, and $\otimes$ denotes the Kronecker product. All factors were assumed to be independent, except direct and indirect genetic effects, for which the assumed prior distribution was: $\begin{bmatrix}\mathbf{d}\\ \mathbf{s}\end{bmatrix}|\mathbf{G_0}\sim\mathrm{MVN}(\mathbf{0},\mathbf{G_0}\otimes\mathbf{A})$, where $\mathbf{A}$ is the numerator relationship matrix between individuals and $\mathbf{G_0}$ is the covariance matrix, containing the following elements:

$$\mathbf{G_0} = \begin{bmatrix} \sigma^2_{d_1} & \sigma_{d_1,d_2} & \sigma_{d_1,d_3} & \sigma_{d_1,s_1} & \sigma_{d_1,s_2} & \sigma_{d_1,s_3} \\ \sigma_{d_1,d_2} & \sigma^2_{d_2} & \sigma_{d_2,d_3} & \sigma_{d_2,s_1} & \sigma_{d_2,s_2} & \sigma_{d_2,s_3} \\ \sigma_{d_1,d_3} & \sigma_{d_2,d_3} & \sigma^2_{d_3} & \sigma_{d_3,s_1} & \sigma_{d_3,s_2} & \sigma_{d_3,s_3} \\ \sigma_{d_1,s_1} & \sigma_{d_2,s_1} & \sigma_{d_3,s_1} & \sigma^2_{s_1} & \sigma_{s_1,s_2} & \sigma_{s_1,s_3} \\ \sigma_{d_1,s_2} & \sigma_{d_2,s_2} & \sigma_{d_3,s_2} & \sigma_{s_1,s_2} & \sigma^2_{s_2} & \sigma_{s_2,s_3} \\ \sigma_{d_1,s_3} & \sigma_{d_2,s_3} & \sigma_{d_3,s_3} & \sigma_{s_1,s_3} & \sigma_{s_2,s_3} & \sigma^2_{s_3} \end{bmatrix}$$

where $\sigma^2_{d_i}$ are the direct genetic variances for each trait i = 1, 2 and 3; $\sigma^2_{s_i}$ are the indirect genetic variances for each trait i = 1, 2 and 3; and the off-diagonal elements represent covariances, either between direct and indirect genetic effects within, σ_{d_i,s_i}, or across traits, σ_{d_i,s_j}; or for the same genetic effect across traits, i.e. direct genetic effects (σ_{d_i,d_j}) or indirect genetic effects (σ_{s_i,s_j}).

Variance components were estimated by using Bayesian procedures. Flat priors were used for the systematic effects ($\mathbf{b}$) and for all variance components previously described, i.e. $\mathbf{P_0}$, $\mathbf{L_0}$, $\mathbf{G_0}$ and $\mathbf{R_0}$. Marginal posterior distributions of the variance components were sampled using the Gibbs sampling algorithm, with the gibbs2f90 program (Misztal et al., 2015). Chains of 1,000,000 samples were run and the first 100,000 iterations were discarded in order to allow the algorithm to converge to the posterior distributions. Then, one sample every 10 iterations was saved. Convergence of the Markov chains was assessed by visual inspection of the trace plots. Figure S1 [see Additional file 1 Figure S1] contains the trace plots of the Markov chains for the genetic correlations and heritabilities of the three traits. Then, marginal posterior distributions of the genetic parameters (ratios of variances and correlations) and genetic responses under different evaluation procedures and economic conditions were characterized based on the saved samples of the joint posterior distribution of the variance components.

To characterize the marginal posterior distribution of response to selection (RS) stochastic simulation was used. Each replicate of the stochastic simulation was defined by three arguments: (a) the variance components used for generation of data, which was based on a saved sample from the posterior distibutions, (b) the genetic evaluation procedure, i.e. SAM or AM, and (c) the selection index used to ranking candidates. The last two arguments define the relevant scenarios in our study, with the uncertainty of RS due to the uncertainty about the variance components being evaluated based on changes in the first argument across the different replicates.

Due to computational time constraints, we did not use all saved samples from the joint posterior distribution of the variance components. Instead, we used a random subset of 1000 vectors from the joint distribution to characterize the marginal posterior distributions of the expected genetic responses under different scenarios. For a particular replicate within a given scenario, the simulation to evaluate RS started by taking one sample from the posterior distribution of the variance components. Based on these variance components, new ADG, BF and FCR records were generated using a SAM that was similar to the model used for analysis of the Duroc data, i.e. with random litter, pen, DGE and IGE effects, along with litter size, parity order, and batch effects as systematic factors. The simulations were conducted assuming an infinitesimal model (Fisher, 1918), i.e., breeding values were sampled from a multivariate normal distribution.

For the genetic evaluation, only BF and ADG records were considered, using either the SAM or the AM. For the SAM, predictions of breeding values were obtained by solving the mixed model equations with variance components equal to those used in the simulation (best linear unbiased prediction (BLUP)). For the AM, predictions of breeding values were obtained by solving the mixed model equations associated with the AM, with variance components equal those obtained in a previous residual maximum likelihood (REML) step (REML-BLUP) on the data generated in that replicate. The programs used to obtain the predictions of breeding values were blupf90 and remlf90 (Misztal et al., 2015).

Within each scenario, the complete procedure was repeated for each one of the 1000 samples of the posterior variance components retained. The simulated datasets mimicked the management of a pig selection nucleus of 400 sows and 20 boars, where mating between close relatives, i.e. with common grand-parents, was avoided. Reproduction was organized in four batches per generation, but the genetic evaluations and selection process were performed using the first two batches of each generation. The other two batches generated information for genetic evaluation in the next generation. Each batch comprised approximately 2500 selection candidates (half females) in pens of eight animals, litters were processed by order, thus, in general, each pen included animals from more than one litter; in general, less than 25% of the pens were formed by animals from a single litter. The best 200 females from the batch were selected and the males were selected within sire families, thus the best offspring from each sire family was selected. Given that candidates were generated in two batches the average ratio offspring/sow was 12.5

The alternative scenarios to evaluate RS were defined by the different indexes used to rank the animals. The objective was to reduce BF while increasing ADG, but with different assigned weights. When the genetic evaluation relied on REML-BLUP predictions from the AM, selection indexes were defined by assigning alternative weights to breeding value predictions for ADG and BF (Table 2). When the SAM was used to evaluate animals (BLUP), two sets of weights were considered in the selection index, one to define the strength on one trait versus the other (ADG or BF) and the other to control the strength on DGE or IGE (Table 2). Thus, the resulting total number of scenarios assessed was the combination of these two and reached 25 (Table 2). The following equation defines the selection index value for individual i:

$$\hat{I}_i = W_{ADG} * \left(W_{DGE} * \widehat{ADG_{DGE_i}} + W_{IGE} * 7 * \widehat{ADG_{IGE_i}}\right)$$
$$-W_{BF} * \left(W_{DGE} * \widehat{BF_{DGE_i}} + W_{IGE} * 7 * \widehat{BF_{IGE_i}}\right), \qquad (2)$$

where $\widehat{ADG_{DGE_i}}$, $\widehat{ADG_{IGE_i}}$, $\widehat{BF_{DGE_i}}$, and $\widehat{BF_{IGE_i}}$ are predicted breeding values of DGE and IGE for ADG and BF of individual i; W_{DGE} and W_{IGE} are economic weights for DGE and IGE, respectively, the number 7 represents the number of pen mates (n-1), i.e. the IGE of individual i is exerted over seven pen mates; and W_{ADG} and W_{BF} are economic weights for ADG and BF, respectively. In order to evaluate the accuracy of the selection index, we calculated the correlations between true and predicted breeding values of the traits included in the index and the correlations between true and predicted indexes values for all scenarios.

As it has been stated, during the data generation ADG, BF and FCR records were obtained in the first two batches in each generation; ADG and BF information was used to take selection decisions while FCR was just used to assess the correlated response after selection for the proposed indexes. In addition, three profit traits (€), B1, B2 and B3, were derived based on three profit functions that represent three Spanish or European markets: B1 was based on a market without any constraint on BF; B2 represents a lean meat production market in which a penalty is applied if BF is outside the 6 to 10 mm range; and B3 represents a fat meat production market, in which a penalty is applied if BF is outside the 10 to 20 mm range. The general equation used to compute these profit traits was:

$$B_i = (FBW_i * P_{BW}) -$$

$$\left(P_{pl} + FCR_i * (FBW_i - IBW_i) * \ P_{fd} + P_{fx} * \frac{FBW_i - \ IBW_i}{ADG_i}\right) -$$

$$PenaltyBF_i, \qquad (3)$$

where B_i is the profit for individual i, FBW_i is the live body weight at the end of the fattening period (assumed constant = 110 kg) of individual i, P_{BW} is the price per kg (1.164 €/kg), P_{pl} is the price of a piglet (35 €/piglet), FCR_i is the FCR of individual i, IBW_i is the initial body weight (assumed constant = 20 kg) of individual i, P_{fd} is the price of feed (0.252 €/kg), P_{fx} is the fixed costs for daily maintenance of pigs on the farm (0.09 €/d), and $PenaltyBF_i$ is the penalty that is applied based on BF. In both scenarios with penalties on BF (B2 and B3), the penalization is based on a price reduction per BF mm outside of the valid limits (0.012 €/mm). The assumed production costs and the prices needed to define the profit function were based on the Spanish market (Davis, 2017).

The simulation was run for five generations and responses for the three biological traits and the three profit traits were defined as linear regression coefficients of the average phenotype of traits across selection candidates in a given generation on generation number. One thousand regression coefficients were obtained for each trait and scenario, one for each sample from the joint posterior distribution of the variance components in the SAM. Thus, each regression coefficient can be interpreted as a sample from the marginal posterior distribution of the RS for that trait for a given scenario. Based on this procedure, we can characterize the expected RS as well as the uncertainty of this expectation, the latter being a consequence of errors in the estimates of variance components.

The simulation process was implemented in a software pipeline that combined own Fortran90 code for data generation and R code to edit the data and to compose parameter files needed to run the genetic evaluation programs (remlf90 or blupf90) and to create the list of the selected males and females, which was then read by the Fortran90 program for us as parents of the next generation. This complete pipeline package is available upon request.

Table 2 Economic weights assigned in the selection index to average daily gain (ADG) and backfat thickness (BF)

	Five scenarios AM[a]	25 scenarios SAM[b]	
	$W_{ADG} - W_{BF}$ (%)	$W_{ADG} - W_{BF}$ (%)	$W_{DGE} - W_{IGE}$ (%)
Economic values	0–100	0–100	0–100
	25–75	25–75	25–75
	50–50	50–50	50–50
	75–25	75–25	75–25
	100–0	100–0	100–0

[a] The five scenarios with the classic animal model. Index for AM: $\widehat{I_J} = W_{ADG} * \widehat{ADG_J} - W_{BF} * \widehat{BF_J}$

[b] The 25 scenarios with the animal model including direct (DGE) and indirect (IGE) genetic effects are obtained by combining each element of the column $W_{DGE} - W_{IGE}$ (%) – weights on the DGE or the IGE - with the weights in the column to its left. Index for SAM: $\widehat{I_J} = W_{ADG} * \left(W_{DGE} * \widehat{ADG_{DGEJ}} + W_{IGE} * 7 * \widehat{ADG_{IGEJ}}\right) - W_{BF} * \left(W_{DGE} * \widehat{BF_{DGEJ}} + W_{IGE} * 7 * \widehat{BF_{IGEJ}}\right)$.

The complete procedure, i.e. based on simulations using samples of the posterior distribution of the variance components from the SAM, was repeated for samples from the posterior distribution of variance components obtained from the AM. The AM had the same factors and prior structure as the SAM, except that a single additive genetic effect was fitted for each trait instead both DGE and IGE. Thus, the genetic covariance matrix under this model was a 3x3 matrix. The simulated data for assessment of RS was based on an AM that fitted litter, pen, and additive genetic effects as random factors, and litter size, parity order, and batch as systematic effects. The genetic evaluation conducted each generation was based on the same AM that generated the data by setting the variance components to those used for generating the data (BLUP). In this assessment, which did not fit social genetic effects, the same scenarios as those considered when data were generated with SAM but the evaluation was conducted with the AM were assessed (Table 2).

Results

For the three biological traits, we estimated genetic parameters using the SAM (see Table 3). Estimates of heritability (h^2) for ADG, BF, and FCR were moderate to high, 0.31±0.09, 0.39±0.10 and 0.25±0.07, respectively. The ratios of total breeding value variance and total phenotypic variance (T^2) were clearly larger than h^2 for all three traits, which shows the importance of IGE for these traits. Another argument in favour of using the SAM to fit our dataset is that the Deviance Information Criteria (DIC) value (Spiegelhalter et al., 2002) associated with this model was clearly lower, than for the AM, i.e., 7268.53 versus 7524.59. For each trait, the genetic correlation between DGE and IGE (Table 3) was not statistically different from zero because the marginal posterior probabilities of the genetic correlation being greater than zero was not greater than 0.95 or less than 0.05. Estimates of genetic correlations of DGE between traits (Table 3) were similar to those obtained with the AM (parameter estimates based on the AM are in Table S1 [see Additional file 2 Table S1]). The estimated genetic correlations were positive between ADG and BF and between BF and FCR, whereas the estimated correlation between ADG and FCR was not statistically different from zero. With the SAM, the only estimated genetic correlation between IGE that could be considered as statistically different from zero was between ADG and BF (0.59±0.26). For estimate of genetic correlations between IGE and DGE, only the correlation between DGE of FCR and IGE of ADG was statistically different from zero (0.70±0.25).

Table 3 Posterior Mean (Posterior SD)[a] of direct heritability, total heritability, genetic correlations, and variances of direct and indirect genetic effects (diagonal)

Trait	h^2	T^2	σ^2_{Phe}	Genetic effect of traits	ADG$_{\mathrm{DGE}}$	ADG$_{\mathrm{IGE}}$	BF$_{\mathrm{DGE}}$	BF$_{\mathrm{IGE}}$	FCR$_{\mathrm{DGE}}$	FCR$_{\mathrm{IGE}}$
ADG[b]	0.31(0.09)	0.63(0.22)	0.75(0.05)	ADG$_{\mathrm{DGE}}$	0.24(0.08)	-0.29(0.25)	0.52(0.17)*	-0.19(0.34)	-0.03(0.22)	-0.35(0.32)
				ADG$_{\mathrm{IGE}}$		$4\mathrm{x}10^{-3}(1\mathrm{x}10^{-3})$	0.24(0.29)	0.59(0.26)*	0.70(0.25)*	0.18(0.36)
BF	0.39(0.10)	0.74(0.27)	11.84(0.84)	BF$_{\mathrm{DGE}}$			4.69(1.24)	-0.09(0.36)	0.33(0.19)*	-0.34(0.31)
				BF$_{\mathrm{IGE}}$				0.04(0.02)	-0.07(0.38)	0.33(0.38)
FCR	0.25(0.07)	0.93(0.43)	4.44(0.44)	FCR$_{\mathrm{DGE}}$					1.10(0.34)	-0.17(0.37)
				FCRI$_{\mathrm{GE}}$						0.03(0.02)

[a] Estimates obtained using the multi-trait social animal model

[b]ADG: average daily gain, BF: backfat thickness, FCR: feed conversion ratio, DGE: direct genetic effect, IGE: indirect genetic effect, h^2: ratio of direct genetic effect variance to total phenotypic variance, T^2: ratio of the total breeding value variation and the total phenotypic variance, σ^2_{Phe}: the total phenotypic variance.

*Probability of being higher than 0 was higher than 0.95 or lower than 0.05.

Table 4 shows the estimates of RS for ADG, BF, and FCR, and for B1, B2, and B3. In total, 25 scenarios were assessed based on different economic weights assigned to the traits in the selection index (ADG and BF) and to the genetic effects (DGE and IGE). In general, estimates of correlated responses in FCR were not statistically different from zero for any scenario, i.e. the posterior probability of the response being positive or negative was less than 0.9 (positive response) or less than 0.1 (negative response). There were only two exceptions to this general pattern, which was when all the weight was allocated to the IGE (W_IGE = 100%), with a distribution of the weight across traits of W_ADG = 75%–W_BF = 25% and W_ADG = 100%–W_BF = 0%, in these cases unfavourable positive responses (i.e. 0.07) were predicted. For responses in profit, only profit in the lean meat production market resulted in favourable responses that were statistically different from zero, primarily for the scenarios with an economic weight of at least 50% on BF. Among these scenarios, the best two were when the same weight was assigned to ADG and BF and the weight on genetic effects were W_DGE = 100%–W_IGE = 0% and W_DGE = 75%–W_IGE = 25% (2.35 and 2.24 €/pig, respectively). Unfavourable economic responses were estimated when all weight was assigned to the IGE (W_DGE = 0%–W_IGE = 100%) and the distribution of this weight across traits were W_ADG = 75%–W_BF = 25% and W_ADG = 100%–W_BF = 0% (-3.26 and -3.34 €/pig respectively). In these two scenarios unfavourable responses on FCR were also estimated. Table 4 also includes the accuracy of the index predictions, i.e. the correlations between predicted and true values for the indexes. As the weight was moved from IGE to DGE, the accuracy of the indexes increased from 0.54-0.58 to 0.63-0.70, depending on the weights assigned to the traits. In general, accuracy of the indexes also increased when the weight assigned to BF increased. More details are in Tables S2, S3 and S4 [see Additional file 3], which also present the accuracies of predictions of IGE, DGE and TBV.

When the data were generated using SAM and genetic evaluations were based on the AM, the overall pattern of correlated responses in FCR was similar to that described for genetic evaluation based on SAM (Table 5). Estimated responses in FCR were not statistically different from zero for any economic weight distribution between BF and ADG.

Table 4. Posterior Mean (Posterior SD)[a] of the responses to selection for 25 indexes.

$W_{ADG}-W_{BF}$, % [b]	0–100	25–75	50–50	75–25	100–0
$W_{DGE}-W_{IGE}$, %	0–100	0–100	0–100	0–100	0–100
ADG, kg	-0.01(0.02)	0.00(0.02)	0.01(0.02)	0.02(0.02)	0.02(0.02)
BF, mm	-0.88(1.24)	-0.56(1.26)	0.74(0.97)	1.50(0.97)*	1.54(0.99)*
FCR, kg/kg	-0.04(0.05)	-0.02(0.06)	0.03(0.05)	0.07(0.05)*	0.07(0.05)*
B1, €	0.71(1.26)	0.44(1.32)	-0.62(1.26)	-1.28(1.16)	-1.31(1.13)
B2, €	1.53(1.82)	0.93(1.93)	-1.62(1.42)	-3.26(1.67)*	-3.34(1.71)*
B3, €	0.46(1.37)	0.17(1.43)	-1.30(1.22)	-2.64(1.52)*	-2.72(1.54)*
$\rho(I,\hat{I})$	0.54(0.08)	0.54(0.08)	0.54(0.09)	0.58(0.08)	0.57(0.08)
$W_{ADG}-W_{BF}$, %	0–100	25–75	50–50	75–25	100–0
$W_{DGE}-W_{IGE}$, %	25–75	25–75	25–75	25–75	25–75
ADG, kg	-0.03(0.02)*	-0.02(0.02)	0.01(0.02)	0.04(0.02)*	0.04(0.02)*
BF, mm	-2.02(0.99)*	-1.83(1.03)*	0.02(0.75)	1.84(0.88)*	2.01(0.89)*
FCR, kg/kg	-0.03(0.05)	-0.02(0.05)	0.03(0.05)	0.05(0.05)	0.05(0.05)
B1, €	0.20(1.25)	0.09(1.26)	-0.54(1.20)	-0.81(1.16)	-0.75(1.16)
B2, €	2.01(1.44)*	1.78(1.50)	-0.59(1.28)	-3.23(1.65)*	-3.40(1.70)*
B3, €	-0.31(1.41)	-0.33(1.41)	-0.69(1.17)	-2.53(1.55)*	-2.68(1.61)*
$\rho(I,\hat{I})$	0.57(0.08)	0.56(0.08)	0.49(0.09)	0.56(0.07)	0.57(0.07)
$W_{ADG}-W_{BF}$, %	0–100	25–75	50–50	75–25	100–0
$W_{DGE}-W_{IGE}$, %	50–50	50–50	50–50	50–50	50–50
ADG, kg	-0.04(0.02)*	-0.03(0.02)*	0.01(0.01)*	0.05(0.01)*	0.05(0.01)*
BF, mm	-2.45(0.74)*	-2.41(0.73)*	-0.87(0.45)*	1.54(0.86)*	1.93(0.81)*
FCR, kg/kg	-0.02(0.05)	-0.02(0.05)	-0.01(0.05)	0.01(0.05)	0.01(0.05)
B1, €	-0.27(1.25)	-0.11(1.26)	0.48(1.13)	0.35(1.1)	0.28(1.16)
B2, €	1.81(1.29)*	1.97(1.31)*	1.55(1.28)	-1.68(1.71)	-2.27(1.73)*
B3, €	-0.99(1.37)	-0.79(1.39)	0.56(1.12)	-1.02(1.57)	-1.53(1.66)
$\rho(I,\hat{I})$	0.65(0.07)	0.65(0.07)	0.58(0.07)	0.60(0.07)	0.61(0.06)
$W_{ADG}-W_{BF}$, %	0–100	25–75	50–50	75–25	100–0
$W_{DGE}-W_{IGE}$, %	75–25	75–25	75–25	75–25	75–25
ADG, kg	-0.04(0.02)*	-0.03(0.02)*	0.00(0.01)	0.04(0.02)*	0.04(0.02)*
BF, mm	-2.35(0.76)*	-2.32(0.77)*	-1.21(0.65)*	0.74(0.95)	1.29(0.89)*
FCR, kg/kg	-0.01(0.06)	-0.02(0.06)	-0.04(0.06)	-0.03(0.05)	-0.02(0.05)
B1, €	-0.49(1.27)	-0.16(1.32)	0.85(1.23)	1.09(1.07)	0.98(1.06)
B2, €	1.56(1.30)*	1.88(1.35)*	2.24(1.48)*	0.11(1.77)	-0.72(1.70)
B3, €	-1.14(1.41)	-0.79(1.43)	0.83(1.21)	0.44(1.42)	-0.13(1.51)
$\rho(I,\hat{I})$	0.69(0.06)	0.70(0.06)	0.65(0.07)	0.63(0.07)	0.63(0.06)
$W_{ADG}-W_{BF}$, %	0–100	25–75	50–50	75–25	100–0
$W_{DGE}-W_{IGE}$, %	100–0	100–0	100–0	100–0	100–0
ADG, kg	-0.04(0.02)*	-0.03(0.02)*	0.00(0.01)	0.03(0.02)*	0.04(0.02)*
BF, mm	-2.24(0.80)*	-2.23(0.81)*	-1.38(0.80)*	0.26(1.03)	0.84(0.96)
FCR, kg/kg	0.00(0.06)	-0.01(0.06)	-0.04(0.06)	-0.05(0.05)	-0.04(0.05)
B1, €	-0.61(1.28)	-0.22(1.34)	0.86(1.26)	1.33(1.12)	1.27(1.05)
B2, €	1.40(1.31)	1.78(1.37)*	2.35(1.52)*	0.95(1.83)	0.15(1.77)
B3, €	-1.18(1.42)	-0.79(1.46)	0.74(1.24)	0.94(1.34)	0.53(1.42)
$\rho(I,\hat{I})$	0.69(0.06)	0.70(0.06)	0.66(0.07)	0.63(0.07)	0.63(0.06)

[a] Data were simulated using variance component samples from the marginal posterior distribution of the social animal model and the responses were obtained in five generations of selection evaluating candidates using the social animal model.

[b] ADG: average daily gain, BF: backfat thickness, FCR: feed conversion ratio, $W_{ADG}-W_{BF}$: proportion of

economic weight assigned to ADG and BF in the selection index, $W_{DGE} - W_{IGE}$: proportion of economic weight assigned to direct (DGE) and indirect (IGE) genetic effects of traits in the selection index, B1: economic benefit in a non-BF-constrained market, B2: economic benefit with BF penalty out of the range 6 to 10 mm, B3: economic benefit with BF penalty out of the range 10 to 20 mm, $\rho(I, \widehat{I})$: correlation between predicted $(\widehat{I})$ and true value (I) of the index.

*Probability of being higher than 0 was higher than 0.95 or lower than 0.05.

For profit traits, only B2 had responses that were statistically different from zero, which occurred when the weight on BF was at least 50%, i.e. 2.02, 1.72 and 1.43 €/pig, for weights on BF of 50, 75 and 100%, respectively. The pattern of the correlations between the predicted values of the indexes and the real values of the index computed based on TBV predictions (Table 5) was also similar to that of the accuracies of the index when data were both simulated and analysed with the SAM (Table 4). These correlations increased as the weight assigned to BF increased and were comparable to those reported in Table 4 when the same weight was assigned to IGE and DGE (W_IGE = 50 and W_DGE = 50). As expected, these correlations were higher when the SAM (Table 4) was used for the genetic evaluation than when the AM was used (Table 5). These higher correlations for SAM have consequences on direct responses for ADG and BF, which were slightly higher when the SAM was used for genetic evaluation (Table 4). It should be noted, however, that data were generated using SAM for both these cases.

Table 5. Posterior Mean (Posterior SD)[a] of the responses to selection for five indexes.

W_{ADG}–W_{BF}, %[b]	0–100	25–75	50–50	75–25	100–0
ADG, kg	-0.04(0.02)*	-0.03(0.02)*	0.00(0.01)	0.04(0.02)*	0.04(0.02)*
BF, mm	-2.29(0.74)*	-2.29(0.74)*	-1.21(0.66)*	0.86(0.94)	1.36(0.85)*
FCR, kg/kg	0.00(0.05)	-0.01(0.05)	-0.03(0.05)	-0.02(0.05)	-0.02(0.04)
B1, €	-0.62(1.20)	-0.34(1.25)	0.64(1.17)	0.96(1.01)	0.89(0.99)
B2, €	1.43(1.22)*	1.72(1.28)*	2.02(1.41)*	-0.18(1.67)	-0.90(1.59)
B3, €	-1.21(1.35)	-0.92(1.38)	0.62(1.14)	0.22(1.34)	-0.28(1.42)
$\rho(I_{TBV}, \widehat{I})$	0.60(0.09)	0.60(0.09)	0.53(0.1)	0.52(0.1)	0.54(0.1)

[a] Data were simulated using variance component samples from the marginal posterior distribution of the social animal model and the responses were obtained in five generations of selection evaluating candidates using the classical animal model. [b]ADG: average daily gain, BF: backfat thickness, FCR: feed conversion ratio, $W_{ADG} - W_{BF}$: proportion of economic weight assigned to ADG and BF in the selection index, B1: economic benefit in a

non-BF-constrained market, B2: economic benefit with BF penalty out of the range 6 to 10 mm, B3: economic benefit with BF penalty out of the range 10 to 20 mm, $\rho(I,\widehat{I})$: correlation between predicted $(\widehat{I})$ index value and true value of the total breeding value (TBV).

*Probability of being higher than 0 was higher than 0.95 or lower than 0.05.

Table 6 Posterior Mean (Posterior SD)^a of the responses to selection for five indexes when data were generated with the animal model.

W_{ADG}–W_{BF}, %^{b}	0–100	25–75	50–50	75–25	100–0
ADG, kg	-0.01(0.01)	-0.01(0.01)	0.01(0.01)*	0.03(0.01)*	0.03(0.01)*
BF, mm	-2.11(0.56)*	-2.04(0.55)*	-1.15(0.52)*	0.44(0.94)	0.95(0.87)
FCR, kg/kg	-0.05(0.02)*	-0.05(0.02)*	-0.02(0.03)	0.01(0.04)	0.02(0.04)
B1, €	0.92(0.60)*	0.96(0.61)*	0.70(0.74)*	0.03(0.89)	-0.22(0.85)
B2, €	3.04(0.75)*	3.05(0.77)*	2.09(1.11)*	-0.56(1.89)	-1.48(1.79)
B3, €	0.53(0.57)	0.61(0.60)	0.74(0.71)*	-0.42(1.34)	-1.03(1.42)
$\rho(I,\widehat{I})$	0.67(0.07)	0.69(0.07)	0.61(0.11)	0.58(0.08)	0.58(0.07)

^{a}Data were simulated using variance component samples from the marginal posterior distribution of the classical animal model and the responses were obtained in five generations of selection evaluating candidates using also the classical animal model. ^{b}ADG: average daily gain, BF: backfat thickness, FCR: feed conversion ratio, $W_{ADG} - W_{BF}$: proportion of economic weight assigned to ADG and BF in the selection index, B1: economic benefit in a non-BF-constrained market, B2: economic benefit with BF penalty out of the range 6 to 10 mm, B3: economic benefit with BF penalty out of the range 10 to 20 mm, $\rho(I,\widehat{I})$: correlation between predicted $(\widehat{I})$ and true value (I) of the index. *Probability of being higher than 0 was higher than 0.95 or lower than 0.05.

As a baseline situation, we explored the genetic responses when IGE were ignored during the process of data generation (i.e. AM) and also during the genetic evaluation of the candidates, which was conducted by applying an AM with the variance components set to values that were used for the simulation in each replicate (Table 6). The most remarkable feature of this baseline situation was the decrease in the magnitude of the standard deviations of the marginal posterior distributions of the responses compared to those in Tables 4 and 5. In this case, the maximum value of the ratio between posterior standard deviation and posterior mean, across traits and scenarios, was 29.7, while it was only 9.3 when the SAM was used for simulation and genetic evaluations was conducted using the AM (Table 5) and as high as 37.5 when the genetic evaluation was by SAM (Table 4). When data were simulated using the AM, responses in FCR were statistically different from 0 for the two scenarios in which most of the weight was assigned to BF. In these two scenarios, favourable economic responses were also estimated not only for markets with and without constraints on BF (3.04 and 3.05 €/pig for B2 and 0.92 €/pig and 0.96 €/pig for B1). In addition, positive economic responses were obtained in the scenario where ADG and BF had similar weights for both B1 and B2 (0.70 €/pig and 2.09 €/pig, respectively), but in this case the response in FCR was not statistically different from 0. In the baseline scenario, the accuracy of the selection indexes ranged from 0.58 to 0.69, and the largest accuracies were obtained in the scenarios where most of the weight was assigned to BF.

Discussion

In general, genetic parameters estimated with the SAM are subject to large estimation errors. In our case, these errors were particularly large because of the small size of our data set, but other studies that used much larger datasets reported a similar magnitude of errors (Arango et al., 2005; Chen et al., 2009; Canario et al., 2010; Lu et al., 2017; Nielsen et al., 2018). Thus, this could be due to the limited amount of information in pig datasets to separate direct from indirect genetic effects, as well as the within-pen sum of indirect genetic effects from other factors such as pen effects (Cantet and Cappa, 2008). Consequently, the assessment of response to selection when a SAM is proposed to evaluate selection candidates has to take such estimation errors into account. To accomplish this, we used Monte Carlo methods to integrate variation of the posterior distribution of the variance components on genetic response predictions out. Since the function to assess the genetic response is complex, i.e. based on stochastic simulation, we took advantage of the availability of a computational cluster to afford the computations.

As expected, the uncertainty of the expected responses was much larger when the SAM was used for generating the data and for evaluation than when the AM was used. Direct responses in ADG and BF were only slightly lower when AM was used to rank the candidates (Table 5) than when SAM was used to rank the candidates and the same weight was assigned to both IGE and DGE (Table 4). These findings indicate that using a different model to that used for data generation is not the most important factor for a decrease in accuracies and responses. The fact that similar patterns of direct responses in ADG and BF were observed when the evaluation was conducted using SAM or AM could be explained by the large uncertainty on the model parameters for generating the data, which dominated the results for both models. In situations where these errors would have a lower magnitude, using the wrong model for genetic evaluation is expected to have a stronger impact. Previous studies have addressed the theoretical magnitude of the estimation errors of genetic parameters with the SAM and reported difficulties associated with estimation based on such models (Arango et al., 2005; Van Vleck and Casady, 2005; Cantet and Cappa, 2008). However, to the best of our knowledge, none of these studies have addressed the consequences that these large estimation errors can have on the expected genetic responses to selection.

Our initial hypothesis was that using SAM for the genetic evaluation would allow us to take advantage of genetic correlations among DGE and IGE of traits that might help to alleviate the unfavorable genetic correlations that exist between BF and ADG, or between ADG and FCR. For example, a negative genetic correlation between IGE of FCR and DGE of ADG. Based on our results, this hypothesis does not hold for the population under study because the highest economic responses were obtained when the AM was used for genetic evaluation (Table 6). As mentioned, this result can be explained by the fact that the use of a complex model introduces large uncertainty on genetic parameter estimates, which translates to uncertainty in responses to selection. This, in turn, prevented responses from SAM that were of similar magnitude to those estimated when AM was used to be declared as significantly different from zero. This larger uncertainty on model parameters of the more complex models also reduces prediction accuracies (Tables 4, 5 and 6, and Table S2 [see Additional file 3]), particularly when most of the weight is assigned to IGE or to ADG, which also has consequences for observed responses to selection.

In spite of the overall rejection of our hypothesis, it should be noted that when the genetic evaluation was conducted using SAM (Table 4), the best economic responses were achieved when both BF and ADG had the same weight but the selection index relied exclusively on DGE. Note that, in the simulation phenotypes were generated considering the concept of total breeding value (DGE + (n-1)*IGE). This result partially supports our hypothesis, in the sense that the largest correlated response on FCR was obtained when DGE and IGE were weighted different from their weights in TBV, i.e. 0 versus (n-1) on IGE.

Another point that could explain the failure our initial hypothesis is that the correlations that could eliminate the antagonistic relationship between traits did not reach a relevant magnitude in the population under study. This could happen, for example, if the correlation of IGE for ADG with DGE for BF was low. Thus, one trait could be modified by selecting on the IGE and the other by selecting on DGE. Then, a correlated response in FCR could be expected if the correlation between IGE for ADG and IGE for FCR was negative and that between DGE of BF and DGE of FCR was positive. Some of these requirements for our hypothesis to hold were fulfilled in our case, i.e., the posterior mean of the correlation between IGE for ADG and DGE for BF was lower than that of the correlation between DGE for the two traits. However, other requirements were not satisfied. The correlations meant just above are only a part of the whole correlation structure, for example those between IGE and DGE across traits should be also considered. In order to account for the whole structure is the reason why we conducted an assessment of responses based on simulation to explore the consequences of different selection indexes combining IGE and DGE.

Regarding the applied problem addressed in our study, i.e. indirect improvement of FCR by joint selection on ADG and BF, our results indicate that, in this Duroc pig population, response in FCR is highly driven by a reduction in BF, and selecting only on ADG, ignoring BF, would lead to economic losses. When the data were generated with the AM, the economic responses resulted from both a direct reduction in BF and a correlated response in FCR. However, when the SAM was used to generate the data, the achieved economic benefit did not result from improved FCR but only from a reduction in BF, which was of value in some of the markets assessed.

The magnitude of genetic parameters is known to depend on the population under study, and for the traits considered here, a wide range of estimates have been reported in the literature for different lines and breeds. Although the genetic correlation between ADG and BF tends to be positive (Suzuki et al., 2005; Do et al., 2013), some studies on other Duroc lines have reported nearly zero correlations (Kuhlers et al., 2003). Estimates of genetic correlations between BF and FCR and between ADG and FCR show a wider range of variability, with both having both negative and positive estimates (Kuhlers et al., 2003; Suzuki et al., 2005; Do et al., 2013). In Suzuki et al., (2005) and Kuhlers et al., (2002), the observed responses in the implemented selection experiments clearly matched the estimated parameters. Thus, we can state that the general pattern of the genetic correlations that we estimated, both for IGE and DGE, is compatible with previously reported estimates of genetic parameters, although they were obtained with the AM.

Conclusions

Using the SAM in genetic evaluation to indirectly improve FCR by selection on ADG and BF does not overcome the unfavourable genetic correlations that exist between the traits when they are evaluated with the traditional AM. On the one hand, this is due to the large magnitude of the estimation errors of the genetic parameters estimated in more complex models such as SAM. On the other hand, the correlations between IGE and DGE that could help overcome the unfavourable genetic correlations between DGE did not reach sufficiently high magnitudes.

Additional files

Additional file 1 Figure S1

Title: Trace plots of Markov Chains of the genetic parameters for the social animal model
Description: Contains the trace plots of the Markov chains for the genetic correlations and heritabilities of ADG, BF and FCR. This can be used to assess that our Markov chains have an acceptable rate of mixing.

Additional file 2 Table S1

Title: Posterior Mean (Posterior SD) of genetic (above diagonal) and phenotypic (below diagonal) correlations, and heritabilities (diagonal)
Description: Contains the estimated genetic parameters for ADG, BF and FCR using the AM. This estimates can be compared to those obtained when SAM (Table 3) was used for the analysis of the available dataset.

Additional file 3 Table S2

Title: Posterior mean (posterior SD) of the correlation between true and predicted breeding values using SAM
Description: Contains the correlation between true and predicted values of DGE and IGE of traits included in the selection index (ADG and BF) for the 25 studied scenarios using the SAM. This table also contains the correlation between true and predicted values of an index calculated based on the total breeding value definition of the involved traits.

Additional file 3 Table S3

Title: Posterior mean (posterior SD) of the correlation between true figures for total breeding value, direct and indirect genetic effects, and breeding values predictions obtained with the AM.
Description: Contains the correlation between predicted values of EBV using the AM and the true values of DGE, IGE, and TBV used in the simulation, using SAM, for the traits included in the selection index (ADG and BF).

Additional file 3 Table S4

Title: Posterior mean (posterior SD) of the correlation between true and predicted breeding values using AM for data generation and evaluation
Description: Contains the correlations between true and predicted values of EBV for traits included in the selection index (ADG and BF) when both simulation and genetic evaluations are conducted using the AM.

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Authors' contributions

JPS designed the study. WHC performed the analysis and wrote the manuscript. JPS helped in data analysis, helped in interpreting results and improving the manuscript. Both authors read and approved the final manuscript.

Ethics approval and consent to participate

Animals used in this study come from a commercial population raised under selection nucleus conditions, following all the applicable Spanish and European Union laws with regard to welfare and health control. The fattening period of the animals was conducted at the Institut de Recerca i Tecnologia Agroalimentàries (IRTA) experimental facilities, and for this control period a research protocol was approved by IRTA's Animal Care and Use Committee.

Competing interests

The authors declare that they have no competing interests.

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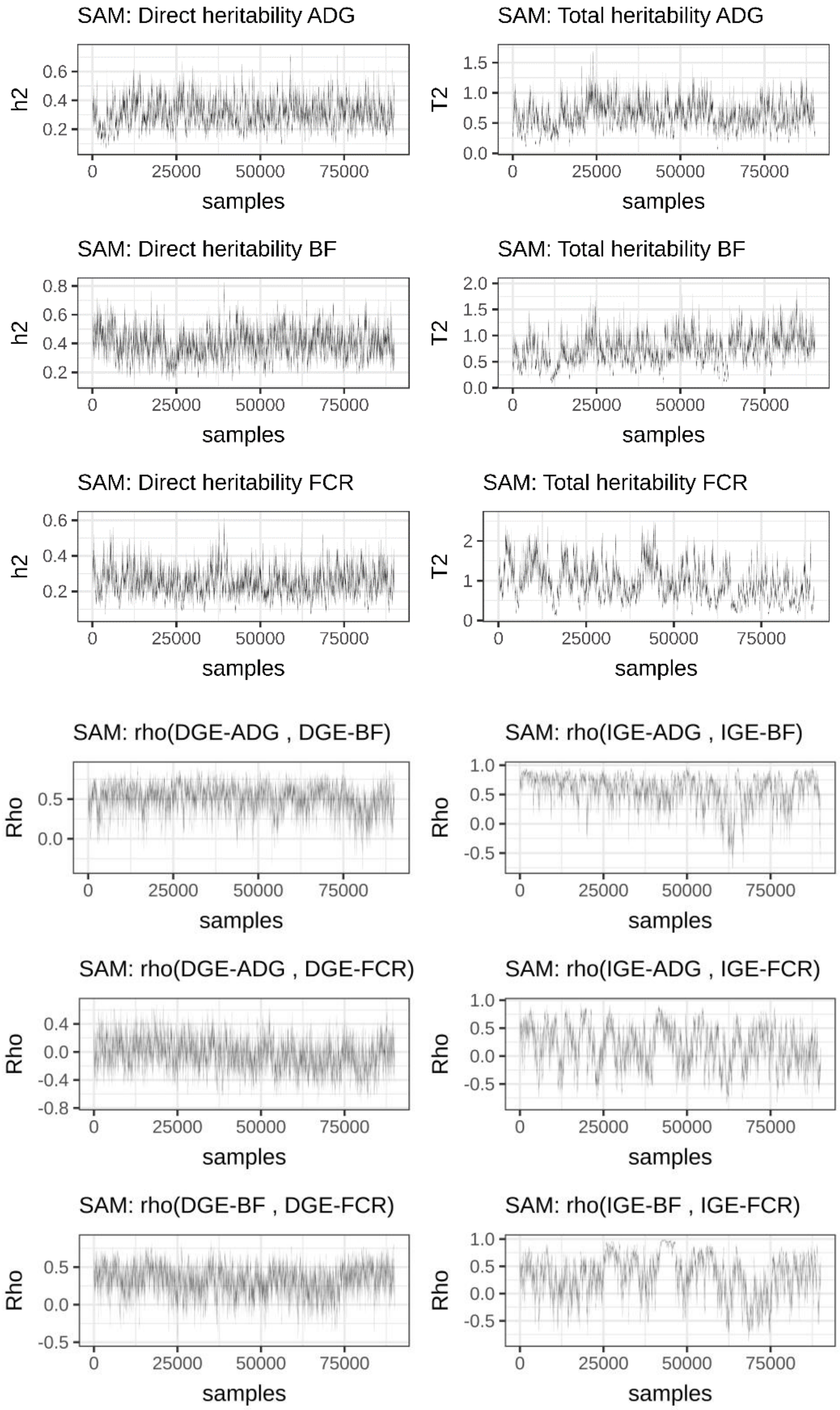
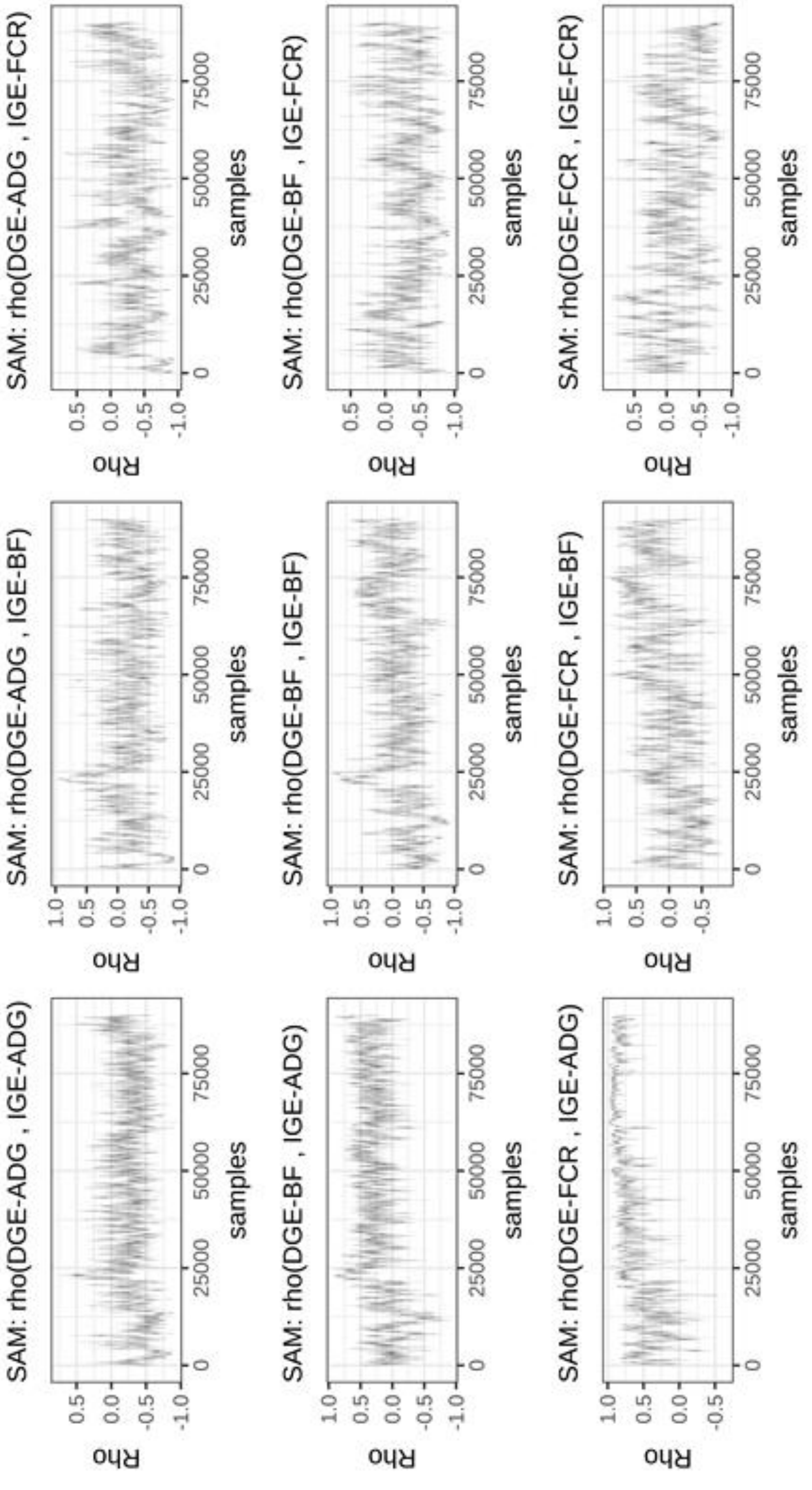
Additional file 1

Figure S1 Trace plots of Markov Chains of the genetic parameters for the social animal model




SAM: rho(DGE-ADG , IGE-ADG)
SAM: rho(DGE-ADG , IGE-BF)
SAM: rho(DGE-ADG , IGE-FCR)
SAM: rho(DGE-BF , IGE-ADG)
SAM: rho(DGE-BF , IGE-BF)
SAM: rho(DGE-BF , IGE-FCR)
SAM: rho(DGE-FCR , IGE-ADG)
SAM: rho(DGE-FCR , IGE-BF)
SAM: rho(DGE-FCR , IGE-FCR)
Rho
samples
1.0
0.5
0.0
-0.5
-1.0
0
25000
50000
75000

Additional file 2

Table S1 Posterior Mean (Posterior SD)[a] of genetic (above diagonal) and phenotypic (below diagonal) correlations, and heritabilities (diagonal)

	ADG [b]	BF	FCR
ADG	0.20(0.08)	0.50(0.24)*	0.46(0.46)
BF	0.59(0.03)*	0.37(0.10)	0.65(0.27)*
FCR	-0.04(0.04)	0.31(0.03)*	0.18(0.10)

[a] Estimates obtained using the classical multi-trait animal model

[b] ADG: average daily gain, BF: backfat thickness, FCR: feed conversion ratio.

*Probability of being higher than 0 was not higher than 0.95 or lower than 0.05.

Additional file 3

Table S3 Posterior mean (posterior SD) of the correlation between true figures for total breeding value, direct and indirect genetic effects, and breeding values predictions obtained with the AM[a]

$W_{ADG} – W_{BF}$, % [b]	0 – 100	25 – 75	50 – 50	75 – 25	100 – 0
$\rho(DGE_{ADG}, \widehat{EBV_{ADG}})$	0.63(0.08)	0.64(0.08)	0.63(0.09)	0.57(0.09)	0.58(0.08)
$\rho(IGE_{ADG}, \widehat{EBV_{ADG}})$	-0.04(0.20)	-0.03(0.20)	0.05(0.21)	0.05(0.19)	0.02(0.18)
$\rho(TBV_{ADG}, \widehat{EBV_{ADG}})$	0.56(0.10)	0.58(0.10)	0.61(0.11)	0.55(0.10)	0.54(0.10)
$\rho(DGE_{BF}, \widehat{EBV_{BF}})$	0.66(0.06)	0.66(0.07)	0.72(0.06)	0.72(0.06)	0.70(0.06)
$\rho(IGE_{BF}, \widehat{EBV_{BF}})$	0.06(0.23)	0.05(0.23)	0.05(0.26)	0.07(0.27)	0.07(0.26)
$\rho(TBV_{BF}, \widehat{EBV_{BF}})$	0.60(0.09)	0.60(0.08)	0.66(0.09)	0.66(0.09)	0.65(0.09)

[a] Accuracy in generation five. The data were simulated from samples of the marginal posterior distribution of the social effects animal model but the classical animal was used for genetic evaluation.

[b] $W_{ADG} – W_{BF}$: proportion of economic weight assigned to average daily gain (ADG) and backfat thickness (BF) in the selection index.

Table S4 Posterior mean (posterior SD) of the correlation between true and predicted breeding values using AM for data generation and evaluation[a]

$W_{ADG} – W_{BF}$, % [b]	0 – 100	25 – 75	50 – 50	75 – 25	100 – 0
$\rho(EBV_{ADG}, \widehat{EBV_{ADG}})$	0.63(0.07)	0.63(0.07)	0.63(0.07)	0.58(0.07)	0.58(0.07)
$\rho(EBV_{BF}, \widehat{EBV_{BF}})$	0.67(0.07)	0.68(0.07)	0.72(0.06)	0.72(0.07)	0.72(0.07)

[a] Accuracy in generation five. The data were simulated from samples of the marginal posterior distribution of the classical animal model (AM) and the same model was used for genetic evaluation.

[b] $W_{ADG} – W_{BF}$: proportion of economic weight assigned to average daily gain (ADG) and backfat thickness (BF) in the selection index, $W_{DGE} – W_{IGE}$: proportion of economic weight assigned to the EBV’s of traits in the selection index

Table S2 Posterior mean (posterior SD) of the correlation between true and predicted breeding values using SAM[a]

W_{ADG} – W_{BF}, % [b]	0 – 100	25 – 75	50 – 50	75 – 25	100 – 0
W_{DGE} – W_{IGE}, %	0 – 100	0 – 100	0 – 100	0 – 100	0 – 100
$\rho(DGE_{ADG}, \widehat{DGE_{ADG}})$	0.69(0.06)	0.68(0.06)	0.69(0.06)	0.69(0.06)	0.69(0.06)
$\rho(IGE_{ADG}, \widehat{IGE_{ADG}})$	0.61(0.07)	0.62(0.08)	0.62(0.08)	0.58(0.07)	0.57(0.08)
$\rho(TBV_{ADG}, \widehat{TBV_{ADG}})$	0.61(0.07)	0.62(0.08)	0.62(0.08)	0.58(0.07)	0.57(0.08)
$\rho(DGE_{BF}, \widehat{DGE_{BF}})$	0.74(0.06)	0.74(0.06)	0.73(0.06)	0.74(0.05)	0.74(0.06)
$\rho(IGE_{BF}, \widehat{IGE_{BF}})$	0.54(0.08)	0.54(0.08)	0.59(0.08)	0.59(0.07)	0.57(0.07)
$\rho(TBV_{BF}, \widehat{TBV_{BF}})$	0.54(0.08)	0.54(0.08)	0.59(0.08)	0.59(0.07)	0.57(0.07)
$\rho(I_{TBV}, \widehat{I})$	0.25(0.24)	0.20(0.27)	0.00(0.25)	0.18(0.19)	0.25(0.18)
W_{ADG} – W_{BF}, %	0 – 100	25 – 75	50 – 50	75 – 25	100 – 0
W_{DGE} – W_{IGE}, %	25 – 75	25 – 75	25 – 75	25 – 75	25 – 75
$\rho(DGE_{ADG}, \widehat{DGE_{ADG}})$	0.69(0.06)	0.69(0.06)	0.69(0.06)	0.69(0.06)	0.69(0.06)
$\rho(IGE_{ADG}, \widehat{IGE_{ADG}})$	0.60(0.07)	0.61(0.08)	0.63(0.08)	0.59(0.07)	0.59(0.07)
$\rho(TBV_{ADG}, \widehat{TBV_{ADG}})$	0.60(0.07)	0.61(0.07)	0.63(0.08)	0.58(0.07)	0.57(0.07)
$\rho(DGE_{BF}, \widehat{DGE_{BF}})$	0.73(0.06)	0.73(0.06)	0.74(0.06)	0.73(0.06)	0.72(0.06)
$\rho(IGE_{BF}, \widehat{IGE_{BF}})$	0.56(0.07)	0.55(0.08)	0.59(0.08)	0.58(0.08)	0.58(0.07)
$\rho(TBV_{BF}, \widehat{TBV_{BF}})$	0.57(0.08)	0.57(0.08)	0.63(0.08)	0.60(0.08)	0.59(0.08)
$\rho(I_{TBV}, \widehat{I})$	0.51(0.16)	0.49(0.17)	0.26(0.21)	0.40(0.14)	0.46(0.13)
W_{ADG} – W_{BF}, %	0 – 100	25 – 75	50 – 50	75 – 25	100 – 0
W_{DGE} – W_{IGE}, %	50 – 50	50 – 50	50 – 50	50 – 50	50 – 50
$\rho(DGE_{ADG}, \widehat{DGE_{ADG}})$	0.69(0.06)	0.69(0.06)	0.68(0.07)	0.66(0.06)	0.67(0.06)
$\rho(IGE_{ADG}, \widehat{IGE_{ADG}})$	0.61(0.07)	0.61(0.07)	0.63(0.07)	0.63(0.07)	0.63(0.07)
$\rho(TBV_{ADG}, \widehat{TBV_{ADG}})$	0.64(0.06)	0.66(0.06)	0.67(0.07)	0.62(0.06)	0.61(0.06)
$\rho(DGE_{BF}, \widehat{DGE_{BF}})$	0.70(0.06)	0.71(0.06)	0.75(0.06)	0.73(0.06)	0.72(0.06)
$\rho(IGE_{BF}, \widehat{IGE_{BF}})$	0.59(0.07)	0.58(0.07)	0.59(0.08)	0.59(0.08)	0.59(0.08)
$\rho(TBV_{BF}, \widehat{TBV_{BF}})$	0.65(0.07)	0.66(0.07)	0.71(0.07)	0.69(0.07)	0.68(0.07)
$\rho(I_{TBV}, \widehat{I})$	0.65(0.07)	0.65(0.07)	0.58(0.07)	0.60(0.07)	0.61(0.06)
W_{ADG} – W_{BF}, %	0 – 100	25 – 75	50 – 50	75 – 25	100 – 0
W_{DGE} – W_{IGE}, %	75 – 25	75 – 25	75 – 25	75 – 25	75 – 25
$\rho(DGE_{ADG}, \widehat{DGE_{ADG}})$	0.69(0.06)	0.70(0.06)	0.68(0.06)	0.64(0.06)	0.64(0.06)
$\rho(IGE_{ADG}, \widehat{IGE_{ADG}})$	0.62(0.07)	0.62(0.06)	0.62(0.07)	0.63(0.07)	0.63(0.08)
$\rho(TBV_{ADG}, \widehat{TBV_{ADG}})$	0.68(0.06)	0.69(0.06)	0.69(0.06)	0.64(0.06)	0.63(0.06)
$\rho(DGE_{BF}, \widehat{DGE_{BF}})$	0.69(0.06)	0.70(0.06)	0.75(0.06)	0.74(0.06)	0.73(0.06)
$\rho(IGE_{BF}, \widehat{IGE_{BF}})$	0.59(0.07)	0.59(0.07)	0.59(0.07)	0.59(0.08)	0.60(0.07)
$\rho(TBV_{BF}, \widehat{TBV_{BF}})$	0.69(0.06)	0.69(0.06)	0.75(0.06)	0.75(0.06)	0.73(0.06)
$\rho(I_{TBV}, \widehat{I})$	0.60(0.09)	0.60(0.1)	0.50(0.11)	0.49(0.11)	0.51(0.12)
W_{ADG} – W_{BF}, %	0 – 100	25 – 75	50 – 50	75 – 25	100 – 0
W_{DGE} – W_{IGE}, %	100 – 0	100 – 0	100 – 0	100 – 0	100 – 0
$\rho(DGE_{ADG}, \widehat{DGE_{ADG}})$	0.69(0.06)	0.70(0.06)	0.69(0.06)	0.64(0.06)	0.63(0.06)
$\rho(IGE_{ADG}, \widehat{IGE_{ADG}})$	0.63(0.07)	0.62(0.07)	0.61(0.07)	0.62(0.07)	0.63(0.07)
$\rho(TBV_{ADG}, \widehat{TBV_{ADG}})$	0.69(0.06)	0.70(0.06)	0.69(0.06)	0.64(0.06)	0.63(0.06)
$\rho(DGE_{BF}, \widehat{DGE_{BF}})$	0.69(0.06)	0.69(0.06)	0.74(0.06)	0.75(0.05)	0.74(0.06)
$\rho(IGE_{BF}, \widehat{IGE_{BF}})$	0.59(0.07)	0.59(0.07)	0.59(0.07)	0.59(0.07)	0.59(0.07)
$\rho(TBV_{BF}, \widehat{TBV_{BF}})$	0.69(0.06)	0.69(0.06)	0.74(0.06)	0.75(0.05)	0.74(0.06)
$\rho(I_{TBV}, \widehat{I})$	0.55(0.12)	0.55(0.13)	0.45(0.14)	0.39(0.16)	0.41(0.16)

[a] Accuracy in generation five. The data were simulated from samples of the marginal posterior distribution of the social effects animal model and the same model was used for genetic evaluation. [b] W_{ADG} – W_{BF}: proportion of

economic weight assigned to average daily gain (ADG) and (backfat thickness) BF in the selection index, W_{DGE} – W_{IGE}: proportion of economic weight assigned to direct (DGE) and indirect (IGE) genetic effects of traits (DGE and IGE) in the selection index.

3.3. Prediction of individual feed intake from group records in growing Duroc pigs: Cross-validation assessment under different data structures

Authors:

William Herrera-Cáceres and Juan Pablo Sánchez

Abstract

The objective of this study was to evaluate the prediction accuracy of individual feed intake (IFI) when different proportions of individual and group feed intake (GFI) records are present in the dataset for the genetic evaluations. Phenotypic records for average daily gain (ADG), body weight (MBW), backfat thickness (BFT) and IFI on 1,384 Duroc pigs distributed in 118 pens were available. GFI was computed as the pen average of IFI records. Variance components of these traits were estimated employing a 5-trait linear animal model using Bayesian procedures. A 7-folds cross-validation procedure was used on 11 datasets, derived from the original data set, having different proportions of animals with IFI or GFI. The prediction quality of IFI records on the different data structures was evaluated assessing the Pearson correlation coefficient between observed and predicted IFI. The estimated heritability for IFI and for GFI was fairly the same (0.27), and both the genetic and the phenotypic correlations between them were around 0.96. The prediction accuracy of IFI did not show a clear pattern with the proportion of IFI records in the analysis, and the variation (0.71-0.79) we observed between the different distributions of individual and pen average feed intake record must be understood as uncertainty in the prediction accuracies. Most likely, our results are conditioned by the fact that other individually recorded traits are considered in the evaluation. Thus, we could postulate that when several individually recorded traits are jointly considered with pen average feed intake information, the added value of this pooled records is rather limited.

Introduction

The feed represents an important cost of the pig production (Pomar and Remus, 2019). For this reason, feed efficiency traits are considered paramount for pig production industry and breeding programs. Nevertheless, to collect feed intake individual records is still expensive and can only be accomplish by relatively large breeding companies (Jiao *et al*., 2014). This is why in many selection programs aiming to improve the efficiency of the raising animals indirect criteria based on easy-to-measure traits are considered, like for example back fat thickness (BFT) or daily growth (ADG) (Kuhlers *et al*., 2003). Another alternative could be to derive breeding value predictions for feed efficiency traits jointly considering traits representing animals' needs, like for example ADG or BFT, jointly with pen average feed intake records. This approach has been recently proposed for rabbits by Piles and Sánchez (2019), in this study the reported heritably estimate for the derived, i.e. obtained from cage feed intake averages, residual feed intake traits was 0.22. The value of this approach to successfully improve the feed efficiency within a selection program will depend on the actual ability of cage feed intake to inform about breeding values for individual feed efficiency or individual feed intake traits. The objective in this study was to assess the value of pen feed intake records to predict individual feed intake data in different data structures with respect to the proportion of individual and group average records.

Material and Methods

Animal material:

Phenotypic information during growing period on 1,384 Duroc pigs were recorded in 12 batches from 2007 to 2019 at the Center of Porcine Evaluation (Monells, Girona, Spain) using IVOG feeding stations (Insentec, Markenesse, The Netherland). Animals belonged to 530 litters sired by 103 boars and from 495 different sows. The completely known pedigree comprises 4,573 records from 533 sires and 2,658 dams. Animals were fed ad libitum on a standard diet containing: 15.0% CP, 4.7% fibre, 4.5% fat, 0.9% lysine and 0.3% methionine, having 3,200 Kcal of metabolic energy per Kg of feed. This Duroc line is being selected as a maternal line since 1991 (Tibau *et al*., 1999), receiving most of the weight in the selection index the prolificacy traits and backfat thickness. The studied animals were housed in 118 single sexed pens, the size of the pens ranged from 7 to 15 animals with an average of 12.0 animals per pen. The average (standard deviation) age of the animals at the beginning of the fattening period was 70(6) days of age and at the end of the fattening period was 180(10) days of age.

Description of traits:

Records of individual body weight (BW, kg) were collected from 4 to 11 times during the whole fattening period. Backfat thickness (BFT, mm) was also measured several times (3-5) during the fattening period, the assessment was done using ultrasounds (PIGLOG 105, SFK-Technology, Herlev, Denmark) at 5 cm of the midline between the third and fourth last ribs. From these raw BFT records, BFT at 180 days of age was computed following the procedure described by Herrera-Cáceres *et al*. (2020). Average daily gain (ADG, kg) was also obtained using a within-animal linear regression model of BW on age, i.e.: $BW_{ij} = \alpha_i + ADG_i * age_{ij} + e_{ij}$. The metabolic body weight (MBW, kg) of animals was computed as the mid body weight along the fattening period, i.e. average between initial and final BW to the power 0.75. Individual records of daily feed intake were collected using the single-space electronic feeder installed in each pen, the raw information generated by the feeders were processed as described by Sánchez *et al*. (2017) to generate average (along the fattening period) individual daily feed intake records (IFI, kg/d). From these individual records, group records were generated averaging across pen members within pen (GFI, kg/d). Basic statistics of the studied traits (ADG, MBW, BFT, IFI and GFI) are shown in Table 1.

Table 1 Descriptive statistics of traits in growing Duroc pigs

Trait	Abbreviation	No. of observations	Min.	Mean	Max.	SD
Average daily gain, kg/d	ADG	1,384	0.23	0.83	1.07	0.09
Mid metabolic body weight, kg	MBW	1,384	15.85	23.81	29.74	1.98
Backfat thickness at 180 d, mm	BFT	1,384	7.67	18.71	32.74	4.36
Individual daily feed intake, kg/d	IFI	1,384	1.19	2.73	4.40	0.46
Group daily feed intake, kg/d	GFI	1,384	1.98	2.72	3.55	0.35

Statistical models:

In an initial analysis, a multi-trait linear animal model was used to jointly fit ADG, MBW, BFT IFI and GFI. The same systematic effects were considered for all the traits: batch (12 levels), sex (2 levels: female and castrated male), age at the end of the fattening period (covariate) and number of pigs per pen (covariate). Pen, litter, additive genetic and environmental effects were also included in the model. In matrix notation, the model is represented by the following equation:

$$\begin{bmatrix} \boldsymbol{y_1} \\ \boldsymbol{y_2} \\ \boldsymbol{y_3} \\ \boldsymbol{y_4} \\ \boldsymbol{y_5} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X_1} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{X_2} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{X_3} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{X_4} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{X_5} \end{bmatrix} \begin{bmatrix} \boldsymbol{b_1} \\ \boldsymbol{b_2} \\ \boldsymbol{b_3} \\ \boldsymbol{b_4} \\ \boldsymbol{b_5} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{p_1}} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{Z_{p_2}} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{Z_{p_3}} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{Z_{p_4}} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{Z_{p_5}} \end{bmatrix} \begin{bmatrix} \boldsymbol{p_1} \\ \boldsymbol{p_2} \\ \boldsymbol{p_3} \\ \boldsymbol{p_4} \\ \boldsymbol{p_5} \end{bmatrix}$$

$$+ \begin{bmatrix} \boldsymbol{Z_{l_1}} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{Z_{l_2}} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{Z_{l_3}} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{Z_{l_4}} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{Z_{l_5}} \end{bmatrix} \begin{bmatrix} \boldsymbol{l_1} \\ \boldsymbol{l_2} \\ \boldsymbol{l_3} \\ \boldsymbol{l_4} \\ \boldsymbol{l_5} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{a_1}} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{Z_{a_2}} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{Z_{a_3}} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{Z_{a_4}} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{Z_{a_5}} \end{bmatrix} \begin{bmatrix} \boldsymbol{a_1} \\ \boldsymbol{a_2} \\ \boldsymbol{a_3} \\ \boldsymbol{a_4} \\ \boldsymbol{a_5} \end{bmatrix}$$

$$+ \begin{bmatrix} \boldsymbol{Z_{pe_1}} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{Z_{pe_2}} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{Z_{pe_3}} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{Z_{pe_4}} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{Z_{pe_5}} \end{bmatrix} \begin{bmatrix} \boldsymbol{pe_1} \\ \boldsymbol{pe_2} \\ \boldsymbol{pe_3} \\ \boldsymbol{pe_4} \\ \boldsymbol{pe_5} \end{bmatrix} + \begin{bmatrix} \boldsymbol{e_1} \\ \boldsymbol{e_2} \\ \boldsymbol{e_3} \\ \boldsymbol{e_4} \\ \boldsymbol{e_5} \end{bmatrix}$$

Where $\boldsymbol{y_1}$, $\boldsymbol{y_2}$, $\boldsymbol{y_3}$, and $\boldsymbol{y_4}$ are the vector of observations for individual records of ADG, MBW, BFT and IFI, respectively, $\boldsymbol{b}$ is a vector of systematic effects with incidence matrix $\boldsymbol{X}$; $\boldsymbol{p}$ is a vector of pen effects with incidence matrix $\boldsymbol{Z_p}$; $\boldsymbol{l}$ is a vector of litter effects with incidence matrix $\boldsymbol{Z_l}$; $\boldsymbol{a}$ is a vector of additive genetic effects with incidence matrix $\boldsymbol{Z_a}$; $\boldsymbol{pe}$ is a vector of environmental effects with incidence matrix $\boldsymbol{Z_{pe}}$; $\boldsymbol{e}$ is the vector of residuals. Whereas for the case of $\boldsymbol{y_5}$, this vector includes the observations for group records of feed intake, that is, GFI for each pen and the effects for this trait are the same as in $\boldsymbol{b}$, $\boldsymbol{p}$, $\boldsymbol{l}$, $\boldsymbol{a}$, $\boldsymbol{pe}$, and $\boldsymbol{e}$, however in this case, the matrices $\boldsymbol{Z_p}$, $\boldsymbol{Z_l}$, $\boldsymbol{Z_a}$ and $\boldsymbol{Z_{pe}}$, instead of including 0's and 1's, they contain real numbers corresponding to the proportions of the different levels of the factor which explain that particular pen average. For example, if the animals in a pen of 10 come from two different litters (7 and 3), the elements in the row of $\boldsymbol{Z_l}$ that apply to that particular pen will be 0.7 and 0.3, selecting with these proportions the appropriate levels of the litter effect vector.

Variance components for the studied traits were estimated using Bayesian procedures. Flat priors were assumed for systematic effects ($\boldsymbol{b}$) and for the rest of factors in the model the following prior distributions were assumed:

$\boldsymbol{p}|\boldsymbol{P_0}\sim N(\boldsymbol{0},\boldsymbol{P_0} \otimes \boldsymbol{I})$; $\boldsymbol{l}|\boldsymbol{L_0}\sim N(\boldsymbol{0},\boldsymbol{L_0} \otimes \boldsymbol{I})$; $\boldsymbol{a}|\boldsymbol{G_0}\sim N(\boldsymbol{0},\boldsymbol{G_0} \otimes \boldsymbol{A})$; $\boldsymbol{pe}|\boldsymbol{T_0}\sim N(\boldsymbol{0},\boldsymbol{T_0} \otimes \boldsymbol{I})$ and $\boldsymbol{e}|\boldsymbol{R_0}\sim N(\boldsymbol{0},\boldsymbol{R_0} \otimes \boldsymbol{I})$, where ***I*** are identity matrices of appropriate dimensions, $\boldsymbol{A}$ is the numerator relationship matrix between individuals and $\boldsymbol{P_0}$, $\boldsymbol{L_0}$ $\boldsymbol{G_0}$, $\boldsymbol{T_0}$ and $\boldsymbol{R_0}$ are covariance matrices of dimension 5, containing pen, litter, additive genetic effects, environmental effects and residual (co)variances of the five studied traits and $\otimes$ denotes the kronecker product. In this model, random factors were assumed to be independent, therefore:

$$\boldsymbol{Var}\begin{bmatrix}\boldsymbol{p}\\ \boldsymbol{l}\\ \boldsymbol{a}\\ \boldsymbol{pe}\\ \boldsymbol{e}\end{bmatrix}=\begin{bmatrix}\boldsymbol{P_0}\otimes\boldsymbol{I} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0}\\ \boldsymbol{0} & \boldsymbol{L_0}\otimes\boldsymbol{I} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0}\\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{G_0}\otimes\boldsymbol{A} & \boldsymbol{0} & \boldsymbol{0}\\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{T_0}\otimes\boldsymbol{I} & 0\\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{R_0}\otimes\boldsymbol{I}\end{bmatrix}$$

Like ***b***, flat uniform priors were assumed for all the covariance matrices. Pen effects for GFI and environmental effects for IFI are necessary factors in this multi-trait approach to estimate the covariance between these effects for both GFI and IFI, if environmental effect were not included in the model part of its effect would be captured by the additive genetic covariance. Note that in univariate setting the pen effect for GFI and the environmental effects for ADG, MBW, BFT and IFI would not be distinguish from the residual term, in a multi-trait setting the covariance structure between traits allows the identification (Piles and Sánchez, 2019).

Despite this partition of the environmental effects the final environmental effects are defined as the sum of pen, environmental and residual effects. Therefore, the residual variance (σ_{re}^2) for ADG, MBW, BFT and IFI was $\sigma_{re}^2 = \sigma_p^2 + \sigma_{pe}^2 + \sigma_e^2$ while that for GFI was $\sigma_{re}^2 = \sigma_p^2 + \sigma_{pe}^2 + m * \sigma_e^2$, where m is the average of animals per pen, in our study it was 12, σ_p^2 is the pen effect variance and σ_{pe}^2 is the environmental effect variance. The expression $m * \sigma_e^2$ is necessary because σ_e^2 for GFI represents the mean of the residual for a group and the groups are composed by 12 animals as average. Hence, the total phenotypic variance for this model was $\sigma_{Phe}^2 = \sigma_a^2 + \sigma_l^2 + \sigma_{re}^2$, where σ_a^2 is de additive genetic effect variance and σ_l^2 is the litter effect variance.

The marginal posterior distributions of all unknown parameters were obtained using the Gibbs Sampling algorithm, with the program gibbs2f90 (Misztal *et al*., 2015). Chains of 1,000,000 samples were run and the first 300,000 iterations were discarded to allow the algorithm to reach convergence to the marginal posterior distributions. Then, one sample every 10 iterations was saved, thus the autocorrelation of the chain was reduced. Convergence of the Markov chains was assessed by visual inspection of the trace plots included in the Additional files A1 and A2. In addition, the coda R package was used to convergence diagnostics, particularly using Geweke test (Plummer *et al*., 2006).

Prediction accuracy of IFI under different data structures:

Eleven different datasets were artificially created from the above described material. In these datasets the pens were distributed as either having IFI or GFI. When the individuals of a pen were declared to have IFI their GFI were assumed to be missing; and the other way around, when a pen was defined by GFI all the animals in that pen were assumed to have missing IFI.

As the combination between batch by sex comprised 15 levels, in order to guarantee that all the levels of this combination were present both in IFI and GFI records, we defined four data sets by choosing one, two, three or four pens within batch by sex combination with GFI and letting the rest of pens within batch y sex combination to have IFI records. Other four data sets were defined under the same structure, but instead of setting the chosen pens as having GFI records they were set to have IFI records, letting the rest of the pens within batch by sex combination to have GFI information. Another dataset was defined considering only IFI records for all the individuals, and the last two were defined considering only GFI records. In one of these two last cases the cross validation was conducted leaving out one IFI record per pen, and in the other all the records of randomly chosen pens were leaved out for validation. In this way, these IFI records were never considered in the training, in the previous case the IFI records were considered during the training as part of the pen averages. During the analysis of the last three datasets the respective 4-trait models were used instead of the general above described 5-trait model. Thus, the assessed scenarios comprised data structures having 0, 15, 30, 45, 58, 60, 73, 88, 103 and 118 pens with IFI and the complementary pens up to the total of 118 having GFI records.

For each one of these data structures we conducted a 7-folds cross validation procedure (Bengio and Grandvalet, 2004) randomly repeated 3 times. In each fold one individual per pen was randomly selected and excluded from the training, the minimum number of animals in a pen was 7, thus in order to minimize the correlation between folds we conducted this 7-fold cross validation, in order to increase the number of replicates the procedure was repeated 3 times. Under this validation structure the size of the validation dataset was constant and equal to 118 IFI records, one per pen. This validation procedure, jointly with the way the different data structures were created, conducted to two different groups of individuals in the validation data set: i) those not having any IFI information in the training dataset, i.e. those belonging to pens that kept their original IFI; and ii) those that their information was considered in the training data set throughout its pen average GFI. The proportion of ones versus the others would depend on the data set under study. In the results, we distinguish the accuracy for both types of animals. This accuracy was defined as the Pearson correlation coefficient between observed and predicted IFI records in the validation dataset. As previously indicated, the prediction was done using the same 5-trait model as described above for the data structures having both IFI and GFI, but in this case the EM-REML algorithm, as implemented in the remlf90 program (Misztal *et al*., 2015). In those data structures only having IFI or GFI the corresponding 4-trait sub-models were used. The accuracy report was presented as the average and the standard deviation of the Pearson correlations across folds and replicates.

Results and Discussion

The estimated variance component parameters for ADG, MBW, BFT, IFI and GFI are shown in Table 2. The heritability for these traits ranged from 0.19 to 0.34, the portion of phenotypic variance explained by litter effects ranged from 0.12 to 0.15 and the portion of phenotypic variance explained by residual effects ranged from 0.51 to 0.69.

Table 2 Posterior mean (posterior SD) of the ratios of variance components to the phenotypic variances and of the genetic (above diagonal) and phenotypic (below diagonal) correlations.

Trait	h^2	l^2	re^2	σ^2_{Ph}	ADG	MBW	BFT	IFI	GFI
ADG	0.23(0.06)	0.15(0.03)	0.62(0.05)	0.73(0.03)	--	0.69(0.12)*	0.66(0.12)*	0.87(0.05)*	0.95(0.02)*
MBW	0.19(0.06)	0.12(0.03)	0.69(0.05)	3.28(0.39)	0.76(0.02)*	--	0.33(0.18)*	0.52(0.14)*	0.58(0.14)*
BFT	0.34(0.07)	0.15(0.04)	0.51(0.06)	11.37(0.56)	0.60(0.02)*	0.50(0.03)*	--	0.72(0.09)*	0.70(0.11)*
IFI	0.28(0.06)	0.12(0.03)	0.60(0.06)	12.40(0.64)	0.82(0.01)*	0.62(0.03)*	0.67(0.02)*	--	0.97(0.01)*
GFI	0.27(0.06)	0.12(0.03)	0.61(0.07)	12.96(0.86)	0.81(0.02)*	0.61(0.04)*	0.66(0.03)*	0.96(0.01)*	--

ADG: average daily gain, MBW: metabolic body weight, BFT: backfat thickness, IFI: individual daily feed intake, GFI: group daily feed intake. σ^2_{Ph}: total phenotypic variance, h^2: heritability, l^2: ratio of litter effect variance to the phenotypic variance, re^2: ratio of the environmental variance to the phenotypic variance. *Probability of correlation being greater than 0≥0.95 or ≤0.05.

These figures match well previous estimates obtained in the same (Herrera-Cáceres *et al*., 2020) and other populations (Do *et al*., 2013). The range of genetics and phenotypic correlations for those traits that were previously studied, also match reasonably well those previous estimates (Labroue *et al*., 1997; Johnson *et al*., 1999; Chen *et al*., 2002;). For the aim of our study one of the most relevant result is the fact that the same ratios of variances to the phenotypic variance were estimated for IFI and GFI, and also very high genetic (0.97) and phenotypic (0.96) correlations were estimated between GFI and IFI. This result could be expected since within pen IFI means include the same information as that considered when analyzing raw IFI records.

During the cross validation procedure variance components were obtained using REML for the training data sets in all the replicates and scenarios, the averages and the standard deviations across replicates of the genetic correlations for the different data set structures are presented in Table 3. As it could be expected all the genetic correlation involving any trait except GFI presented a fairly constant patter across the different scenarios and their values were similar to those reported in the initial analysis considering the whole dataset. This applies even for the correlations involving IFI, in the case in which only 15 cages have IFI information, the estimated genetic correlations with the other traits (ADG, MBW and BFT) are in the range of those estimated with the whole data set or in scenarios with most of the data being recorded individually.

For the genetic correlations involving GFI the variation of the estimates across scenarios was much larger, and they were also different to those reported in the analysis with the whole dataset (Table 2). Nonetheless not a clear pattern across the different scenarios can be evidenced. For the case in which only 15 cage records were considered, being the rest of the information treated as IFI, except 118 animals (one per pen) that was considered in the validation set, the estimated correlations between GFI and the other traits was always 0.01, very different to the estimates reported in Table 2, between 0.58 for the correlation between MBW and GFI, and 0.97 for the correlation between IFI and GFI. This result could be expected since in this particular scenario amount of GFI records is very low.

Table 3 Mean(SD) across replicates of the estimated genetic correlations for the different proportions of pens with IFI.

Dataset[a]	$\rho_{(ADG,MBW)}$	$\rho_{(ADG,BFT)}$	$\rho_{(ADG,IFI)}$	$\rho_{(ADG,GFI)}$	$\rho_{(MBW,BFT)}$	$\rho_{(MBW,IFI)}$	$\rho_{(MBW,GFI)}$	$\rho_{(BFT,IFI)}$	$\rho_{(BFT,GFI)}$	$\rho_{(IFI,GFI)}$
118 IFI	0.74(0.02)	0.66(0.05)	0.81(0.02)	-	0.29(0.05)	0.51(0.03)	-	0.76(0.03)	-	-
103 IFI	0.75(0.02)	0.64(0.03)	0.81(0.02)	0.01(0.00)	0.30(0.05)	0.50(0.05)	0.01(0.00)	0.77(0.03)	0.01(0.00)	0.01(0.00)
88 IFI	0.73(0.03)	0.70(0.04)	0.80(0.03)	0.86(0.03)	0.28(0.05)	0.48(0.05)	0.43(0.05)	0.70(0.03)	0.76(0.04)	0.69(0.06)
73 IFI	0.74(0.04)	0.72(0.06)	0.85(0.02)	0.58(0.08)	0.33(0.05)	0.56(0.04)	0.63(0.09)	0.78(0.03)	0.15(0.09)	0.55(0.09)
60 IFI	0.75(0.04)	0.70(0.05)	0.83(0.03)	0.73(0.06)	0.29(0.05)	0.48(0.05)	0.52(0.06)	0.72(0.03)	0.41(0.07)	0.87(0.03)
58 IFI	0.73(0.03)	0.68(0.07)	0.79(0.03)	0.47(0.14)	0.28(0.05)	0.50(0.04)	0.31(0.22)	0.80(0.04)	0.62(0.14)	0.72(0.08)
45 IFI	0.75(0.03)	0.71(0.05)	0.78(0.04)	0.85(0.05)	0.31(0.05)	0.40(0.07)	0.63(0.09)	0.70(0.04)	0.54(0.11)	0.71(0.10)
30 IFI	0.74(0.04)	0.70(0.06)	0.85(0.04)	0.56(0.07)	0.28(0.07)	0.40(0.07)	0.59(0.07)	0.92(0.02)	0.12(0.09)	0.39(0.09)
15 IFI	0.73(0.03)	0.70(0.05)	0.73(0.06)	0.84(0.04)	0.27(0.04)	0.34(0.07)	0.79(0.04)	0.71(0.05)	0.46(0.07)	0.52(0.07)
0 IFI	0.73(0.02)	0.69(0.05)	-	0.83(0.05)	0.26(0.05)	-	0.68(0.07)	-	0.37(0.12)	-
0 IFI[b]	0.73(0.03)	0.68(0.05)	-	0.83(0.03)	0.25(0.06)	-	0.70(0.09)	-	0.40(0.11)	-

ADG: average daily gain, MBW: metabolic body weight, BFT: backfat thickness, IFI: individual daily feed intake, GFI: group daily feed intake.

[a] The number refers to the number of pens having IFI, the remaining up to 118 had GFI. Pigs in the training dataset without IFI records had GFI records, i.e. pigs with GFI had IFI=0.

[b] In this scenario the validation set was created selecting complete pens, instead of choosing one animal per pen, as it was done in the other scenario.

Despite these changes in the genetic correlation estimates across the different scenarios the prediction accuracy of the validation data set remains fairly constant across the different data structure scenario (Table 4).

Table 4 Prediction accuracy[a] of IFI for animals in the validation data set, one animal per pen.

Pens having IFI & GFI	Animals whose IFI record was part of pen averages in the training	Animals whose IFI record was not used at all in the training.
118 IFI – 0 GFI	-	0.75(0.04)
103 IFI – 15 GFI	0.75(0.11)	0.74(0.05)
88 IFI – 30 GFI	0.74(0.08)	0.76(0.06)
73 IFI – 45 GFI	0.77(0.04)	0.71(0.07)
60 IFI – 58 GFI	0.79(0.04)	0.74(0.07)
58 IFI – 60 GFI	0.76(0.04)	0.76(0.06)
45 IFI – 73 GFI	0.74(0.06)	0.78(0.06)
30 IFI – 88 GFI	0.76(0.04)	0.71(0.08)
15 IFI – 103 GFI	0.71(0.04)	0.73(0.12)
0 IFI – 118 GFI	0.78(0.04)	-
0 IFI – 118 GFI[b]	-	0.75(0.05)

IFI: individual daily feed intake, GFI: group daily feed intake.

[a] Average across 7 folds and 3 replicates (21 values) of the correlation between observed and predicted IFI records

[b] In this scenario the validation set was created selecting complete pens, instead of choosing one animal per pen as it was done in the other scenario. In this was the IFI predictions was done for animals whose IFI was never used in the training.

The average prediction accuracy presented certain variation across scenarios, but as this variation did not follow a pattern according to the distribution of IFI and GFI records we interpret such variation as noise. Thus, we could say that regardless the distribution of IFI and GFI records the same predict accuracy of IFI records was observed, and this holds both for the case in which IFI was never used during the training or when these IFI records to predict were part of pen averages included during the training. These results were certainly unexpected, since a drop in the prediction accuracy when IFI records were moved to GFI records was expected.

Nonetheless, we believe there are a number of issues in our cross-validation scheme that could explain this find. The sampling design was done to allow for a proper identification of all the levels of the systematic effects in the training sets, thus, even in the case in which very little information was available, as the systematic effects are properly identified, its contribution to the prediction could be very important. Even in the cases with less amount of IFI information, 15 pens with IFI, we were still considering in the training set an average of around 150-160 individuals with IFI. In spite of this last indicated point, in the case in which no IFI was used at all during the training, and the predicted IFI records were never used as part of pen averages (0 IFI – 118 GFI[b]), accuracies of around 0.75 we observed. Thus, the most likely factor to explain our results could be that we rely our predictions on results from multivariate analysis, thus part of the information for predicting random effects for IFI might not directly come from the trait itself, but also from the other traits (MWB, ADG or BFT) and this information from correlated traits is always present regardless the distribution of IFI or GFI. On this regard Ma *et al*. (2020) showed that the accuracy of breeding value prediction greatly increased when a pooled trait is jointly evaluated with an individually recorded trait, and they discussed that the added value of considering group records to predict breeding values of individually recorded traits is rather limited.

A number of studies have been conducted in different species to handle group performance records to allow for genetic parameter estimates as well as to conduct genetic evaluations, these studies include laying hens (Biscarini *et al*., 2008), mink (Madsen *et al*., 2020), cattle (Cooper *et al*., 2010), rabbits (Piles and Sánchez, 2019) and even pigs (Sánchez *et al*., 2014; Su *et al*., 2018). In spite of this, we are not aware of any study evaluating the actual impact within a breeding program, i.e. in terms of prediction accuracy or increase in the genetic responses, of considering such groups performance records as complementary information or as an alternative easy-to-measure trait that might replace information from other trait that could be difficult to record, as could be the case of IFI. We aimed this in our study, but must regard that the fact of relying our conclusions on results from multivariate models blur the actual impact of considering different data structures with regard to the availability of IFI or GFI information. In future studies we will reconsider the problem assessed in this study by using simulation tools, in a similar way as we have already done for exploring the role of social animal models in breeding programs of pigs (Herrera-Cáceres and Sánchez, 2020). With this simulation we will assess the role of GFI in terms of genetic responses, and one of the factors to consider in the simulation design will be to consider either single or multiple trait evaluations.

Conclusions

No changes in the prediction accuracies of IFI were observed across data structures having different proportions of IFI or GFI records. Most likely, this is a consequence of jointly considering in the evaluations other three individual traits. We could conclude that the added value of GFI for predicting IFI when other correlated traits a jointly considered in the evaluation is rather limited.

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Ethics approval and consent to participate

Animals used in this study come from a commercial population raised under selection nucleus conditions, following all the applicable Spanish and European Union laws with regard to welfare and health control. The fattening period of the animals was conducted at the Institut de Recerca i Tecnologia Agroalimentàries (IRTA) experimental facilities, and for this control period a research protocol was approved by IRTA's Animal Care and Use Committee.

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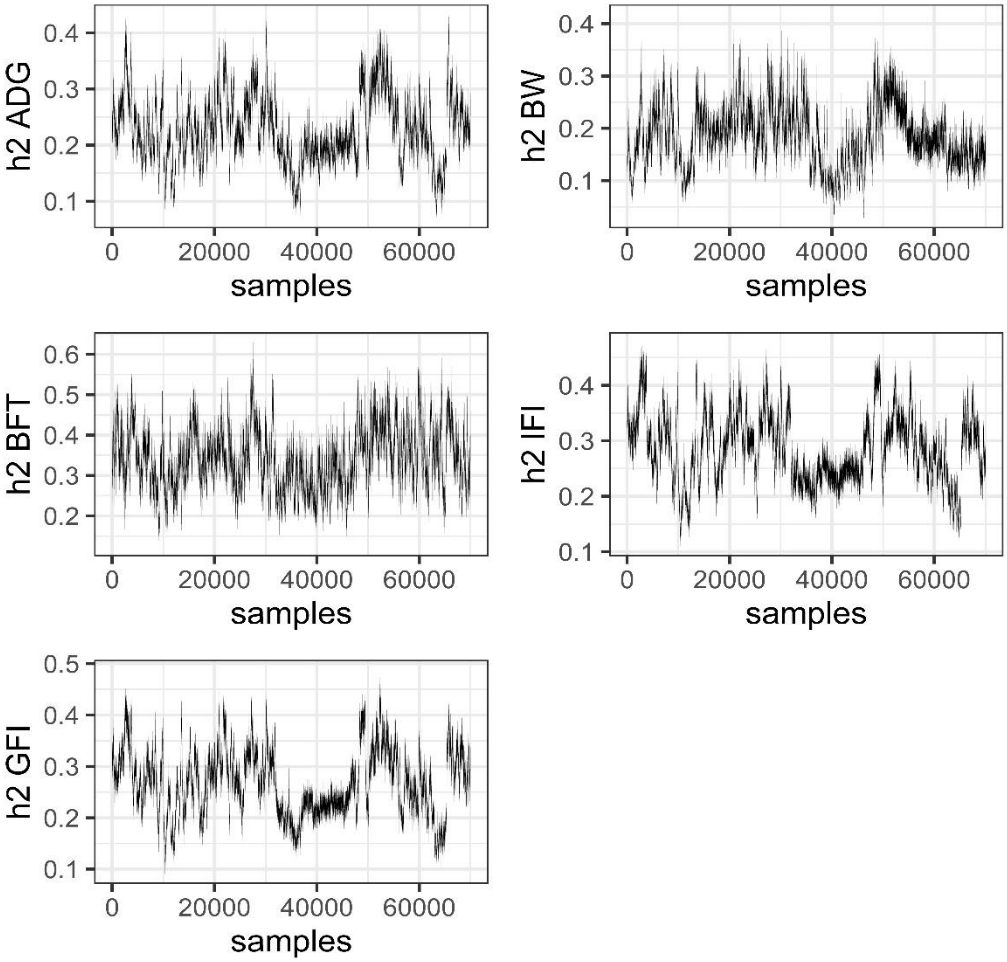
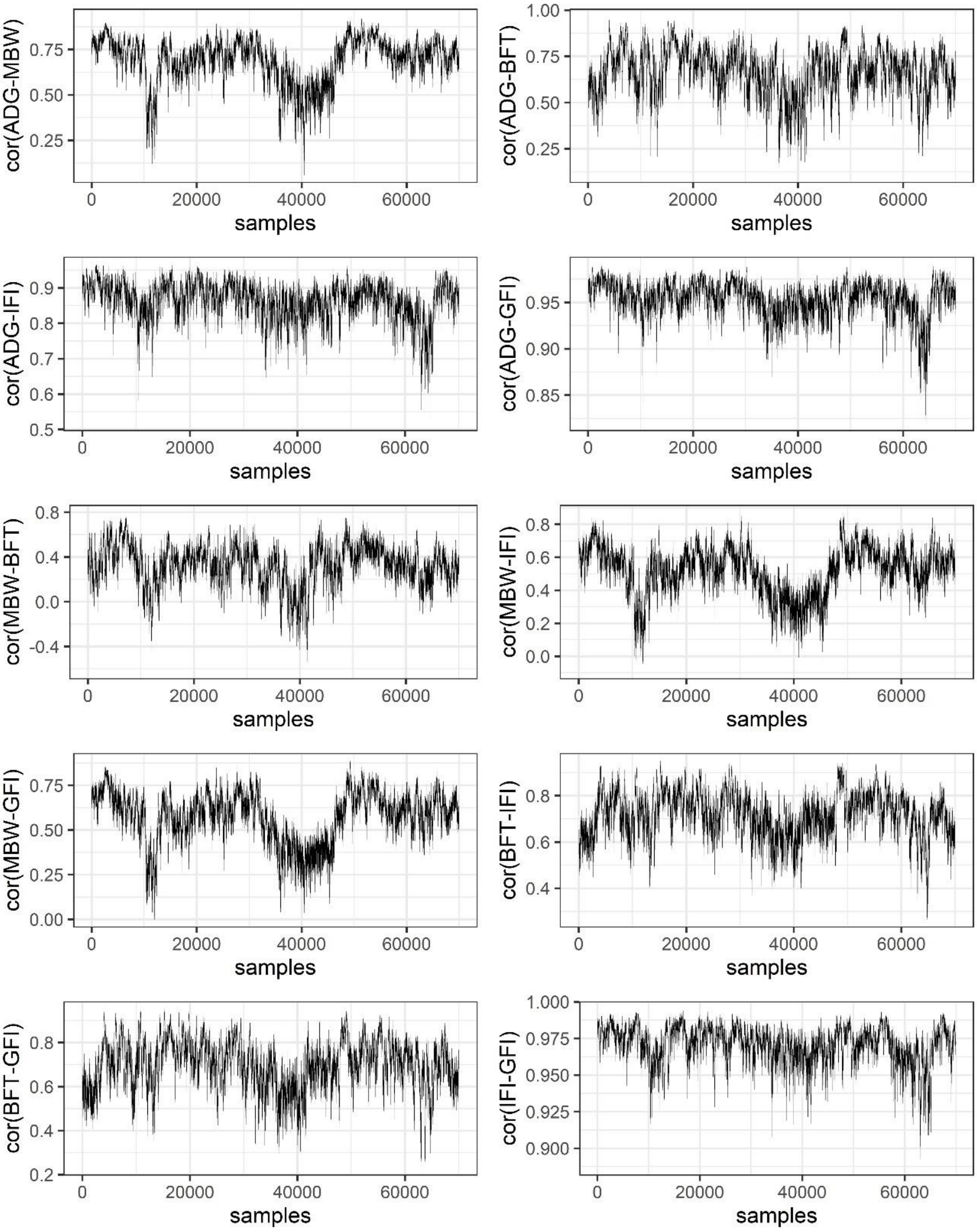
Additional File A1

Figure A1 Trace plots of Markov Chains of the estimated heritability for average daily gain, metabolic body weight, backfat thickness, individual feed intake and group feed intake.



Additional File A2

Figure A2 Trace plots of Markov Chains of estimated genetic correlations for average daily gain, metabolic body weight, backfat thickness, individual feed intake and group feed intake.



3.4. Longitudinal modelling of performance and feed efficiency traits in growing Duroc pigs

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Abstract

In this study we used the phenotypic information of 1,499 Duroc pigs, recorded longitudinally since 110 to 200 days of age for individual daily feed intake (DFI), backfat thickness (BF) and alive body weight (BW). Our aim was to estimate the genetic parameters for production and feed efficiency traits during the fattening period, with the objective to define, based on these parameters, the optimal moment for recording the phenotypes in order to maximize the expected response in a selection program to improve feed efficiency. In the analysis, addition to the aforementioned traits, other three traits were derived: average daily gain (ADG), a linear approximation of feed conversion ratio (FCR) and residual feed intake (RFI). The variance components for these traits were estimated through Bayesian procedures and using a multi-trait random regression animal model fitting Legendre polynomial of degree one. The estimated heritability patterns along the fattening were quite flat, around 0.17, 0.33, 0.26, 0.20 and 0.24 for DFI, BF, DWG, FCR and RFI, respectively. The only trait that shown variation in the heritability estimate along the fattening period was BW, from 0.15 to 0.07. For all the traits, the correlations between performance at different moments of the fattening period and those at 120 days, was always higher than 0.86. These results clearly point to a constant genetic determinism for the traits and period considered. Thus, regardless the age in which traits are recorded the same genetic response would be expected, since fairly the same genetic parameters are estimated along the fattening period.

Introduction

The costs associated to feeding growing pigs is the most important portion of the whole production costs in pig production (Gutierrez and Patience, 2012). Therefore, to reduce the daily feed intake (DFI) of growing pigs is expected to result in economic benefits and for this reason such trait is often considered, either directly or indirectly, in breeding programs for pigs (Stewart, 1990). Any direct consideration of feed efficiency traits, such as feed conversion ratio (FCR) or residual feed intake (RFI) (Merks *et al*., 2012), would request recording both performance traits like for example daily weight gain (DWG), backfat thickness (BF) or live body weight (BW); as well as feed intake records. Nonetheless important improvements on feed efficiency can be also achieved by indirect selection of performance traits genetically correlated with FCR or RFI. In this regard, the role of BF is paramount and most of the commercial pig breeding programs rely on the reduction of BF to enhance the efficiency of the growing animals.

The availability of longitudinal records, i.e. multiple measurements recorded throughout the fattening period, on performance and feed intake traits allows the study of the evolution of genetic parameters involved in the control of these traits, heritabilities and genetic correlation between the traits. There are already evidences that the genetic correlations between production and feed efficiency traits change with the age (Cai *et al*., 2011; Wetten *et al*., 2012), as well as the genetic variances and the heritabilities of traits (Shirali *et al*., 2017; Tran *et al*., 2017; Chaudhary *et al*., 2019). This variation in the genetic parameters along the fattening period could be the responsible of the changes in the accuracy of the estimated breeding values for DWG, DFI, FCR and RFI from early to late ages during the fattening period (Arthur *et al*., 2008). The objective of this study was to estimate the genetic parameters trend along the fattening period for performance and feed efficiency traits in a Duroc population, with the additional aim of identifying the optimal moment in which to record performance traits to indirectly improve overall feed efficiency in the studied population.

Material and Methods

Phenotypic records of 1,499 Duroc pigs were collected in 13 batches from 2007 to 2019 at the experimental Center of Porcine Evaluation (Monells, Girona, Spain). These batches comprised a total of 128 pens (pigs per pen averaged 11.8 ± 1.4) with an individual-space IVOG electronic feeding station (Insentec, Markenesse, the Netherlands) in each pen. The complete known pedigree for these animals is composed of 6,179 individuals. The Duroc line was founded in 1991 (Tibau *et al*., 1999) initially selected as a multipurpose line but later, at around 2005, the line was specialized as a maternal line focusing on increasing prolificacy while reducing backfat thickness (BF). The average (range) age at the first live weight control was 70 (53-85) days, while that for the last control was 180 (160-200) days. Despite this, as the recording of BF only was systematically conducted when the animals were older than 110 days old, we limit the period of study from this age onward, i.e. 90 days from 110 d to 200 d.

During the fattening period, animals were fed *ad libitum* with a standard diet satisfying their nutritional requirements. Measures for individual body weight (BW, kg) and BF (mm) were recorded several times during the fattening period, there were variation on the number of measurements per animal, ranging from 3 – 10 records per animal. BF was measured using ultrasonic technics (PIGLOG 105, SFK-Technology, Herlev, Denmark). The individual feed intake (DFI, kg) records were collected using electronic feeders following the procedure described by Sánchez *et al.* (2017). Descriptive statistics of the three raw studied traits are presented in the Table 1.

Table 1 Descriptive statistics for studied traits in three different periods along fattening.

	DFI (kg/d)			BW (kg)			BF (mm)		
Period	MEAN	SD	N	MEAN	SD	N	MEAN	SD	N
110 d - 140 d	2.58	0.63	28,27	66.03	10.47	2,40	10.75	2.57	1,67
141 d - 170 d	2.96	0.73	37,99	92.49	12.67	2,78	14.98	3.85	1,83
171 d - 200 d	2.96	0.85	15,08	117.85	14.04	1,58	20.0	4.6	1,49

DFI: daily feed intake, BW: live body weight, BF: backfat thickness.

A multi-trait random regression animal model was fitted to DFI, BW and BF. The same model was considered for the three traits and its equation, in scalar form, is the following:

$$\mathrm{Y}_{\mathrm{jklmiot}} = \mathrm{B}_{\mathrm{jt}} + \mathrm{S}_{\mathrm{kt}} + \boldsymbol{\Phi}_{\mathbf{3}}'(\mathrm{age}_{\mathrm{io}}) \times \boldsymbol{\beta}_{\mathrm{t}} + \boldsymbol{\Phi}_{\mathbf{1}}'(\mathrm{age}_{\mathrm{io}}) \times \mathbf{c}_{\mathrm{mt}} + \boldsymbol{\Phi}_{\mathbf{1}}'(\mathrm{age}_{\mathrm{io}}) \times \mathbf{l}_{\mathrm{lt}} \\ + \boldsymbol{\Phi}_{\mathbf{1}}'(\mathrm{age}_{\mathrm{io}}) \times \mathbf{p}_{\mathrm{it}} + \boldsymbol{\Phi}_{\mathbf{1}}'(\mathrm{age}_{\mathrm{io}}) \times \mathbf{a}_{\mathrm{it}} + \mathrm{e}_{\mathrm{jklmiot}}$$

Where the subscript t refers to each one of the tree studied traits (DFI, BW and BF), the considered systematic effects were the batch (B_{jt}, 13 levels), the sex (S_{kt}, 2 levels: females and castrated males) and a Legendre polynomial regression of degree three on the age, $\boldsymbol{\beta}_{\mathrm{t}}$ is a vector that includes, the effects associated to the four coefficients, $\boldsymbol{\Phi}_{\mathbf{3}}{}'(\mathrm{age}_{\mathrm{io}})$, of the Legendre polynomial. These Legendre coefficients are a function of the age of the animal i when its o$^{\mathrm{th}}$ record was obtained. Similarly; pen ($\mathbf{c}_{\mathrm{mt}}$, 128 levels), litter ($\mathbf{l}_{\mathrm{lt}}$, 562 levels), permanent environmental ($\mathbf{p}_{\mathrm{it}}$, 1,499 levels) and additive genetic ($\mathbf{a}_{\mathrm{it}}$, 6,179 levels) effects were fitted as regression on Legendre functions of degree 1 (two coefficients) for the age of the animal i when its o$^{\mathrm{th}}$ record was obtained. The residual term ($\mathrm{e}_{\mathrm{jklmiot}}$) was assumed to be heteroskedastic with respect to the age, see below.

Model parameters were estimated using a Bayesian MCMC procedure, thus prior distribution of all the unknowns had to be specified. Uniform and independent distributions were *a priori* assumed for the elements of $\mathbf{B}$, $\mathbf{S}$ and $\boldsymbol{\beta}$, i.e. batch, sex and regression coefficients on Legendre functions of age. Pen, litter, permanent environment and additive genetic effects were assumed, *a priori*, to follow independent multivariate normal distributions with these specifications: $\mathbf{c}|\mathbf{C_0}\sim MVN(\mathbf{0},\mathbf{C_0}\otimes\mathbf{I})$; $\mathbf{l}|\mathbf{L_0}\sim MVN(\mathbf{0},\mathbf{L_0}\otimes\mathbf{I})$; $\mathbf{p}|\mathbf{P_0}\sim MVN(\mathbf{0},\mathbf{P_0}\otimes\mathbf{I})$ and $\mathbf{a}|\mathbf{G_0}\sim MVN(\mathbf{0},\mathbf{G_0}\otimes\mathbf{A})$, respectively. The identity matrices $\mathbf{I}$ have dimensions equal to the number of levels of the different factors previously described and **A** is the numerator relationship matrix between individuals in the pedigree. $\mathbf{C_0}$, $\mathbf{L_0}$, $\mathbf{P_0}$ and $\mathbf{G_0}$ contain the co-variances associated with the two regression coefficients for each one of the studied traits, i.e. dimension 6. The operator ⊗ denotes the Kronecker product. As it has been stated, heterogeneous residual variances were assumed, three different residual co-variance matrices were defined for the intervals 110-140,141-170 and 171-200. The normal prior distribution for the residuals can be expressed as $\mathbf{e}|\mathbf{R}\sim MVN(\mathbf{0},\mathbf{R})$, where the covariance matrix has the following form:

$$\mathbf{R}=\begin{bmatrix}\mathbf{R}_{\mathbf{0},110-140}\otimes\mathbf{I}_{110-140} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{R}_{\mathbf{0},141-170}\otimes\mathbf{I}_{141-170} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{R}_{\mathbf{0},171-210}\otimes\mathbf{I}_{171-200}\end{bmatrix}$$

$\mathbf{R}_{\mathbf{0},110-140}$, $\mathbf{R}_{\mathbf{0},141-170}$ and $\mathbf{R}_{\mathbf{0},171-200}$ are 3x3 matrices with the residual (co)variances between traits in the respective periods; and $\mathbf{I}_{110-140}$, $\mathbf{I}_{141-170}$ and $\mathbf{I}_{171-200}$ are identity matrices with dimension equal to the number of records in each period.

Similarly to the systematic effects, uniform prior within their valid domain were assumed for all the elements of the variance component matrices: $\mathbf{C_0}$, $\mathbf{L_0}$, $\mathbf{P_0}$, $\mathbf{G_0}$, $\mathbf{R_{0}}_{,110-140}$, $\mathbf{R_{0}}_{,141-170}$ and $\mathbf{R_{0}}_{,171-200}$.

Marginal posterior distribution of the variance components were sampled using the Gibbs Sampling algorithm using the program gibbsf90test, which is a new version of the gibbs3f90 program (Misztal *et al*., 2015). Chains of 1,000,000 samples were run and the first 600,000 iterations were discarded in order to allow the algorithm to reach convergence to the marginal posterior distributions. Then, one sample every 10 iterations was saved. Convergence of the Markov chains was assessed using the Geweke test function in coda R package (Plummer *et al*., 2006). Another criterion to assess for convergence was just the visual inspection of the chain trace plots (see Additional Figure B1 and B2). We also run two chains having the same random seed but with different starting values, in one of them the starting values were set to the estimates obtained in a previous EM-REML analysis using the software remlf90 (Misztal *et al*., 2015). In the other chain the starting values were set to those in the first iterations of the EM-REML algorithm. By comparing the posterior mean obtained with both chains we could assess whether the effect of the starting value vanished.

From the saved samples of the marginal posterior distribution of the variance components in the aforementioned model, it was possible to derive variance components of other related traits. One of this was daily weight gain (DWG), this trait was obtained from the first derivative of the Legendre polynomial functions of BW for pen, litter, permanent environmental and additive genetic effects. From the polynomial functions of the different factors for DFI, BW, BF and DWG, the last one based on their first derivative, variances components were obtained for all the days under study (110-200 days), this was done for pen, litter, permanent environmental, additive genetic and residual effects.

Once matrices of variance covariance for all the factors and traits were defined on a daily basis, then variance components for feed efficiency related measurements were obtained. We consider residual feed intake (RFI) and feed conversion ratio

(FCR), for RFI the same procedure used as that used Piles and Sánchez (2019), previously proposed by Strathe *et al*. 2014, was used. This method relies on considering RFI as a DFI conditioned on BF, BW and DWG; thus, for each day (d) along the fattening period it was needed to obtain the regression coefficient vector ($\mathbf{B}_{\mathrm{d}}$) that allows to obtain the conditioned traits:

$$\mathbf{b}_{\mathrm{d}} = [1 \quad -\mathrm{b}_{\mathrm{BW,d}} \quad -\mathrm{b}_{\mathrm{BF,d}} \quad -\mathrm{b}_{\mathrm{DWG,d}}]$$

$\mathrm{b}_{\mathrm{BW,d}}$, $\mathrm{b}_{\mathrm{BF,d}}$ and $\mathrm{b}_{\mathrm{DWG,d}}$ are phenotypic regression coefficients for the day d obtained from the 4x4 phenotypic co-variance matrix on the day d.

$$\begin{bmatrix} \mathrm{b}_{\mathrm{BW,d}} \\ \mathrm{b}_{\mathrm{BF,d}} \\ \mathrm{b}_{\mathrm{DWG,d}} \end{bmatrix} = \begin{bmatrix} \sigma^2_{\mathrm{Phe,BW,d}} & \sigma_{\mathrm{Phe,BW-BF,d}} & \sigma_{\mathrm{Phe,BW-DWG,d}} \\ \sigma_{\mathrm{Phe,BW-BF,d}} & \sigma^2_{\mathrm{Phe,BF,d}} & \sigma_{\mathrm{Phe,BF-DWG,d}} \\ \sigma_{\mathrm{Phe,BW-DWG,d}} & \sigma_{\mathrm{Phe,BF-DWG,d}} & \sigma^2_{\mathrm{Phe,DWG,d}} \end{bmatrix}^{-1} \begin{bmatrix} \sigma_{\mathrm{Phe,DFI-BW,d}} \\ \sigma_{\mathrm{Phe,DFI-BF,d}} \\ \sigma_{\mathrm{Phe,DFI-DWG,d}} \end{bmatrix}$$

The phenotypic covariance matrix was obtained as $\mathbf{Phe}_{\mathrm{d}} = \mathbf{C}_{\mathrm{d}} + \mathbf{L}_{\mathrm{d}} + \mathbf{P}_{\mathrm{d}} + \mathbf{G}_{\mathrm{d}} + \mathbf{R}_{\mathrm{d}}$. Pen, litter, permanent environmental, additive genetic and residual variances for RFI on the day d were defined as:

$$\sigma^2_{\mathrm{C,RFI,d}} = \mathbf{b}_{\mathrm{d}} \times \mathbf{C}_{\mathrm{d}} \times \mathbf{b}'_{\mathrm{d}};$$
$$\sigma^2_{\mathrm{L,RFI,d}} = \mathbf{b}_{\mathrm{d}} \times \mathbf{L}_{\mathrm{d}} \times \mathbf{b}'_{\mathrm{d}}\ ;$$
$$\sigma^2_{\mathrm{P,RFI,d}} = \mathbf{b}_{\mathrm{d}} \times \mathbf{P}_{\mathrm{d}} \times \mathbf{b}'_{\mathrm{d}};$$
$$\sigma^2_{\mathrm{G,RFI,d}} = \mathbf{b}_{\mathrm{d}} \times \mathbf{G}_{\mathrm{d}} \times \mathbf{b}_{\mathrm{d}}' \text{ and}$$
$$\sigma^2_{\mathrm{R,RFI,d}} = \mathbf{b}_{\mathrm{d}} \times \mathbf{R}_{\mathrm{d}} \times \mathbf{b}_{\mathrm{d}}'$$

Similarly, covariances between days can be obtained with this general equation:

$$\sigma_{\mathrm{x,RFI,d1,d2}} = \mathbf{b}_{\mathrm{d1}} \times \mathbf{X}_{\mathrm{d1,d2}} \times \mathbf{b}'_{\mathrm{d2}}$$

In this context **X** aims to represent to any one of the effects in the model: pen, litter, permanent environmental, additive genetic and residual, as well as the covariance matrix between days associated to it. $\mathbf{X}_{\mathrm{d1,d2}}$ would contains the covariances within (in the diagonal) and between (out of the diagonal) traits for the effects referring to d1 and d2. The phenotypic variance of RFI on the day d can be defined as $\sigma^2_{\mathrm{Phe,RFI,d}} = \sigma^2_{\mathrm{C,RFI,d}} + \sigma^2_{\mathrm{L,RFI,d}} + \sigma^2_{\mathrm{P,RFI,d}} + \sigma^2_{\mathrm{G,RFI,d}} + \sigma^2_{\mathrm{R,RFI,d}}$.

Following a similar procedure, phenotypic and genetic variances were obtained for a linear approximation of the FCR. We used the procedure described by Lin (1980), he proposed to approximate any ratio trait by a liner index of the component traits yielding the same response to that obtained when selection is directly performed on the ratio trait. In our case this imply that the following vector would be used in quadratic forms of the variance components:

$$\mathbf{w}_{\mathrm{d}} = [\mathrm{w}_{\mathrm{FI,d}} \quad 0 \quad 0 \quad \mathrm{w}_{\mathrm{DWG,d}}]$$

Being the non-null elements of the vector the following:

$$\begin{bmatrix} \mathrm{w}_{\mathrm{DFI,d}} \\ \mathrm{w}_{\mathrm{DWG,d}} \end{bmatrix} = \begin{bmatrix} \sigma^2_{\mathrm{Phe,DFI,d}} & \sigma_{\mathrm{Phe,DFI-DWG,d}} \\ \sigma_{\mathrm{Phe,DFI-DWG,d}} & \sigma^2_{\mathrm{Phe,DWG,d}} \end{bmatrix}^{-1} \begin{bmatrix} \sigma^2_{\mathrm{G,DFI,d}} & \sigma_{\mathrm{G,DFI-DWG,d}} \\ \sigma_{\mathrm{G,DFI-DWG,d}} & \sigma^2_{\mathrm{G,DWG,d}} \end{bmatrix} \begin{bmatrix} 1 \\ -\left(\frac{\overline{\mu_{DFI,d}}}{\overline{\mu_{DWG,d}}}\right) \end{bmatrix},$$

where $\frac{\overline{\mu_{DFI,d}}}{\overline{\mu_{DWG,d}}}$ is the ratio between the mean DFI and the mean DWG on the day d. These raw mean estimates were obtained after applying the same fixed Legendre polynomial regressions (4 coefficients) included in the initial model to the raw DFI and BW data. DWG mean on the day d were obtained deriving with respect to the day the Legendre polynomial function of BW.

The variance components associated to the different factors would be, assuming that the order of the trait in the variance components matrix is DFI, BW, BF and DWG,

$$\sigma^2_{\mathrm{C,FCR,d}} = \mathbf{w}_{\mathrm{d}} \times \mathbf{C}_{\mathrm{d}} \times \mathbf{w}'_{\mathrm{d}};$$

$$\sigma^2_{\mathrm{L,FCR,d}} = \mathbf{w}_{\mathrm{d}} \times \mathbf{L}_{\mathrm{d}} \times \mathbf{w}'_{\mathrm{d}};$$

$$\sigma^2_{\mathrm{P,FCR,d}} = \mathbf{w}_{\mathrm{d}} \times \mathbf{P}_{\mathrm{d}} \times \mathbf{w}'_{\mathrm{d}};$$

$$\sigma^2_{\mathrm{G,FCR,d}} = \mathbf{w}_{\mathrm{d}} \times \mathbf{G}_{\mathrm{d}} \times \mathbf{w}'_{\mathrm{d}} \text{ and}$$

$$\sigma^2_{\mathrm{R,FCR,d}} = \mathbf{w}_\mathrm{d} \times \mathbf{R}_\mathrm{d} \times \mathbf{w}'_\mathrm{d}$$

Also, covariance terms between days can be obtained in the same way as it was defined for RFI. Similarly, to RFI, the phenotypic variance of FCR on the day d was defined as:

$$\sigma^2_{\mathrm{Phe,FCR,d}} = \sigma^2_{\mathrm{C,FCR,d}} + \sigma^2_{\mathrm{L,FCR,d}} + \sigma^2_{\mathrm{P,FCR,d}} + \sigma^2_{\mathrm{G,FCR,d}} + \sigma^2_{\mathrm{R,FCR,d}}$$

Daily variances for RFI ($\sigma^2_{\mathrm{X,RFI,d}}$), FCR ($\sigma^2_{\mathrm{X,FCR,d}}$) and DWG ($\sigma^2_{\mathrm{X,DWG,d}}$) and covariances between days (for example for RFI = $\sigma_{\mathrm{X,RFI,d1,d2}}$) can be organized in 90 x 90 matrices (90 = 200 d – 110 d). In this notation we use X to refer to any model effect: pen, litter, permanent environmental, additive genetic and residual. We can name these matrices: $\mathbf{C}_{\mathrm{all,RFI}}$, $\mathbf{L}_{\mathrm{all,RFI}}$, , $\mathbf{P}_{\mathrm{all,RFI}}$, $\mathbf{G}_{\mathrm{all,RFI}}$ and $\mathbf{R}_{\mathrm{all,RFI}}$ for RFI; $\mathbf{C}_{\mathrm{all,FCR}}$, $\mathbf{L}_{\mathrm{all,FCR}}$, , $\mathbf{P}_{\mathrm{all,FCR}}$, $\mathbf{G}_{\mathrm{all,FCR}}$ and $\mathbf{R}_{\mathrm{all,FCR}}$ for FCR and $\mathbf{C}_{\mathrm{all,DWG}}$, $\mathbf{L}_{\mathrm{all,DWG}}$, , $\mathbf{P}_{\mathrm{all,DWG}}$, $\mathbf{G}_{\mathrm{all,DWG}}$ and $\mathbf{R}_{\mathrm{all,DWG}}$ for DWG .

From these matrices we can obtain overall (averages along the whole fattening period) variance components for the different factors with these quadratic forms:

$$\sigma^2_{\mathrm{C,oRFI}} = \mathbf{h} \times \mathbf{C}_{\mathrm{all,RFI}} \times \mathbf{h}';$$
$$\sigma^2_{\mathrm{L,oRFI}} = \mathbf{h} \times \mathbf{L}_{\mathrm{all,RFI}} \times \mathbf{h}';$$
$$\sigma^2_{\mathrm{P,oRFI}} = \mathbf{h} \times \mathbf{P}_{\mathrm{all,RFI}} \times \mathbf{h}';$$
$$\sigma^2_{\mathrm{G,oRFI}} = \mathbf{h} \times \mathbf{G}_{\mathrm{all,RFI}} \times \mathbf{h}' \text{ , and}$$
$$\sigma^2_{\mathrm{R,oRFI}} = \mathbf{h} \times \mathbf{R}_{\mathrm{all,RFI}} \times \mathbf{h}'$$

The equivalent expressions for oFCR being:

$$\sigma^2_{\mathrm{C,oFCR}} = \mathbf{h} \times \mathbf{C}_{\mathrm{all,FCR}} \times \mathbf{h}';$$
$$\sigma^2_{\mathrm{L,oFCR}} = \mathbf{h} \times \mathbf{L}_{\mathrm{all,FCR}} \times \mathbf{h}';$$
$$\sigma^2_{\mathrm{P,oFCR}} = \mathbf{h} \times \mathbf{P}_{\mathrm{all,FCR}} \times \mathbf{h}';$$
$$\sigma^2_{\mathrm{G,oFCR}} = \mathbf{h} \times \mathbf{G}_{\mathrm{all,FCR}} \times \mathbf{h}' \text{ and}$$

$$\sigma^2_{\mathrm{R,oFCR}} = \mathbf{h} \times \mathbf{R}_{\mathrm{all,FCR}} \times \mathbf{h}';$$

And those for oDWG:

$$\sigma^2_{\mathrm{C,oDWG}} = \mathbf{h} \times \mathbf{C}_{\mathrm{all,DWG}} \times \mathbf{h}';$$
$$\sigma^2_{\mathrm{L,oDWG}} = \mathbf{h} \times \mathbf{L}_{\mathrm{all,DWG}} \times \mathbf{h}';$$
$$\sigma^2_{\mathrm{P,oDWG}} = \mathbf{h} \times \mathbf{P}_{\mathrm{all,DWG}} \times \mathbf{h}';$$
$$\sigma^2_{\mathrm{G,oDWG}} = \mathbf{h} \times \mathbf{G}_{\mathrm{all,DWG}} \times \mathbf{h}' \text{ and}$$
$$\sigma^2_{\mathrm{R,oDWG}} = \mathbf{h} \times \mathbf{R}_{\mathrm{all,DWG}} \times \mathbf{h}';$$

$\mathbf{h}$ is a vector weighting the different days along the fattening period we assigned the same weight to all the days thus all the elements of vector $\mathbf{h}$ were equal to $\frac{1}{90}$. Finally, phenotypic variances of oRFI, oFCR and oDWG were obtained as:

$$\sigma^2_{\mathrm{Phe,oRFI}} = \sigma^2_{\mathrm{C,oRFI}} + \sigma^2_{\mathrm{L,oRFI}} + \sigma^2_{\mathrm{P,oRFI}} + \sigma^2_{\mathrm{G,oRFI}} + \sigma^2_{\mathrm{R,oRFI}} ;$$
$$\sigma^2_{\mathrm{Phe,oFCR}} = \sigma^2_{\mathrm{C,oFCR}} + \sigma^2_{\mathrm{L,oFCR}} + \sigma^2_{\mathrm{P,oFCR}} + \sigma^2_{\mathrm{G,oFCR}} + \sigma^2_{\mathrm{R,oFCR}} \text{ , and}$$
$$\sigma^2_{\mathrm{Phe,oDWG}} = \sigma^2_{\mathrm{C,oDWG}} + \sigma^2_{\mathrm{L,oDWG}} + \sigma^2_{\mathrm{P,oDWG}} + \sigma^2_{\mathrm{G,oDWG}} + \sigma^2_{\mathrm{R,oDWG}}$$

All the above-mentioned computations of parameters for the derived traits were conducted within each sample of the marginal posterior distribution of the model parameters, thus it was possible to fully characterize the marginal posterior distribution of genetic parameters for the derived traits.

Results and Discussion

Figure 1 shows the heritability patterns for the studied traits DFI, BW, BF, DWG, FCR and RFI. To properly quantify the magnitude of the estimates for the different moments along the fattening period the estimates every 15 days are presented in the Table 2. Fairly constant heritability patterns were observed for DFI (0.17), BF (0.33) and DWG (0.26). BW is the trait for which the largest differences in heritability across age were observed, from around 0.15 at 110 d. to around 0.07 at 200 d. The heritability of feed efficiency traits (FE) also shown constant patterns, 0.20 for FCR and around 0.24 for RFI.

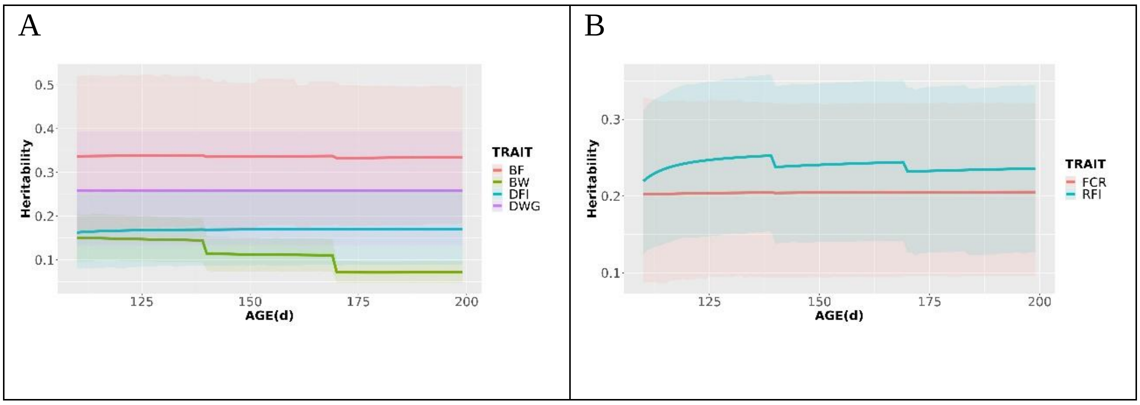

Figure 1 Heritability patterns along the fattening period for daily feed intake (DFI), live body weight (BW), backfat thickness (BF) and daily weigh gain (DWG) (panel A); and for feed efficiency traits (panel B), feed conversion ratio (FCR) and residual feed intake (RFI). The solid lines represent posterior means, and the colored transparent areas represent 95HPD regions.

The observed broken-line pattern for the heritabilities of BW and RFI is consequence of the assumed heterogeneous residual variance pattern, with jumps at 140 and 170 days, this pattern gets translated to the phenotypic covariance structure and thus, if the transition from one period to the other is not smooth them it could be possible to observe it in the phenotypic variance pattern, i.e. the denominator of the heritability.

Table 2 Marginal posterior Mean(SD) of the heritabilities for production and feed efficiency traits at different ages during the fattening period.

Age	DFI	BW	BF	DWG	FCR	RFI
110, d	0.16(0.04)	0.15(0.03)	0.34(0.09)	0.26(0.07)	0.20(0.06)	0.22(0.05)
125, d	0.17(0.04)	0.15(0.03)	0.34(0.09)	0.26(0.07)	0.20(0.06)	0.25(0.05)
140, d	0.17(0.04)	0.11(0.02)	0.34(0.08)	0.26(0.07)	0.20(0.06)	0.24(0.05)
155, d	0.17(0.04)	0.11(0.02)	0.34(0.08)	0.26(0.07)	0.20(0.06)	0.24(0.05)
170, d	0.17(0.04)	0.07(0.01)	0.33(0.08)	0.26(0.07)	0.20(0.06)	0.23(0.06)
185, d	0.17(0.04)	0.07(0.01)	0.33(0.08)	0.26(0.07)	0.21(0.06)	0.23(0.06)
200, d	0.17(0.04)	0.07(0.01)	0.33(0.08)	0.26(0.07)	0.21(0.06)	0.24(0.06)

DFI: daily feed intake, BW: live body weight, BF: backfat thickness, DWG: daily weight gain, FCR: feed conversion ratio, RFI: residual feed intake.

The estimated heritabilities for DFI, BF, DWG and FCR are in the range of previous estimates obtained in the same population when studies based on single-measure traits were conducted (Herrera-Cáceres *et al*., 2020). Regarding the heritability of the overall FE and the overall growth we observed that the posterior mean (posterior standard deviation) of oRFI, oFCR and oDWG were 0.24(0.05), 0.19(0.08) and 0.26(0.00), respectively.

In order to assess the magnitude of the genetic correlations within each trait across the fattening period we report in Table 3 the marginal posterior mean (standard deviations) of the genetic correlations between the trait recorded at different days along the fattening period and the trait recorded at day 120 of age. Extremely high correlations were observed for all the traits, the lowest value (0.86) was observed in the estimated correlation between BW at 120 d and BW at the end of the control period. This result, jointly with the constant heritabilities along the fattening period are clear indications of a common genetic control of the traits along the fattening period. In previous studies (Huisman *et al*., 2002; Coyne *et al*., 2017) a general result or conclusion was the opposite, there certain degree of variation on the genetic control along the fattening period. Our result could be highly dependent on the fact that a polynomial of degree one was considered in the random regression. This reduced degree imposes the constraint that only linear changes in the variance components could be evidenced. In other published studies (Cai *et al*., 2011) higher degree was assumed, increasing the flexibility of the functions, thus non-linear patterns could be evidenced. We decided to keep the polynomial function on its minimum degree in order to avoid a number of artifacts that were evidenced when higher degree is employed, for example, the correlations between BF and BW were extremely negative. We assumed that these artifacts were a consequence of the reduced number of records available for this study.

The pattern of daily genetic correlations between performance and FE traits are shown in Figure 2. To quantitatively assess the magnitude of these correlations we also show the values (posterior means (posterior standard deviations)) of these correlation estimates every 15 days in the Table 4.

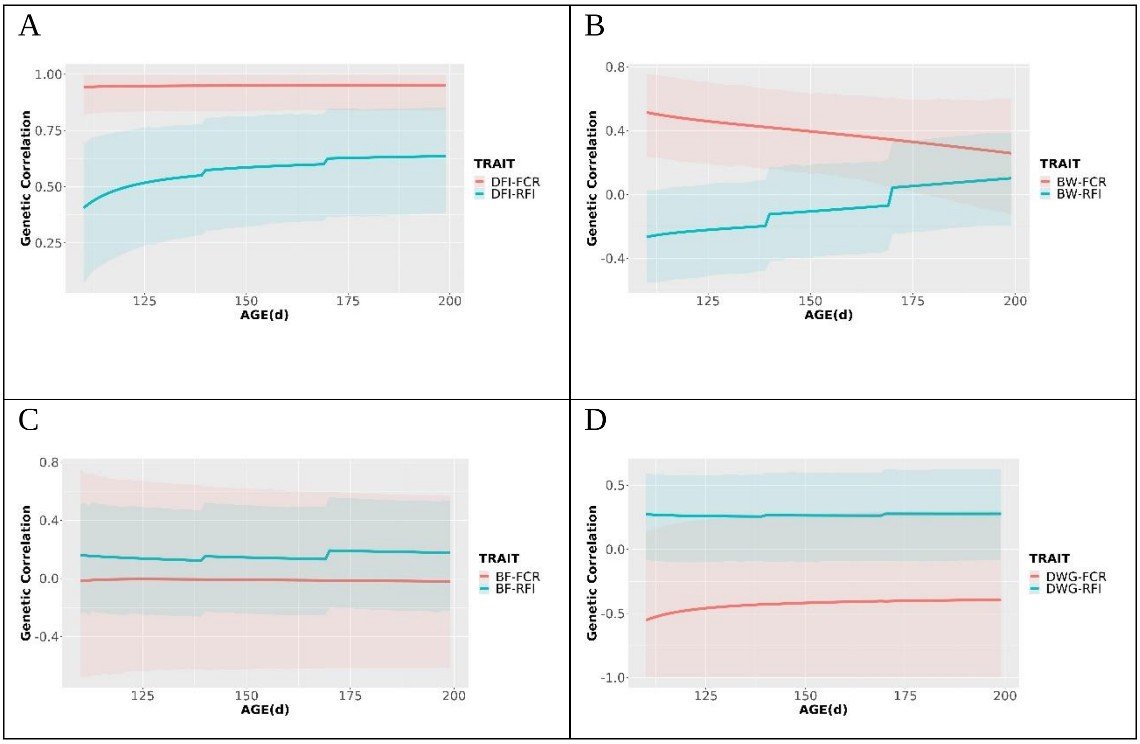

Figure 2 Pattern along the fattening period of estimated genetic correlations between production (DFI: daily feed intake, BW: live body weight, BF: backfat thickness and DWG: daily weight gain) and feed efficiency traits (FCR: feed conversion ratio and RFI: residual feed intake). Solid lines represent posterior means, and the colored transparent areas represent 95HPD regions.

The only genetic correlations that seems to show a non-constant pattern along the fattening period are the two involving BW and the feed efficiency definitions. That between BW and FCR changed from 0.51 at the beginning of the control period to 0.26 at the end. For that between BW and RFI the pattern increased from -0.27 at 110 days to 0.10 at 200 days, in this pattern, however, the only correlation that could be said to be statistically different from zero was that at 110 days of age for the estimated correlation between RFI and BW.

The correlations between both FE and BF were close to zero (Table 4). Although the point estimates of the correlation between DWG and RFI were positive its associated error prevent to statistically define their sign. The same happened for the correlation between DWG and FCR, but in this case the point estimates were negative. The genetic correlations between DFI and both FE are clearly positive, those with FCR close to 1, and those with RFI ranging from 0.41 to 0.64.

In general, the observed patterns make sense according to the definition of the FE. For example, as it would be expected the magnitude of the correlations are much higher for those involving FCR than for those involving RFI. For FCR a negative correlation with DWG (denominator of the ratio) was expected, while that with DFI would be expected to be positive both with FCR and RFI. Herrera-Cáceres *et al*. (2020) reported for the same population non-statistically different from zero genetic correlations between FCR and BF at 180 days, and between FCR and average daily gain. These results could be said to be compatible with our longitudinal patterns, since in both cases zero is included in the uncertainty regions of our estimates.

It would be relevant to assess how the daily estimates for FE and daily growth get averaged along the control period, this can be done by assessing the correlation patterns along the fattening period between performance traits and the two overall feed efficiency definitions (oRFI and oFCR) and the overall growth (oDWG) (Figure 3 and Table 5).

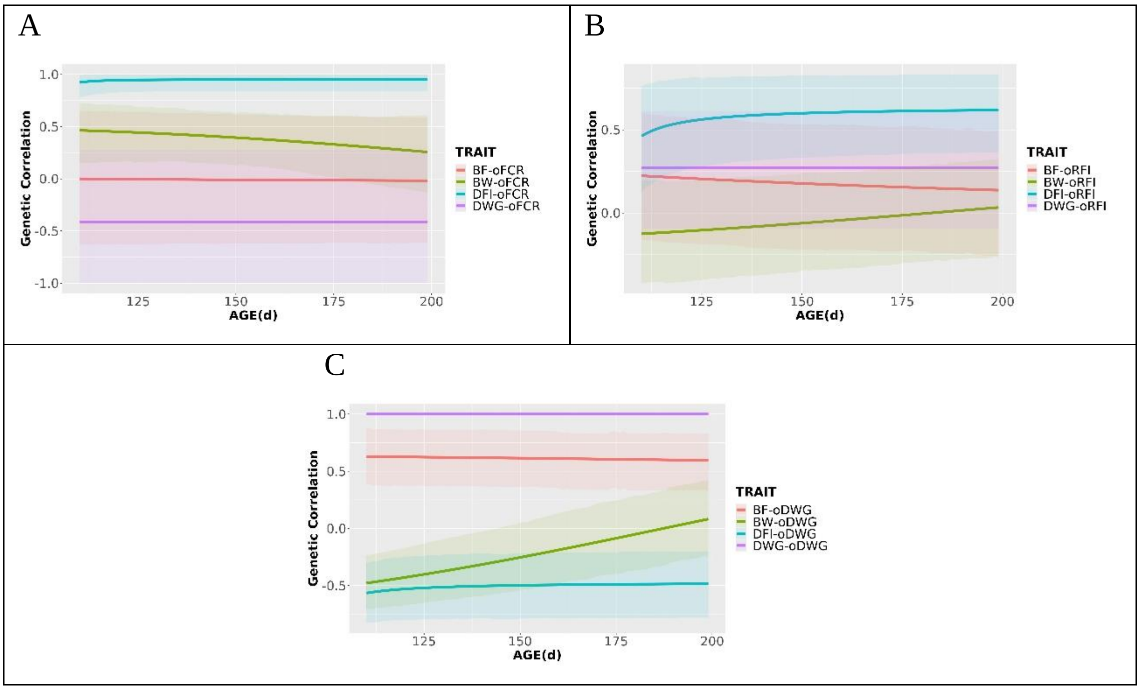

Figure 3. Pattern along the fattening period of the genetic correlations between production (DFI: daily feed intake, BW: live body weight, BF: backfat thickness and DWG: daily weight gain) and overall feed efficiency traits (oFCR: overall feed conversion ratio, oRFI: overall residual feed intake and oFCR: overall daily weight gain). The solid lines represent posterior means, and the colored transparent areas represent 95HPD regions.

Table 3 Marginal posterior Mean(SD) of the genetic correlation between each trait at different ages and that particular trait at 120 days of age.

Age	$r(DFI, DFI_{120})$	$r(BW, BW_{120})$	$r(BF, BF_{120})$	$r(DWG, DWG_{120})$	$r(FCR, FCR_{120})$	$r(RFI, RFI_{120})$
110, d	0.99(0.00)*	1.00(0.00)*	1.00(0.00)*	1.00(0.00)*	0.98(0.04)*	0.99(0.00)*
125, d	1.00(0.00)*	1.00(0.00)*	1.00(0.00)*	1.00(0.00)*	1.00(0.00)*	1.00(0.00)*
140, d	1.00(0.00)*	0.99(0.00)*	1.00(0.00)*	1.00(0.00)*	0.99(0.01)*	0.99(0.00)*
155, d	0.99(0.00)*	0.97(0.01)*	0.99(0.00)*	1.00(0.00)*	0.99(0.02)*	0.99(0.00)*
170, d	0.99(0.00)*	0.95(0.02)*	0.99(0.00)*	1.00(0.00)*	0.99(0.02)*	0.97(0.01)*
185, d	0.99(0.00)*	0.91(0.03)*	0.98(0.01)*	1.00(0.00)*	0.98(0.03)*	0.97(0.01)*
200, d	0.99(0.00)*	0.86(0.04)*	0.98(0.01)*	1.00(0.00)*	0.98(0.03)*	0.97(0.01)*

DFI: daily feed intake, BW: live body weight, BF: backfat thickness, DWG: daily weight gain, FCR: feed conversion ratio, RFI: residual feed intake.

Table 4 Marginal posterior Mean(SD) of the genetic correlation between production and feed efficiency traits at different ages during the fattening period.

Age	$r(FCR, DFI)$	$r(RFI, DFI)$	$r(FCR, BW)$	$r(RFI, BW)$	$r(FCR, BF)$	$r(RFI, BF)$	$r(FCR, DWG))$	$r(RFI, DWG)$
110, d	0.94(0.06)*	0.41(0.15)*	0.51(0.14)*	-0.27(0.15)*	-0.02(0.42)	0.16(0.19)	-0.55(0.37)	0.27(0.17)
125, d	0.95(0.05)*	0.52(0.13)*	0.46(0.13)*	-0.22(0.15)	0.00(0.38)	0.14(0.19)	-0.46(0.39)	0.26(0.17)
140, d	0.95(0.05)*	0.57(0.13)*	0.42(0.13)*	-0.12(0.15)	-0.01(0.37)	0.15(0.19)	-0.43(0.39)	0.27(0.18)
155, d	0.95(0.05)*	0.59(0.12)*	0.38(0.13)*	-0.10(0.15)	-0.01(0.36)	0.14(0.19)	-0.41(0.39)	0.26(0.18)
170, d	0.95(0.05)*	0.63(0.12)*	0.34(0.15)*	0.04(0.15)	-0.01(0.35)	0.19(0.20)	-0.40(0.39)	0.28(0.18)
185, d	0.95(0.05)*	0.63(0.12)*	0.30(0.17)	0.07(0.15)	-0.02(0.35)	0.18(0.20)	-0.40(0.39)	0.28(0.18)
200, d	0.95(0.05)*	0.64(0.12)*	0.26(0.19)	0.10(0.15)	-0.02(0.34)	0.18(0.20)	-0.39(0.39)	0.28(0.18)

DFI: daily feed intake, BW: live body weight, BF: backfat thickness, DWG: daily weight gain, FCR: feed conversion ratio, RFI: residual feed intake. *Probability of the correlation being greater than 0 > 0.95 or < 0.05.

Constant patterns of correlation were observed in all the cases (Figure 3), except for that between BW and oDWG. Regarding the correlations involving FE the only ones that could be said to be statistically different from zero were those with DFI, and the pattern between oFCR and BW (Table 5). No previous estimates of the genetic correlation between BW and FCR were obtained in the population under study at any age, nonetheless, results in other populations of this correlation point to the same direction for different breeds (Bidanel *et al*., 1996). It could make sense this correlation to be positive since the larger the animals, the most maintenance needs would be requested, and thus the efficiency drops, i.e. feed conversion ratio increases. In agreement with previous estimates on the genetic correlation between BF and growth (Herrera-Caceres *et al*., 2020) we also obtained a constant pattern along the control period at around 0.6-0.7 (panel C in Figure 3). It was unexpected, however, to detect negative correlations between daily feed intake and overall growth, on this regard it must be noted that our definition of daily weight gain is the derivative of the polynomial function for explaining the body weight, and this could impose some constraints in the relationships between the studied traits, that yields this unexpected result.

The estimated (posterior mean (posterior standard deviation)) genetic correlations between oFCR and oRFI, between oFCR and oDWG, and between oRFI and oDWG were 0.60(0.30), -0.41(0.39) and 0.27(0.18), respectively. The estimation errors were so large that it was not possible the comparison of these figures with other reports. Nonetheless we could say that the estimates between FCR and average daily growth in another study with the same population (Herrera-Cáceres *et al*., 2020) also had large estimation errors.

To finish with the description of the genetic correlation patterns is needed to present the correlations along the fattening period between the performance traits. These traits could be seem as the major criteria driving any indirect selection procedure aiming to improve the feed efficiency of the population. Figure 4 shows these patterns for the correlations between DFI and the performance traits (BW, BF and DWG) as well as the patterns for the genetic correlations between BW and, BF and

DWG; and between BW and BF. Similarly, to the genetic correlation pattern observed between DFI and overall DWG (oDWG), the genetic correlation pattern between DFI and daily weigh gain (DWG) was constant at around -0.5. As it has been said before, this must be linked with the definition of DWG we have considered. Having study DWG as the derivative of the polynomial function could be the reason of observing a linearly increasing pattern on the correlation between BW and DWG. We interpret this result as evidence of some compensatory growth mechanism. The smallest animals at early ages have the highest growth, thus negative correlations (-0.5) were observed at these ages. This pattern can also be observed in the correlation pattern between BW and BF. In previous studies (Herrera-Cáceres *et al*., 2020) of the same population a clearly positive (0.64) genetic correlation was observed between BF at 180 d and average daily feed intake. Thus, observing a constant pattern for the correlation between BF and DFI at around zero was also an unexpected result.

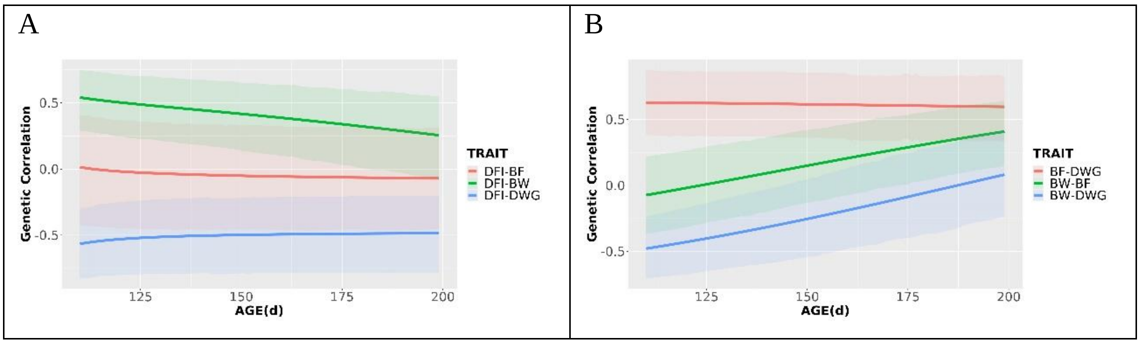

Figure 4. Pattern along the fattening period of the genetic correlations between production traits (DFI: daily feed intake, BW: live body weight, BF: backfat thickness and DWG: daily weight gain).

In this study we aimed to assess whether it would be possible to take advance of any variation in the genetic control along the fattening period of feed efficiency, performance and intake traits in order to overcome certain biological constraints in the genetic correlation structures that exist between the traits that could be considered in an index to indirectly improve feed efficiency (Herrera-Cáceres *et al*., 2020, Sanchez *et al*., 2017), for example, reducing BF while increasing growth.

Table 5 Marginal posterior Mean(SD) of the genetic correlations between production traits at different ages and overall feed efficiency traits.

Age	$r(FCRo, DFI)$	$r(FCRo, BW)$	$r(FCRo, BF)$	$r(FCRo, DWG)$	$r(RFIo, DFI)$	$r(RFIo, BW)$	$r(RFIo, BF)$	$r(RFIo, DWG)$
110, d	0.92(0.07)*	0.46(0.15)*	0.00(0.37)	-0.41(0.39)	0.46(0.16)*	-0.13(0.16)	0.22(0.20)	0.27(0.18)
125, d	0.95(0.06)*	0.44(0.14)*	0.00(0.37)	-0.41(0.39)	0.56(0.13)*	-0.10(0.16)	0.20(0.20)	0.27(0.18)
140, d	0.95(0.05)*	0.42(0.13)*	-0.01(0.36)	-0.41(0.39)	0.59(0.13)*	-0.08(0.15)	0.19(0.20)	0.27(0.18)
155, d	0.95(0.05)*	0.38(0.13)*	-0.01(0.36)	-0.41(0.39)	0.60(0.12)*	-0.05(0.15)	0.17(0.19)	0.27(0.18)
170, d	0.95(0.05)*	0.34(0.15)*	-0.01(0.35)	-0.41(0.39)	0.61(0.12)*	-0.02(0.15)	0.16(0.19)	0.27(0.18)
185, d	0.95(0.05)*	0.30(0.17)	-0.02(0.35)	-0.41(0.39)	0.62(0.12)*	0.01(0.15)	0.15(0.19)	0.27(0.18)
200, d	0.95(0.05)*	0.26(0.20)	-0.02(0.35)	-0.41(0.39)	0.62(0.12)*	0.03(0.15)	0.14(0.19)	0.27(0.18)

DFI: daily feed intake, BW: live body weight, BF: backfat thickness, DWG: daily weight gain, oFCR: overall feed conversion ratio, oRFI: overall residual feed intake.

*Probability of the correlation being greater than 0 > 0.95 or < 0.05.

Our results indicate that there is not such variation in the genetic control along the fattening period, thus it could not be possible to alleviate the aforementioned constrain by recording one trait a given age and the other at a different one, since regardless the age the genetic control of the involved traits is similar. This overall conclusion holds despite the unexpected results we have detected.

Not observing for the traits under study a genetic control that varies with the age it could be said to be something different to previous reports. In general, all the longitudinal studies of FE and performance traits in pigs conclude that the genetic control of this type of traits, to some extent, varies with the age (Cai *et al*., 2011; Wetten *et al*., 2012; Shirali *et al*., 2017; Tran *et al*., 2017; Chaudhary *et al*., 2019). It has to be clarified that in these papers, polynomial of higher degree was used, this allows for further flexibility and some non-linear patterns of the genetic parameters were reported. On this regard we have been cautious reducing the degree of the polynomial to its minimum to skip estimation artifact associated with our limit data set size. In some of the previously indicated studies data sets of similar size to ours are used; and in some cases, suspicious patterns of parameters are reported. In spite of this, the authors, based on these patterns, positively conclude about the genetic heterogeneity of the traits under study along the fattening period. We, in the contrary, want to prevent about the difficulty of using random regression models with limited amount of phenotypic data.

Conclusions

Our initial hypothesis of the performance, intake and feed efficiency traits having a heterogeneous genetic determinism along the fattening period, at least for the period we have considered, must be rejected. Thus, it does not make sense to propose alternative recording ages for the different traits in order to alleviate certain unfavorable correlations that might exist between the traits involved in defining feed efficiency. In spite of this overall conclusion, in line with our final objective, we must also regard the difficulty on fitting random regression models when a limited number of phenotypic records is available. These difficulties can partially be evidenced on certain artifacts or spurious correlations that must be interpreted with caution.

Acknowledgements

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Ethics approval and consent to participate

Animals used in this study come from a commercial population raised under selection nucleus conditions, following all the applicable Spanish and European Union laws with regard to welfare and health control. The fattening period of the animals was conducted at the Institut de Recerca i Tecnologia Agroalimentàries (IRTA) experimental facilities, and for this control period a research protocol was approved by IRTA’s Animal Care and Use Committee.

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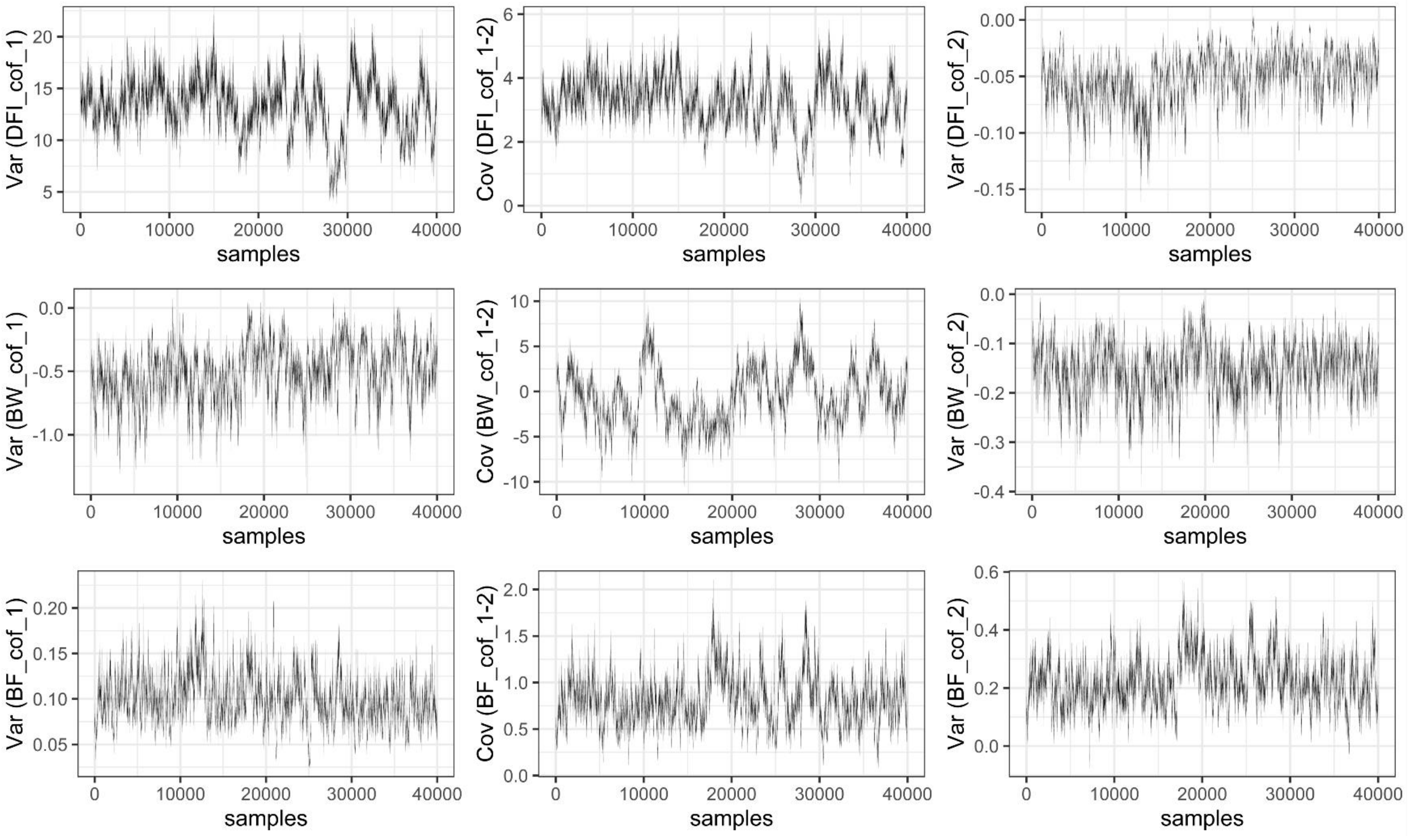
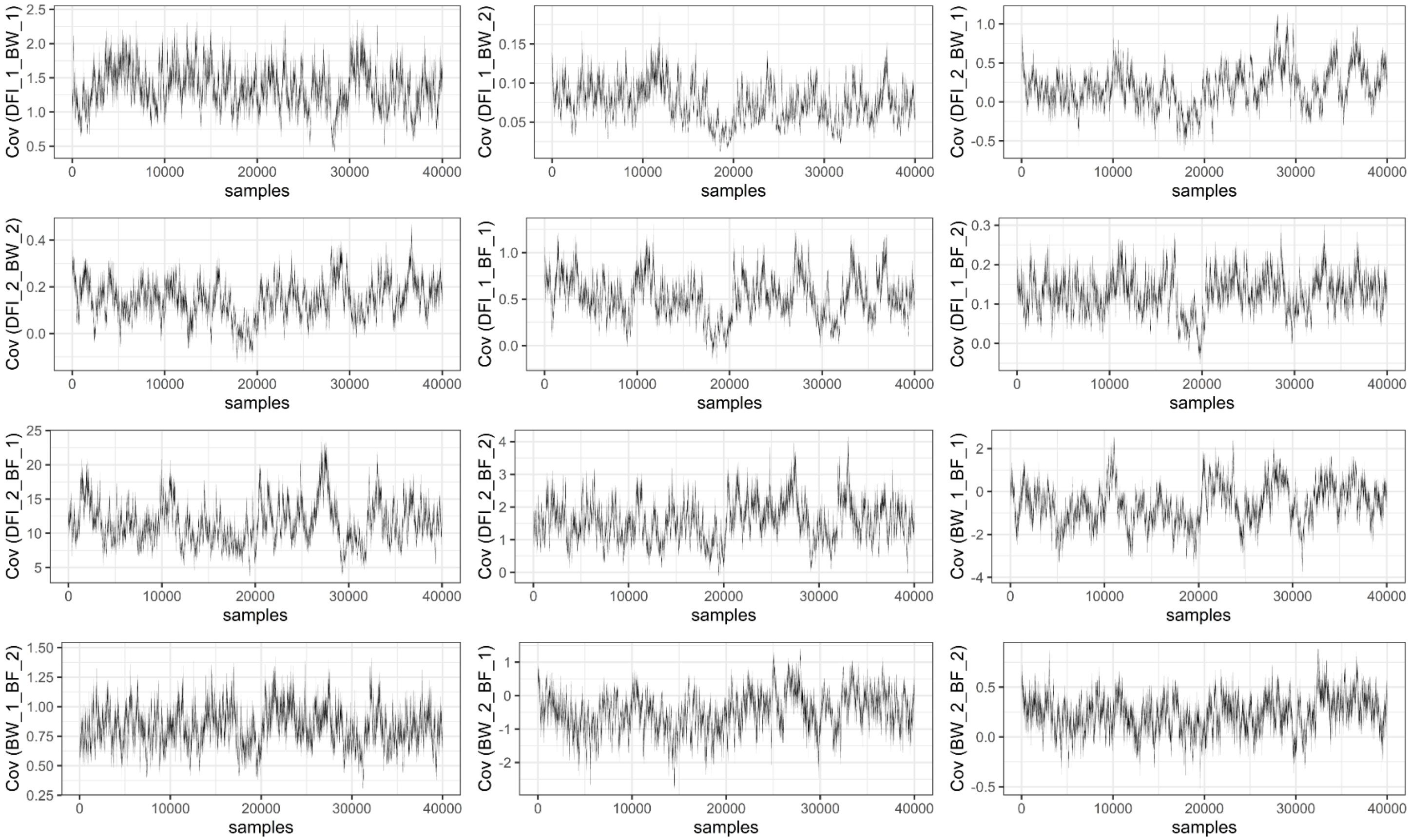
Additional Figure B1

Figure B1. Trace plots of Markov Chains of the estimated (co)variance regression coefficients within traits for daily feed intake, backfat thickness and alive body weight.



Additional Figure B2

Figure B2. Trace plots of Markov Chains of the estimated (co)variance regression coefficients between traits for daily feed intake, backfat thickness and alive body weight.



4. DISCUSIÓN GENERAL

En el contexto de la presente tesis se han explorado diversos puntos de relevancia a considerar en el contexto de programas de mejora genética para incrementar la eficiencia alimentaria de cerdos en periodo de engorde. El primero de ellos es el reconocimiento de que los animales se crían en grupo y unos pueden interactuar con otros, y que parte de esta interacción puede tener un origen genético. Esto planteamiento de modelado se considerada tanto para los caracteres productivos y directamente de eficiencia, como para caracteres de comportamiento alimentario. El segundo de estos puntos supone la consideración, de forma alternativa al consumo individual, de medidas de consumo medio de corral. Y el último punto explorado ha pretendido determinar el grado de variación en el determinismo genético en los caracteres implicados en la definición de la eficiencia alimentaria a lo largo del engorde y cebo de la población bajo estudio.

Los efectos de interacción social resultaron relevantes tanto para los caracteres productivos y de eficiencia como para los caracteres de comportamiento alimentario (velocidad de ingesta de alimento, tiempo en el comedero, número de visitas al comedero y el intervalo de tiempo entre visita). En estudios previos se ha explorado el papel de las interacciones sociales en caracteres productivos y de eficiencia (Muir, 2005; Ellen *et al*., 2014; Fisher and McAdam, 2017). En todos ellos, al igual que en nuestro estudio, se concluye que son factores importantes. Aunque se tiene evidencia de la aplicación de estos modelos de interacción social sobre caracteres de comportamiento alimentario (Lu *et al*., 2007), no se tiene conocimiento de ningún trabajo en el que se hayan aplicado estos modelos de forma multivariada como se hizo en el presente estudio. Una peculiaridad de nuestro estudio es el planteamiento de estos modelos de interacción social de forma multivariada, de manera que hemos podido estimar las correlaciones entre caracteres para los efectos directos, sociales y entre ambos. Con respecto al papel que pueden jugar los caracteres de comportamiento alimentario, más allá de los efectos de interacción social, en el contexto de un programa de mejora genética para eficiencia, se puede afirmar que dado que hay algunas correlaciones genéticas con caracteres productivos que son claramente significativas, pudiéramos concluir que incluir la información de estos caracteres en las evaluaciones genéticas, va, cuanto menos, a ayudar a mejorar la precisión de las evaluaciones genéticas de los caracteres productivos y de eficiencia alimentaria, conclusiones similares a estas ya han sido ofrecidas en otros estudios con animales de otras poblaciones (Lu *et al*., 2017; Kavlak and Uimari, 2019).

Se debe reconocer la dificultad para estimar los parámetros implicados en estos modelos bivariados cuando se consideran efectos de interacción social, dificultad que se evidencia en unos errores de estimación muy grandes. En cualquier caso, estos planteamientos multivariados fueron la semilla sobre la que se ha asentado la hipótesis del segundo trabajo planteado en esta tesis doctoral. Al modelar de forma multivariada con el modelo animal que incluye efectos de interacción social se va a disponer de una estructura de correlación más rica, de manera que pudiera ser factible encontrar combinaciones de efectos directos en unos caracteres e indirectos en otros que permitan actuar de forma más eficiente sobre índices entre cuyos componentes pudiera haber un cierto antagonismo cuando se evalúan con el modelo animal tradicional. Un ejemplo de esto pudiera ser la reducción del espesor de tocino dorsal a la vez que se incrementa el crecimiento, en base a las estimas de correlación genética con el modelo animal, la respuesta esperada para este índice sería muy limitada, pues la correlación genética entre estos caracteres para nuestra población es positiva (Herrera-Cáceres *et al*., 2020), por lo tanto como una alternativa se podría plantear actuar sobre uno de los componentes del índice a través de sus efectos directos y sobre el otro a través de sus efectos indirectos. Son precisamente estos planteamientos los que se exploran mediante simulación en el segundo trabajo de la tesis. En este estudio se definieron 25 índices de selección que consideraban diferentes pesos económicos para los efectos genéticos indirectos y directos de la ganancia de peso diaria y del espesor de tocino dorsal. Para los distintos índices y mediante simulación se evaluó la respuesta en el índice de conversión y en varios índices económicos que representaban varios contextos económicos. A pesar de la relevancia de los efectos sociales en la estructura de las correlaciones genéticas, la respuesta en eficiencia alimentaria cuando se emplearon modelos de interacción social e índices de selección que ponderaban los efectos directos y sociales no fue mayor que la obtenida con un modelo animal tradicional a pesar de haber generado los datos con el modelo que asume interacciones sociales entre los animales que forman los grupos. Estos resultados se explican en primer lugar porque la estructura de correlaciones genéticas en el modelo de interacción social sigue sin permitir actuar sobre un carácter de forma independiente del otro aunque en un caso se haga sobre los efectos directos y en el otro sobre los efectos indirectos, y además porque los errores de las estimas de los parámetros genéticos obtenidos con el modelo animal con efectos sociales generan una gran incertidumbre en las respuestas estimadas, cosa que no ocurre con el modelo animal tradicional al tratarse de un modelo más parsimonioso. La dificultad de estimación de parámetros asociados a los modelos de interacción social ya se ha discutido previamente en un buen número de trabajos (Chen *et al*., 2009; Lu *et al*., 2017; Nielsesn *et al*., 2018). A pesar de la extensa literatura relativa a la estimación de parámetros genéticos cuando se usa el modelo con efectos genéticos indirectos son muy escasas las referencias que ofrecen resultados de la aplicación de estos modelos en esquemas de mejora porcina (Camerlink *et al*., 2014; Camerlink *et al*., 2015) Por lo tanto, es casi imposible comparar nuestros resultados con evidencias empíricas reales del uso de estos modelos en esquemas reales de selección. Una conclusión general de estos estudios en los que se hizo selección empleando modelos de interacción social pueda ser que, aunque parece haberse modificado el comportamiento de los animales, no se aprecia respuesta en el carácter productivo objeto de estudio, en este caso el crecimiento. Quizás una explicación para esto sea la dificultad, que nosotros también hemos encontrado, de estimar con precisión la mayor cantidad de parámetros de los modelos que incluyen los efectos de interacción social.

En el tercer estudio realizado en la presente tesis se trata de cuantificar el valor que en un esquema de mejora pueda tener el uso de información de consumo recogida no de forma individual sino como media de los corrales. Esta cuantificación se hizo mediante una validación cruzada en la que para distintas proporciones de distribución de datos individuales y de grupo se predijo un conjunto de datos individuales que, o bien nunca se usó en el análisis de entrenamiento; o estaban presentes como parte de las medias de algunos corrales. No se observaron diferencias en la capacidad predictiva de los datos individuales entre las distintas proporciones de datos individuales/datos de grupo estudiadas. Lo más probable es que esto se deba a que como se emplearon modelos multivariados donde se incluyeron datos individuales de crecimiento, peso metabólico y espesor de tocino, gran parte de la información para la predicción de los datos individuales no procede de forma directa del fenotipo de consumo considerado, sino que se obtiene a partir de la información de estos otros caracteres correlacionados, que mantienen siempre la misma estructura en todos los escenarios de información de consumo ensayados. Son escasos los trabajos que, de forma práctica, más allá de la estimación de parámetros genéticos, propongan modelos y procedimientos de evaluación del papel de los datos de consumo colectivo en un programa de mejora. En este sentido, recientemente, Ma *et al*. (2020), han mostrado como la información de consumo colectivo cuando ya se dispone de otras medidas individuales es de poca relevancia, un resultado que pudiera ser compatible con los nuestros. En cualquier caso, se debe indicar que, aunque existen modelos que permiten la consideración rigurosa de la información de estos datos de grupo, hay diversos factores que pueden condicionar la precisión de las predicciones basadas en estos datos de grupo, como son por ejemplo el tamaño de los grupos y las relaciones de parentesco dentro de ellos (Olson *et al*., 2006; Peeters *et al*., 2006; Su *et al*., 2006).

En el último trabajo de esta tesis, el objetivo fue explorar la existencia de heterogeneidad genética a lo largo del cebo en el determinismo de los caracteres de los que depende la eficiencia, así como en varias definiciones de esta eficiencia. El propósito de este estudio fue determinar el momento óptimo de recogida de los distintos caracteres de forma que sus heredabilidades sean máximas y las correlaciones genéticas entre ellos óptimas para abordar un programa de mejora de la eficiencia. Es decir, lo mismo que en el segundo trabajo, el objetivo fue buscar definiciones alternativas para un índice de selección que permita maximizar la respuesta. En el segundo trabajo las distintas alternativas las ofrecían distintas ponderaciones de los efectos directos y sociales, y en este último trabajo las alternativas las definen los distintos momentos en los que registrar los diferentes caracteres. Al contrario de los observado en otras poblaciones (Schnyder *el al*., 2001; Schnyder *et al*., 2002, Wetten *et al*., 2012; Huynh-Tran et al., 2017) nuestros resultados indican que no parece existir variación relevante en el control genético a lo largo del período estudiado (110 - 200 días) para los caracteres productivos, de consumo y de eficiencia estudiados: Peso vivo, consumo diario, espesor de tocino dorsal, ganancia diaria, consumo de pienso residual e índice de conversión.

El modelo de estudio considerado usó polinomios de Legendre de grado uno para modelar la relación con la edad de los factores aleatorios. Usar estos polinomios de grado tan reducido supone que sólo va a ser posible detectar cambios lineales de los parámetros bajo estudio, lo que sin duda supone una restricción, pero que creemos necesario asumir dada la limitada cantidad de datos disponibles. Cuando se ensayaron modelos de grado superior se detectaron algunas correlaciones que pudieran calificarse como espurias ya que son muy distintas de las observadas con modelos más sencillos y fuera de toda lógica biológica de relación entre los caracteres considerados.

Por lo tanto, ya en base a los resultados de estimas de parámetros genéticos, se hace difícil aceptar que un índice, que, por ejemplo, considere el espesor de tocino medido a una edad y el peso vivo o la ganancia medidos a otra, pueda dar mayor respuesta que otro definido por ambos caracteres registrados a la misma edad; ya que, como se ha indicado, parece que los caracteres tienen un control genético constante a lo largo del período de estudio. Por lo tanto, no parece necesario llevar a cabo ningún ensayo de cuantificación de la respuesta en base a estos posibles índices que combinen registros de los caracteres tomados a distintas edades.

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5. CONCLUSIONES

1) Los caracteres de comportamiento alimentario recolectados mediante comederos electrónicos aportan información relevante para mejorar las precisiones de las evaluaciones genéticas de los caracteres productivos y de eficiencia alimentaria. Son caracteres con una heredabilidad moderada-alta y algunos están correlacionados con los caracteres productivos y de eficiencia.

2) El efecto de interacción social entre animales que comparten su espacio de alojamiento juega un papel relevante tanto para los caracteres productivos y de eficiencia alimentaria, como también para los caracteres de comportamiento alimentario.

3) A pesar de la relevancia de los efectos de interacción social para los caracteres que definen la eficiencia alimentaria de cerdos en cebo, la consideración de estos modelos en un programa de mejora es difícil. La respuesta que se puede tener en base a índices que combinen efectos directos y sociales es muy similar a la que se obtiene cuando se emplea un modelo animal tradicional para las evaluaciones genéticas.

4) En evaluaciones genéticas multivariadas que incluyen varios caracteres registrados de forma individual, la información de consumo recogida como media del corral parece poco relevante para predecir las medidas de consumo individual.

5) En la población objeto de estudio, todos los caracteres de los que depende la eficiencia alimentaria, así como algunas definiciones directas de esta eficiencia, parecen mostrar un control genético constante a lo largo del período estudiado de engorde y cebo.

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