



Reproductive performance of sows selected for divergent social genetic effects for growth

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Abstract

Social genetic effects (SGE) are genetic effects of an individual that affect the phenotype of its social partners. We determined the reproductive consequences of selection for SGE on growth in pigs. To investigate the influence of social genetic effects on growth, gilts were divided into two groups based on their estimated SGE: positive SGE sows (+SGE) and negative SGE sows (-SGE). At the time of selection, gilts were contemporaries and similarly managed. We recorded the reproductive performance of the two groups based on parity until culling. Reproductive performance included the total number of piglets born (TNB), number of piglets born alive (NBA), average piglet birth weight (BW), coefficient of variation for birth weight (CVBW), age at first farrowing (AFF), weaning to estrus interval (WEI), and gestation length (GL). TNB was 0.5 higher for +SGE sows (13.8) than for -SGE sows ($P = 0.03$, $SEM = 0.06$), and NBA exhibited a higher tendency in +SGE sows ($P = 0.07$, $SEM = 0.06$). Positive SGE for growth was expressed at an earlier AFF ($P = 0.04$, $SEM = 1.10$), and shorter WEI ($P < 0.01$, $SEM = 0.08$) and GL ($P = 0.03$, $SEM = 0.03$). Collectively, the results of this study highlight the opportunities to improve litter size, the age at first farrowing, gestation length, and weaning to estrus interval using SGE.

Key words: reproductive performances, social genetic effects, sow, growth

Introduction

Group housing of gestating sows is common worldwide; it allows social interactions, including aggression during mixing and at feeding time (Barnett *et al.*, 2001). In-group aggression can decrease welfare and performance because of injuries, impaired body condition, and embryonic loss (Brown and Seddon 2014). Recently, a selection method that considers social interactions such as in-group aggression was designed. This selection method accounts for the genetic effect of an individual on trait values of its social partners. The genetic effect of an individual on the phenotypes of its social partners, such as its pen mates, is known as an indirect genetic effect or a social genetic effect (SGE) (Moore *et al.*, 1997; Bijma *et al.*, 2007). Bergsma *et al.* (2008; 2013) reported that pig growth is affected by heritable social interactions among group members. In previous studies, pigs selected for a positive SGE on the growth of their group members

exhibited less non-reciprocal biting and considerably less aggression (Camerlink *et al.*, 2013; 2015). In addition, positive SGE for growth were shown to have positive effects on personality and fear-related behavioral traits in suckling piglets (Reimert *et al.*, 2013). These results demonstrate opportunities to reduce harmful behaviors caused by group housing of pigs. Bergsma *et al.* (2013) reported that in case of positive genetic correlations between social genetic effects and lactation efficiency, selection for growing traits in dam lines could be combined with selection for lactation performance traits.

For practical implementation in the dam line, SGE should be verified in terms of reproductive performance. In addition, the behavioral characteristics of SGE exhibited in previous studies may improve reproductive performance. Thus, We determined the reproductive consequences of selection for SGE on the growth in sow. Reproductive performance parameters included the total number of piglets born (TNB), number of piglets born alive (NBA), average piglet birth weight (BW), coefficient of variation for birth weight (CVBW), age at first farrowing (AFF), weaning to estrus interval (WEI), and gestation length (GL).

Materials and Methods

Estimation of SGE on growth rate

The dataset analyzed in this study consisted of growth rate data obtained from performance tests of 14,624 Yorkshire pigs born from 2009 to 2015 at a nucleus breeding farm in Korea (Tab. 1). The total number of animals in the pedigree was 16,383. The number of individuals for which both parents were known was 16,208. In the whole pedigree, about 96% of the animals were inbred. The average inbreeding coefficient was 0.07 and the range of inbreeding coefficient was 0.00002–0.303. The observed average family size was 4.04, with range of 2–17. The inbreeding coefficient and family size of this breed were determined using the CFC v1.0 software package (Sargolzaei *et al.*, 2006). Performance evaluation for average daily gain (ADG) began when the pigs were 29 ± 3.6 kg (74 ± 3.8 d) and ended when they reached 88 ± 8.8 kg (151 ± 4.4 d) live weight ($ADG 773 \pm 87.1$ g/d). Each pen was 2.5×3.6 m (average 1.3 m²/ pig) with solid concrete flooring and housed 4–10 individuals of the same sex; there were 1–7 full-sibs within each group. Pigs were fed *ad libitum* and water was constantly

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accessible through nipple drinkers. The feeding program was applied in accordance with pig testing standards of

the Korean Animal Improvement Association (<http://www.aiak.or.kr/eng/index.jsp>).

Table 1. Number of animals per study year and means (standard deviation) for group size, full-sib within group, start weight, end weight, age at the end of test, and average daily gain (ADG) in a Yorkshire nucleus herd.

Test year	N	Group size	Full-sib within group	Start weight (kg)	End weight (kg)	Age at the end of test (d)	ADG (g/d)
2009	2,380	6.7 (1.8)	2.1 (0.7)	29 (3.3)	90 (8.6)	151 (4.4)	777 (87.1)
2010	2,512	6.8 (1.7)	2.1 (0.8)	29 (3.5)	90 (10.2)	150 (4.5)	771 (94.4)
2011	2,329	6.7 (1.8)	2.0 (0.7)	27 (3.5)	83 (7.9)	150 (3.4)	745 (88.1)
2012	2,242	6.6 (1.7)	2.1 (0.8)	29 (3.7)	88 (7.8)	151 (2.7)	780 (84.6)
2013	2,138	6.4 (1.7)	2.1 (0.7)	30 (3.4)	87 (6.5)	152 (3.1)	767 (72.4)
2014	2,432	6.8 (1.7)	2.3 (0.9)	30 (3.4)	90 (7.2)	152 (2.8)	797 (80.0)
2015	591	6.2 (1.7)	2.1 (0.9)	30 (3.5)	94 (11.7)	159 (10.1)	767 (101.4)
Total	14,624	6.6 (1.7)	2.1 (0.8)	29 (3.6)	88 (8.8)	151 (4.4)	773 (87.1)

Genetic parameters for ADG were estimated by restricted maximum likelihood (REML) with WOMBAT version 1.0 (Meyer 2007), using the following model that accounted for SGE: $y = Xb + Z_D a_D + Z_S a_S + Wl + Vg + e$, where y is the vector of ADG observations; b is the vector of fixed effects, which included batch (per week), sex (male and female), age at the end of the test, group size, and number of full-sibs within the group; a_D is the vector of random direct additive genetic effects; a_S is the vector of random SGE; l is the vector for the random non-genetic litter effects; g is the vector of random non-genetic group effects (accounting for the group in which the pigs were penned during the finishing period); e is the vector of residuals, and X , Z_D , Z_S , W , and V are the corresponding incidence matrices, respectively.

ADG showed a normal distribution by Shapiro-Wilk test of normality (SAS Institute Inc., Cary, USA). Assumptions for the probability distributions were $g \sim N(0, I\sigma_g^2)$, $l \sim N(0, I\sigma_l^2)$, and $e \sim N(0, I\sigma_e^2)$, in which $N(\cdot)$ indicates a normal distribution; I is an identity matrix of the appropriate dimension; and σ_g^2 , σ_l^2 , and σ_e^2 are the variances of the corresponding effects. Both direct and social additive genetic effects were fitted, which had the following multivariate normal (MVN) distribution: $\begin{bmatrix} a_D \\ a_S \end{bmatrix} \sim MNV(0, C \otimes A)$, in which $C = \begin{bmatrix} \sigma_{a_D}^2 & \sigma_{a_D a_S} \\ \sigma_{a_D a_S} & \sigma_{a_S}^2 \end{bmatrix}$, where $\sigma_{a_D}^2$ is the variance of direct genetic effects, $\sigma_{a_S}^2$ is the variance of social genetic effects, $\sigma_{a_D a_S}$ is the covariance between direct and social genetic effects, A is the relationship matrix among individuals based on pedigree information, and \otimes denotes the Kronecker product.

According to Bijma *et al.* (2007), for traits affected by heritable social effects, the variance of TBV represents the total heritable variation that is exploitable for selection. The TBV of the i^{th} animal is defined as follows: $TBV_i = a_{D,i} + (n-1)a_{S,i}$. The TBV is the heritable effect of an individual on trait values in the

population, which is the sum of its direct genetic effect ($a_{D,i}$) on its own phenotype and its SGE ($a_{S,i}$) on the phenotypes of its $n-1$ group mates. Bijma *et al.* (2007) also stated that the total heritable variance determines the population's potential in response to selection and phenotypic variance.

The total heritable variance can be expressed as: $\sigma_{TBV}^2 = \sigma_{a_D}^2 + 2(n-1)\sigma_{a_D a_S} + (n-1)^2\sigma_{a_S}^2$. The phenotypic variance for such a model can be calculated as follows:

$$\sigma_P^2 = \sigma_{a_D}^2 + (n-1)\sigma_{a_S}^2 + \sigma_g^2 + \sigma_l^2 + \sigma_e^2,$$

where n indicates the average size of social groups ($n = 6.6$). The total heritable variance can be expressed relative to phenotypic variance (Bergsma *et al.*, 2008) as follows:

$$T^2 = \frac{\sigma_{TBV}^2}{\sigma_P^2}.$$

Creation of genetically contrasting groups and reproductive records

To create two contrasting groups, gilts were equally divided at the time (birth year-month) of selection into those with positive estimated social genetic effects (+SGE) and those with negative estimated social genetic effects (-SGE). In total, 43 mating groups (birth year-month) were selected from 2009 to 2012.

Gilts at selection were contemporaries and were managed under the same conditions (individual housing). Age at first mating of gilts was typically 230–250 d and mating was conducted twice (24 h and 36 h after mounting) by artificial insemination. All sows naturally farrowed and the lactation period of sows was 24–28 d. We recorded reproductive traits for sows of the two groups per parity until culling. The reproductive traits included total number of piglets born (TNB), number of piglets born alive (NBA), average piglet birth weight (BW), coefficient of variation for birth weight (CVBW), age at first farrowing (AFF), culling parity (CP), weaning to estrus interval (WEI), and gestation length (GL) (Tab. 2). We only used data from sows with



more than five parities for consideration of the performance following the best period (parity 3 or 4) of sow reproduction. In total, 124 sows produced 753 records of reproductive traits during 1–9 parities. The +SGE sows had a total of 388 records and the frequency of farrowing per parity was 42, 26, 8 and 2 for parities 6–9, respectively. The -SGE sows produced 365 records of reproductive traits and the frequency of farrowing records per parity was 31, 18, 5, and 1 for parities 6–9,

respectively. For comparison of the parities between +SGE and -SGE sows, all records after the seventh parity were consolidated with the seventh parity. Following the Shapiro-Wilk test of normality, significant differences between the +SGE and -SGE sow groups were detected by *t*-test (AFF) and two-way analysis of variance (ANOVA) (GLM procedure) using SAS 9.3 (SAS Institute Inc., Cary, USA). The parity and SGE group were included as fixed effect in the 2-way ANOVA.

Table 2. Number of animals per parity and means (standard deviation) for reproductive traits in a Yorkshire nucleus herd.

Parity	N	DP (d)	DL (d)	WEI, (d)	TNB	NBA	BW (kg)	CVBW (%)
1	124	114 (1.4)	25 (3.0)	6.4 (3.2)	12.9 (2.9)	12.5 (2.8)	1.2 (0.2)	17 (6.1)
2	124	114 (1.5)	25 (3.2)	5.6 (2.3)	12.8 (3.1)	12.5 (2.9)	1.4 (0.2)	17 (6.5)
3	124	114 (1.5)	26 (2.9)	5.5 (2.5)	13.6 (3.4)	13.4 (3.4)	1.3 (0.2)	18 (6.8)
4	124	114 (1.4)	27 (2.7)	5.6 (2.3)	13.9 (3.8)	13.6 (3.7)	1.3 (0.2)	18 (6.8)
5	124	114 (1.5)	24 (7.1)	5.1 (0.5)	13.6 (3.9)	13.3 (3.8)	1.3 (0.2)	20 (15.0)
6	73	114 (1.6)	22 (9.6)	5.4 (1.2)	13.8 (3.4)	13.5 (3.3)	1.3 (0.2)	19 (7.1)
7	44	114 (1.6)	17 (10.7)	5.7 (1.9)	14.8 (3.4)	14.5 (3.4)	1.2 (0.2)	21 (6.3)
8	13	114 (1.1)	14 (12.0)	5.0 (0.0)	14.8 (2.2)	14.1 (1.7)	1.2 (0.2)	22 (6.6)
9	3	114 (0.8)	4 (0.8)	-	16.7 (1.9)	16.3 (1.7)	1.1 (0.0)	20 (5.2)

^aGL = gestation length; DL, duration of lactation; WEI = weaning to estrus interval; TNB = total number of piglets born; NBA = number of piglets born alive; BW = average piglet birth weight; CVBW = coefficient of variation for birth weight.

Results

Estimates of variance and covariance components for ADG are presented in Table 3. The genetic variances were $\sigma_{\alpha_D}^2 = 2,513$, $\sigma_{\alpha_D \alpha_S} = 55$, $\sigma_{\alpha_S}^2 = 9$, and $\sigma_{TBV}^2 = 3,400$. The genetic correlation (*r*) between direct and social effects was 0.38 but did not deviate significantly from zero (*P* = 0.21). The total

heritability (T^2) for ADG was 0.49 which was 0.13 greater than direct heritability (h_D^2). This result indicates that, in addition to being influenced by the environment, social effect for ADG is affected by an additive genetic component, a finding justifying the execution of creation of genetically contrasting groups. This resulted in 62 sows with a +SGE of 0.8 ± 0.47 g/d and 62 sows with a -SGE of -1.4 ± 0.64 g/d, yielding a contrast of 2.2 g/d.

Table 3. Genetic parameters for average daily gain using model that included social genetic effects in a Yorkshire nucleus herd (14,624 pigs born from 2009 to 2015).

$\sigma_{\alpha_D}^2$ ^a	$\sigma_{\alpha_D \alpha_S}$	$\sigma_{\alpha_S}^2$	σ_g^2	σ_l^2	σ_e^2	σ_{TBV}^2	σ_P^2	h_D^2	T^2	<i>r</i>	LogL
2,513	55	9	403	402	3,875	3,400	6,934	0.36	0.49	0.38	-69,551

^a $\sigma_{\alpha_D}^2$ = direct genetic variance; $\sigma_{\alpha_D \alpha_S}$ = covariance between direct and social genetic effects; $\sigma_{\alpha_S}^2$ = social genetic variance; σ_g^2 = group variance; σ_l^2 = litter variance; σ_e^2 = residual variance; σ_{TBV}^2 = the variance of total breeding value; σ_P^2 = phenotype variance; $h_D^2 = \sigma_{\alpha_D}^2 / \sigma_P^2$, direct heritability; $T^2 = \sigma_{TBV}^2 / \sigma_P^2$, total heritability for model including social genetic effects; *r* = genetic correlation between direct and social effects; LogL = maximum likelihood estimate of the model.

Litter performance is shown in Table 4. The TNB was 0.5 higher in +SGE sows (13.8) than in -SGE sows (*P* < 0.05). +SGE sows also tended to have a higher NBA (13.4) than -SGE sows (13.0) (*P* = 0.07). There was no significant difference between +SGE and -SGE sows

for BW (*P* = 0.50) and CVBW (*P* = 0.14). The parity factor exerted a strong effect, regardless of SGE, on all litter performance traits (*P* < 0.01). The interaction between SGE and parity was not significant for any of the litter performance traits measured (*P* > 0.13).



Table 4. Litter performance for sows with positive (+) or negative (-) social genetic effects (SGE) in a Yorkshire nucleus herd.

Item ^a	+SGE sows	-SGE sows	SEM ^b	SGE	P-value	
					Parity	SGE × Parity
Number of records	388	365				
TNB	13.8	13.3	0.06	0.03	<0.01	0.13
NBA	13.4	13.0	0.06	0.07	<0.01	0.13
BW	1.30	1.29	0.00	0.50	<0.01	0.41
CVBW	18.7	17.8	0.14	0.14	<0.01	0.77

^aTNB = total number of piglets born; NBA = number of piglets born alive; BW = average piglet birth weight; CVBW = coefficient of variation for birth weight. ^bSEM = Standard error of the mean.

The values for AFF, WEI, and DP of +SGE and -SGE sows are presented in Table 5. The AFF of +SGE sows was 347.2 d, which was 4.6 d shorter than that of the -SGE sows ($P = 0.04$, $SEM = 1.1$). WEI was 5.4 d for +SGE sows and 5.9 d for WEI sows ($P < 0.01$,

$SEM = 0.08$). The DP of +SGE sows was 114.0, compared with 114.3 for -SGE sows ($P = 0.03$, $SEM = 0.03$). The interaction between SGE and parity was not significant for any of the litter performance traits measured ($P > 0.07$).

Table 5. Mean and SEM for reproductive efficiency traits in managed sows with positive (+) or negative (-) social genetic effects (SGE) in a Yorkshire nucleus herd.

Item ^a	+SGE sows	-SGE sows	SEM ^b	P-value		
				SGE	Parity	SGE × Parity
Number of sows (records)	62 (388)	62 (365)				
AFF	347.2	351.8	1.10	0.04	-	-
WEI	5.4	5.9	0.08	<0.01	<0.01	0.07
GL	114.04	114.29	0.03	0.03	0.80	0.89

^aAFF = age at first farrowing; WEI = weaning to estrus interval; GL = gestation length. ^bSEM = Standard error of the mean.

Discussion

Farrowing performance and SGE

In the present study, +SGE sows had a significantly higher TNB than -SGE sows ($P = 0.03$, $SEM = 0.06$). In addition, +SGE sows tended exhibit positive trends in NBA ($P = 0.07$, $SEM = 0.06$). Sows can be stressed by various factors (mating, gestation and farrowing, among others). Maternal stress during gestation can influence the offspring's physiological development and impair both humoral and cellular immune function in suckling piglets (Tuchscherer *et al.*, 2002). High SGE pigs were better able to manage stressful situations and were less fearful (Camerlink *et al.*, 2013; Reimert *et al.*, 2013; 2014). Therefore, +SGE sows might be less stressed by routine factors, which may lead to healthy fetuses.

Increasing individual growth potential may slightly decrease total litter size and increase perinatal mortality (Johansson 1981; De Nise *et al.*, 1983; Ducos and Bidanel 1996). The SGE represents the genetic effect of an individual on the growth of its social partners (Bijma *et al.*, 2007) and differs from the genetic effect on its own growth. Selection for SGE has been shown to alter social behaviors, which was expressed in lower occurrences of aggressive biting, ear biting (Camerlink *et al.*, 2013; 2015; Reimert *et al.*, 2013; 2014). Biting behaviour is considered an important animal welfare issue. Camerlink *et al.* (2015) reported that various behaviors altered through selection

of SGE appear to reflect an internal state rather than solely social interactions. +SGE could occur because of the apathy of the animal, resulting in reduced negative effects on growth of others (D'Eath *et al.*, 2010; Rodenburg *et al.*, 2010; Camerlink *et al.*, 2015). Further research is needed to estimate the genetic correlation between SGE for growth and DGE (or SGE) for reproductive traits. We did not estimate these genetic correlations because this study was to determine the reproductive consequences of practical selection for SGE on the growth in sow. Bunter *et al.* (2015) investigated the consequences of SGE for reproductive traits in group-housing sows and reported that SGE for reproductive traits also reflected the expression of an unremarked phenotype, such as sow competition. This could suggest that selection including SGE is important not only for group growth in finishing pigs, but also for reproduction in sows.

Reproductive efficiency and SGE

Gilts normally reach first farrowing between 300 and 408 d of age, depending on several factors such as the timing of boar contact and body condition (Soede *et al.*, 2011). Knauer *et al.* (2011) reported that selection for longer estrus and a stronger standing reflex reduced the age at first farrowing. Knauer *et al.* (2011) also reported that the superior estrus behavior of females that were younger at puberty was caused by higher peak concentrations of estradiol compared with that of females that were older at puberty. Among first-litte females,



Sterning *et al.* (1998) estimated a negative genetic correlation between age at puberty and the ability to exhibit the standing reflex and ovulate after weaning. AFF was determined to be moderately heritable (Serenius 2004; Serenius *et al.*, 2008) and the correlation between individual growth rate and AFF has been shown to vary depending on management method (positive: Knauer *et al.*, 2011, negative: Rydhmer *et al.*, 1995, Serenius and Stalder 2004). The AFF is regulated by age at puberty and management practices. In terms of social growth, little is known regarding the effect of SGE (i.e., the genetic effect on a pen mate's ADG) on the AFF. Both the individual and pen mates' ADGs are considered growth traits, but they have different genetic properties (the genetic correlation between both effects is only 0.38, $P = 0.21$). In the present study, +SGE selection resulted in improved AFF. The AFF of +SGE sows was 347 d, i.e., 4.6 d shorter than that of -SGE sows ($P = 0.04$, SEM = 1.1). In the present study, we aimed to keep the influence of farm management on variations in AFF low by assigning the sows equally to selection groups, and consequently farm management did not differ significantly between the +SGE and -SGE groups. Gilts with younger at puberty had higher expression of estrus within genetic lines (Young, 1995; 1998; Moeller *et al.*, 2004).

Sows usually experience lactational anestrus, which is followed by a WEI of 4–6 d. These stages are regulated by positive and negative feedback loops of reproductive hormones that are synthesized in and secreted from the hypothalamus (Soede *et al.*, 2011). A younger age at puberty reduces the WEI in gilts and sows (Knauer *et al.*, 2011), which in turn decreases culling for reproductive failure. In this study, the WEI of +SGE sows (5.4 d) was significantly lower than that of -SGE sows (5.9 d; $P < 0.01$, SEM = 0.08). Based on these results and those reported by Knauer *et al.* (2011), a younger age at first farrowing would reduce the WEI. Therefore, +SGE selection would result in younger age at first farrowing and a shorter WEI. The inhibition of luteinizing hormone during lactation affects both follicle growth and the restart of ovarian activity after weaning (Shaw and Foxcroft 1985; Quesnel *et al.*, 1998). The positive feedback mechanism of estradiol was shown to increase sows' ability to achieve a sufficient luteinizing hormone surge (Sesti and Britt 1993). Our results show that it is important to consider the SGE as a biological feature, similar to estrus behavior and ovulation.

Conclusion

Selection of positive SGE on growth in pigs improved their reproductive performance, as indicated by the higher total number of piglets born. In addition, selection for positive SGE increased overall/life-time reproductive efficiency by reducing the age at first farrowing, gestation length, and weaning to estrus interval. These results demonstrate opportunities to improve reproductive performance of group-living sows by selection for higher social genetic effects on growth rate.

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Authors contributions

JKH carried out the experiment (design), data interpretation and manuscript writing. YMK, KHC and JCP did some manuscript writing. DHL participated in the experiment design. All authors read and approved the final manuscript.

Conflict of interest

The authors declare that they have no competing interests.

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