Associations with four generations of divergent selection for age at puberty in swine

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ABSTRACT: The objective was to evaluate 4 generations of divergent selection for age at puberty (young age at puberty = **YOUNG**; old age at puberty = **OLD**) in swine. Composite Landrace × Large White animals ($n = 4,941$) were reared at the North Carolina Department of Agriculture Tidewater Research Station. At 130 d of age, gilts were exposed to mature boars for 7 min daily. Estrous detection continued for 90 d. Puberty was defined as first observed standing reflex in the presence of a boar. Reproductive and performance traits included: age at puberty (**AGEPUB**), probability of a gilt reaching puberty by 220 d of age (**PUB**), puberty weight (**PUBWT**), pubertal estrus (**LEN1**), length of second estrus (**LEN2**), vulva width at puberty (**VW1**), vulva width at second estrus (**VW2**), gilt birth weight (**BWT**), gilt weaning weight (**WWT**), loin eye area (**LEA**), backfat depth (**BF**), and weight (**WT178**) were measured at 178 d of age on average. Variance components were estimated utilizing an animal model in ASReml 4.1. Models included fixed effects of generation

and sex, a random common litter effect, and a random animal genetic effect. Covariates were fit for reproductive traits (age at boar exposure), **LEA** and **BF** (**WT178**) and **WT178** (age weighed). In generation 4, **YOUNG** and **OLD** gilts had on average a **PUB** of 87% and 64%, respectively, and **AGEPUB** of 163 and 183 d, respectively. Heritability estimates for **AGEPUB**, **PUB**, **PUBWT**, **LEN1**, **LEN2**, **VW1**, **VW2**, **BWT**, **WWT**, **LEA**, **BF**, and **WT178** were 0.40, 0.07, 0.39, 0.19, 0.17, 0.36, 0.48, 0.20, 0.12, 0.42, 0.43, and 0.37, respectively. Common litter effect estimates for **AGEPUB**, **PUB**, **PUBWT**, **LEN1**, **LEN2**, **VW1**, **VW2**, **BWT**, **WWT**, **LEA**, **BF**, and **WT178** were 0.08, 0.14, 0.03, 0.00, 0.01, 0.05, 0.00, 0.03, 0.29, 0.02, 0.10, and 0.11, respectively. Genetic correlations between **AGEPUB** with **PUBWT**, **LEN1**, **LEN2**, **VW1**, **VW2**, **BWT**, **WWT**, **LEA**, **BF**, and **WT178** were 0.83, −0.22, −0.31, 0.25, 0.19, −0.08, −0.29, 0.15, −0.21, and −0.43, respectively. Results suggest selection for reduced **AGEPUB** in swine would decrease **AGEPUB** and increase **PUB**.

Keywords: age at puberty, genetic parameters, swine

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INTRODUCTION

Maximizing salable pigs per female per year, at the least cost, is a goal of the modern swine industry. Recent improvements in sow reproductive efficiency have resulted from improved litter size (Knauer and Hostetler, 2013). Yet problems still exist for other economic sow farm measures such as gilt and sow retention (Stalder et al., 2004).

Reproductive failure continues to be the primary reason for early removal of females from the herd (Stalder et al., 2003). The genetic improvement of gilt and sow retention could be aided by the incorporation of new precursor phenotypic metrics into genetic evaluations. A younger age at puberty or first mating has been associated with improved gilt retention (Knauer et al., 2011; Morrison, 2016) and lifetime sow reproduction (Serenius et al., 2008; Hoge and Bates, 2011). Yet, age at puberty is not typically recorded in nucleus herds (Rydhmer, 2000) as the trait is labor-intensive to capture.

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Decreasing age at puberty may further result in economic gains via reduced gilt development and sow maintenance costs. Decreasing age at first mating reduces gilt nonproductive days which decreases feed, labor, and facility costs associated with gilt development. Decreased body weight at first mating has been associated with reduced gestation and lactation feed required through 3 parities (Newton and Mahan, 1993). Hence, mating gilts at a younger and lighter weight can reduce sow maintenance costs. Yet to achieve an optimal breeding weight, replacement gilts must express puberty before target breeding weight is reached.

Before nucleus farms implement selection for reduced age at puberty or first mating a greater understanding of puberty is needed. The objective of this study was to evaluate associated responses to 4 generations of divergent selection for age at puberty in swine. Variance component estimates and correlated responses to selection for age at puberty are reported for swine estrous, growth, and composition traits.

MATERIALS AND METHODS

Experimental protocols used in this study were approved by the North Carolina State University Institutional Animal Care and Use Committee, IACUC: 15-017A.

Animals

Composite Landrace $\times$ Large White pigs ($n = 4,941$) were reared at the North Carolina

Department of Agriculture Tidewater Research Station (Plymouth, NC). Replacement females were annually batch-farrowed in January. Gilts ($n = 2,428$) from those litters were housed in a curtain-sided building with fully slatted floors and natural ventilation. Sprinkler systems were activated at 27 °C. Stocking density allowed for 0.84 m² per pig (15 pigs per pen). Boars were group-housed on partial slatted floors in an environmentally controlled building separate from females. Diets, shown in Table 1, were formulated to meet or exceed NRC requirements (NRC, 2012).

Estrus detection was performed from mid-May through August. Gilts were first exposed to mature boars at 130 d of age on average and estrus detection continued for 90 d. Estrus was defined using the back-pressure test in the presence of a mature boar (Willemse and Boender, 1966). Boars, older than 12 mo of age, were used once daily to check gilts for expression of estrus. Estrus detection was carried out by bringing a pen of gilts to a harnessed boar and penning them together for 7 min. During that period, 2 additional boars were housed in gestation stalls and had fence-line contact with the females. After 70% of gilts obtained puberty, fence-line boar exposure was used exclusively. Fence-line boar exposure consisted of 2 boars, simultaneously, in front of each gilt pen for 7 min per pen (14 min of total exposure per day).

Estrous traits were measured every 24 h. Age at puberty (AGEPUB) was the first observed standing reflex for the back-pressure test in the presence of a boar. Whether a gilt reached puberty by 220 d

Table 1. Feeding regimen and formulated diets¹ (as-fed basis) of net energy (NE), crude protein (CP), calcium (Ca), and phosphorus (P) for each production phase²

Phase	NE, kcal/kg	CP, %	Lysine, %	Ca, %	P, %
Nursery					
Day 1 to 7	–	21.9	1.59	0.78	0.71
Day 8 to 14	–	20.7	1.52	0.68	0.57
Day 14 to 11 kg	–	20.6	1.51	0.67	0.55
Grower					
11 to 23 kg	2,337	19.0	1.43	0.68	0.52
23 to 41 kg	2,427	15.7	1.16	0.54	0.42
41 to 59 kg	2,496	13.1	0.97	0.52	0.40
59 to 82 kg	2,544	11.3	0.82	0.50	0.38
82 to 105 kg	2,566	10.4	0.72	0.49	0.36
105 kg to mating	2,566	10.4	0.69	0.49	0.36
Gestation	2,277	11.0	0.68	0.85	0.61
Lactation	2,352	16.0	1.10	0.89	0.69

¹Corn and soybean meal were the base ingredients for all diets. Diets were supplemented with Renaissance Nutrition Base mix additives to meet vitamin and mineral requirements suggested by NRC (2012).

²All animals were fed ad libitum from nursery until the final finishing phase. Thereafter, selected animals were fed 2.0 kg (boars) and 2.3 kg (gilts) per day prior to mating. Gilts were fed based on body condition during gestation and sows ate ad libitum during lactation.

of age (**PUB**) was coded as a binary trait (1 = yes, 0 = no). Length of estrus was number of consecutive days during which a gilt exhibited the standing reflex in response to the back-pressure test in the presence of a boar. Both length of estrus at puberty (**LEN1**) and second estrus (**LEN2**) were determined. Vulva width was measured using a dial caliper (S-T Industries Inc., Saint James, MN) at puberty (**VW1**) and second estrus (**VW2**).

Growth and composition traits were collected from gilts and boars at 178 d of age and body weight from gilts at puberty (**PUBWT**). At 178 d of age on average body weight (**WT178**), backfat (**BF**), and loin muscle area (**LEA**) were measured. Composition traits were measured from a cross-sectional 10th rib image obtained by using an Aloka 500V SSD ultrasound machine (Corometrics Medical Systems Inc., Wallingford, CT).

During the breeding period, replacement females were group-housed in a natural ventilated building with partial slats. All matings were by natural service. Gilts were bred once daily by the same boar each day they exhibited the standing reflex. Full-sib and half-sib matings were avoided to minimize inbreeding. After pregnancy was confirmed, gilts were moved to individual stalls for the remainder of the gestation period. Feed allowance was adjusted based on body condition measured using a sow body condition caliper (Knauer and Baitinger, 2015). At day 108 of gestation, females were moved to environmentally controlled farrowing rooms.

Divergent Selection for Age at Puberty

Divergent selection for age at puberty created 2 genetic lines, young and old age at puberty (**YOUNG** and **OLD**, respectively). Generation 0 consisted of 402 composite Landrace $\times$ Large White gilts observed for estrus. Of these, 130 gilts were selected as the founder generation, 65 gilts each for **YOUNG** and **OLD**. The youngest AGEPUB gilts

were selected to create the **YOUNG** line and the 20 oldest AGEPUB gilts and 45 gilts that had not cycled by 220 d of age were selected to create the **OLD** line. Both **YOUNG** and **OLD** gilts were randomly mated to the same 22 boars (13 sire families). Hence, generation 1 progeny from **YOUNG** and **OLD** were half-sib populations. In subsequent generations, selection of animals was again performed at the conclusion of boar exposure to gilts, 220 d. Each year 65 early puberty gilts within **YOUNG** were selected for the breeding pool. Within **OLD**, 30 late puberty gilts and 35 gilts that failed to reach puberty by 220 d were selected for breeding. Boars were selected within line and sire family based on structural conformation and lean growth. Selected animals in generations 1 through 4 were mated within genetic line. Number of mated sires, dams, and offspring produced by generation are presented in Table 2.

Statistical Methods

Variance components were estimated using ASReml 4.1 (Gilmour et al., 2015). Traits were analyzed using both univariate and bivariate animal models. The statistical model fit to the data was,

$$y = Xb + Za + Wl + e$$

where y was a vector of observed traits (AGEPUB, PUB, PUBWT, LEN1, LEN2, VW1, VW2, BWT, WWT, LEA, BF, and WT178); b was a vector of fixed effects including generation, sex, and covariates when applicable (Table 3); a was a vector of additive genetic effects of the animal; l was a vector of random common litter effects; e was a vector of random residuals; X , Z , and W were design matrices associating b , a , l , and e with y , respectively. Probability of puberty was fit as a binary trait using the logit link function. The effects estimated were on the logistic scale with a variance of $\pi^2/3 = 3.2898$ and genetic parameters calculated are also on the logistic scale; thus, 3.2898 was added

Table 2. Number of sows farrowed and sires used by line¹ and generation

Generation	Sows farrowed		Sires		Offspring produced		F , % ²	
	YOUNG	OLD	YOUNG	OLD	YOUNG	OLD	YOUNG	OLD
0	87	22	12	15				
1	45	32	10	13	492	366	0.0	0.0
2	55	36	16	11	576	458	1.8	1.0
3	60	23	10	7	701	251	1.6	2.8
4	60	27	16	15	635	314	3.7	4.7

¹YOUNG = young age at puberty line; OLD = old age at puberty line.

² F = inbreeding percentage.

Table 3. Covariates and fixed effects included in mixed model analysis to estimate genetic parameters

Covariate	Trait ¹							
	AGEPUB	PUBWT	PUB	BWT	WWT	LEA	BF	WT178
Age boar ²	X	X	X					
Sex				X	X	X	X	X
WT178						X	X	
Wean age					X			
Age ³								X

¹AGEPUB = age at puberty; PUBWT = weight at puberty; PUB = probability of reaching puberty; BWT = birth weight; WWT = weaning weight; LEA = loin muscle area; BF = backfat depth; WT178 = weight at 178 d of age on average.

²Age of the animal at first exposure to a boar.

³Age of the animal when WT178, LEA, and BF were recorded.

to the residual variance estimates in all PUB models fit (Gilmour et al., 2015). Gilt age at boar exposure was included as a covariate for AGE PUB, PUB, and PUBWT (Table 3). The model fit assumes that random effects had

$$\text{var} \begin{bmatrix} a \\ l \\ e \end{bmatrix} \sim N \left(\begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \mathbf{A}\sigma_a^2 & 0 & 0 \\ 0 & \mathbf{I}_l\sigma_l^2 & 0 \\ 0 & 0 & \mathbf{I}_e\sigma_e^2 \end{bmatrix} \right)$$

where σ_a^2 was the additive genetic variance; σ_l^2 was the variance due to the common litter effect; σ_e^2 was the variance associated with the residuals; $\mathbf{A}$ was the additive genetic relationship matrix; $\mathbf{I}_l$ was an identity matrix with dimensions equal to the number of litters; and $\mathbf{I}_e$ was an identity matrix with dimensions equal to the number of observations. Covariances between σ_a^2 , σ_l^2 , and σ_e^2 were assumed to be zero. The pedigree used to create $\mathbf{A}$ and calculate inbreeding was traced back 5 generations and contained 5,105 individuals, 420 dams, and 105 sires.

Inbreeding coefficients for all animals in the pedigree were calculated using the INBUPGF90 program (Aguilar and Misztal, 2012). The INBUPGF90 program uses a recursive algorithm assuming nonzero inbreeding values for known parents. All estimated inbreeding values assumed founder animals were unrelated. Reported inbreeding values were averaged among all animals within the population for a given generation (Table 2).

Reported heritability estimates (h^2) and standard errors were averaged across 1 univariate model and 11 bivariate models for which the trait appeared. Phenotypic variance (σ_p^2) was defined as $\sigma_p^2 = \sigma_a^2 + \sigma_l^2 + \sigma_e^2$; thus, h^2 was defined as $h^2 = \sigma_a^2/\sigma_p^2$ and the proportion of variance explained by the common litter environment (c^2) was defined as $c^2 = \sigma_l^2/\sigma_p^2$. Common litter environment effects were fit in all univariate and bivariate models.

Bivariate models used to estimate genetic correlations allowed for covariance between traits for random additive genetic, common litter, and residual effects. To allow convergence, covariance estimates of common litter was fixed to zero in bivariate models containing LEN1, LEN2, and VW2. Residual common litter environmental variance, however, was estimated for the second trait of bivariate models that contained LEN1, LEN2, and VW2.

A bivariate model including PUB and AGE PUB was not fitted; thus, genetic and phenotypic correlations between AGE PUB and PUB were not directly estimable. Rather, genetic relationships between the traits were estimated as a correlation between sire estimated breeding values (EBV). Sires used in the evaluation were limited to those which had 5 or more daughters that were exposed to a boar during puberty detection. Pearson correlation coefficients were calculated between traits in SAS version 9.4 (SAS Institute, 2015) using PROC CORR.

Genetic trends were computed using EBV generated from univariate and bivariate models. Genetic trends for AGE PUB and PUB were produced from univariate models. Trends for all other traits were produced from bivariate linear mixed models, with AGE PUB as the second variate. The use of bivariate models allowed for the estimation of covariance between traits to account for single trait selection pressure for AGE PUB. Direct genetic line differences were calculated by separating EBV by generation and then dividing by the SD of EBV within each line to standardize all traits.

RESULTS AND DISCUSSION

Direct and Correlated Responses to Selection

Least squares estimates and genetic trends for gilt puberty, estrous, growth, and body composition

traits by line and generation are presented in Table 4 and Figs. 1 and 2, respectively. In generation 4, YOUNG and OLD gilts were 87% and 64% pubertal, respectively. Average AGE PUB in generation 4 for YOUNG and OLD gilts was 163 and 183 d, respectively. This is in agreement with Lamberson et al. (1991), who reported response to selection for decreased AGE PUB of 15.7 d after 9 generations of selection when compared to the control line. The same authors did not account for PUB in their results, yet, 99% of gilts reached puberty by 250 d of age. From generation 3 to 4, AGE PUB decreased for OLD gilts (206 vs. 184 d). Perhaps, this is partially explained by the decrease in PUB from generation 3 to 4 in OLD (0.72 vs. 0.64). Additive genetic divergence in generation 4 between YOUNG and OLD for AGE PUB was 1.95 genetic SD units. Similarly, PUB in generation 4 differed between YOUNG and OLD lines by 2.70 genetic SD units. Genetic trends suggest that selection for decreased AGE PUB produces greater additive genetic change in PUB than in AGE PUB (1.93 vs. -0.68 genetic SD units). To our knowledge, few prior studies have quantified the response in PUB by selecting for decreased AGE PUB.

Pubertal weight was reduced in YOUNG when compared to OLD (102 vs. 114 kg). Genetic trends in PUBWT resulted in additive genetic divergence between YOUNG and OLD gilts in generation 4 by 2.14 genetic SD units. This suggests YOUNG gilts could be mated at lighter weights when compared to OLD. Newton and Mahan (1993) reported gilts that are first bred at 120 kg consumed less feed during lactation and gestation across 3 parities when compared to gilts first mated at 135 or 150 kg. Collectively, these results suggest selection for decreased AGE PUB could be used as tool to reduce weight at first breeding and decrease gilt and sow feed costs.

Estimates of Genetic Parameters

Descriptive statistics and estimates of genetic parameters are shown in Table 5. Variance component analysis resulted in a heritability of 0.40 for AGE PUB, similar to a composite of literature estimates (0.37) reported by Rothschild and Ruvinsky (2011). In the current study, variation between heritability estimates between models including AGE PUB was CV = 7.2%. Effects from a common litter environment on AGE PUB were found to be 0.08. These results are consistent with estimates previously reported by Bidanel et al. (1996) and Knauer et al. (2010a) (0.08 and 0.09, respectively).

Combined results suggest litter environment effects impact subsequent reproductive phenotypes such as AGE PUB. Flowers (2012) reported that gilts that were born at heavier weights (>1.59 kg) were predisposed to reach puberty at an earlier age. Similarly, Vallet et al. (2016) reported relationships between preweaning growth rate and colostrum intake with pubertal development in gilts. These studies suggest prenatal and postnatal environmental effects impact the ability of a gilt to reach puberty. Therefore, estimation of common litter variance should be included in mixed models used to estimate variance components for AGE PUB to prevent falsely inflated heritability estimates.

In contrast to AGE PUB, PUB had a lower heritability of 0.07 and a lower CV between heritability estimates between models (6.66%). Common litter environmental variance explained a larger proportion of the total variance in PUB compared to additive genetic effects (0.14 vs. 0.07, respectively), suggesting that pre- and postnatal environment have a stronger relationship with PUB than additive genetic effects. Common litter environmental effects such as sex ratio (Drickamer et al., 1997), preweaning growth rate (Vallet et al., 2016), birth weight (Flowers, 2012), and neonatal litter size (Flowers, 2009) have been shown to influence gilt retention.

Since genetic and phenotypic relationships between AGE PUB and PUB were confounded, the relationship was evaluated as a correlation between sire EBVs. The correlation between sire EBVs for AGE PUB and PUB was -0.78, suggesting that AGE PUB and PUB are genetically similar traits under the control of similar additive genetic mechanisms. To our knowledge, few studies have attempted to quantify the relationship between AGE PUB and PUB. Results from the current study suggest that indirect selection for PUB via selection for AGE PUB would result in greater genetic change in PUB than direct selection.

Genetic and phenotypic correlations between AGE PUB with reproduction, growth, and compositional traits are shown in Table 6. Positive genetic and phenotypic relationships were estimated between AGE PUB and PUBWT (0.83 and 0.80, respectively), suggesting that as gilts reach puberty at an older age they are also heavier in body weight. In agreement, positive correlations between AGE PUB and PUBWT were reported by Eliasson et al. (1991), Rydhmer et al. (1994), Bidanel et al. (1996), and Knauer et al. (2010a). Utilization of this relationship could benefit producers selecting for decreased age at puberty through the development of smaller gilts at first breeding.

Table 4. Least squares means¹ by line² and generation for reproductive, growth, and compositional traits³ in response to selection for age at puberty

Trait	Generation				
	0	1	2	3	4
AGEPUB, d					
YOUNG	199 ± 1.6	176 ± 2.3	176 ± 2.6	168 ± 1.9	163 ± 1.9
OLD		197 ± 2.6	200 ± 2.9	206 ± 3.2	183 ± 3.2
P-value		<0.01	<0.01	<0.01	<0.01
PUB					
YOUNG	0.6 ± 0.03	0.68 ± 0.03	0.50 ± 0.04	0.76 ± 0.03	0.87 ± 0.02
OLD		0.69 ± 0.04	0.43 ± 0.04	0.72 ± 0.04	0.64 ± 0.04
P-value		0.86	0.19	0.44	<0.01
PUBWT, kg					
YOUNG	113 ± 1.1	112 ± 1.4	110 ± 1.6	110 ± 1.2	102 ± 1.2
OLD		115 ± 1.9	114 ± 2.2	113 ± 2.5	114 ± 2.1
P-value		0.27	0.12	0.26	<0.01
LEN1, d					
YOUNG	1.69 ± 0.04	1.63 ± 0.06	1.67 ± 0.07	1.55 ± 0.05	1.70 ± 0.05
OLD		1.47 ± 0.08	1.44 ± 0.09	1.67 ± 0.10	1.46 ± 0.08
P-value		0.10	0.04	0.03	<0.01
LEN2, d					
YOUNG	1.82 ± 0.07	1.87 ± 0.07	1.97 ± 0.08	1.92 ± 0.06	1.99 ± 0.05
OLD		1.93 ± 0.09	1.95 ± 0.11	1.73 ± 0.12	1.55 ± 0.11
P-value		0.60	0.87	0.16	<0.01
VW1, cm					
YOUNG	38.5 ± 0.31	38.7 ± 0.42	38.0 ± 0.47	38.2 ± 0.35	38.0 ± 0.34
OLD		40.3 ± 0.56	38.6 ± 0.64	39.4 ± 0.75	37.3 ± 0.60
P-value		0.02	0.45	0.14	0.28
VW2, cm					
YOUNG	38.3 ± 0.48	39.9 ± 0.49	39.4 ± 0.54	39.9 ± 0.39	38.7 ± 0.36
OLD		40.9 ± 0.62	40.1 ± 0.73	39.6 ± 0.87	38.1 ± 0.76
P-value		0.20	0.43	0.72	0.53
BWT, kg					
YOUNG	1.03 ± 0.007	1.15 ± 0.011	1.11 ± 0.010	1.08 ± 0.009	1.09 ± 0.010
OLD		1.13 ± 0.013	1.10 ± 0.012	0.97 ± 0.016	0.99 ± 0.014
P-value		0.22	0.29	<0.01	<0.01
WWT, kg					
YOUNG	5.5 ± 0.038	5.60 ± 0.051	5.54 ± 0.055	5.94 ± 0.046	5.39 ± 0.045
OLD		5.48 ± 0.059	5.42 ± 0.060	5.51 ± 0.069	5.06 ± 0.062
P-value		0.12	0.07	<0.01	<0.01
LEA, cm ²					
YOUNG	42.2 ± 0.46	43.7 ± 0.48	40.1 ± 0.51	40.4 ± 0.48	40.6 ± 0.48
OLD		45.0 ± 0.55	41.2 ± 0.55	41.4 ± 0.56	41.2 ± 0.55
P-value		<0.01	0.56	0.05	0.23
BF, cm					
YOUNG	1.74 ± 0.042	1.75 ± 0.044	1.66 ± 0.046	1.57 ± 0.044	1.70 ± 0.045
OLD		1.70 ± 0.049	1.74 ± 0.048	1.62 ± 0.052	1.59 ± 0.049
P-value		0.20	0.08	0.24	<0.01
WT178, kg					
YOUNG	116 ± 1.3	115 ± 1.4	112 ± 1.4	123 ± 1.4	119 ± 1.4
OLD		112 ± 1.5	108 ± 1.5	119 ± 1.6	118 ± 1.5
P-value		0.05	<0.01	<0.01	0.75

¹Model included generation, line, generation × line interaction and covariate effects.²YOUNG = young age at puberty line; OLD = old age at puberty line.³AGEPUB = age at puberty; PUBWT = weight at puberty; LEN1 = length of estrus at puberty; LEN2 = length of estrus at second estrus; VW1 = vulva width at puberty; VW2 = vulva width at second estrus; PUB = probability of reaching puberty; BWT = birth weight; WWT = weaning weight; LEA = loin muscle area; BF = backfat depth, WT178 = weight at 178 d.

Figure 1. Direct and correlated response to selection on age at puberty and associated reproductive traits based on average EBV. Average EBVs only include those gilts with phenotypes; OLD = old age at puberty line; YOUNG = young age at puberty line; AGE PUB = age at puberty; LEN = length of pubertal estrus; PUB = probability of reaching puberty (0 or 1); PUBWT = weight at puberty; VW = vulva width at pubertal estrus.

Figure 2. Direct and correlated response to selection on age at puberty and associated production traits based on average EBV. Average EBVs only include those gilts with phenotypes; OLD = old age at puberty line; YOUNG = young age at puberty line; AGE PUB = age at puberty; BF = backfat depth at 178 d; BWT = birth weight; LEA = loin eye area at 178 d; WT178 = body weight at 178 d; WWT = weaning weight at 22 d.

Estimates of genetic relationships between AGE PUB and estrous traits are similar to those reported by Eliasson et al. (1991) and Knauer et al. (2010a). Genetic correlations between AGE PUB with LEN1 and LEN2 (-0.22 and -0.31 , respectively) were negative, implying that as age at puberty decreases length of standing estrus increases, which is within the range (-0.12 to -0.23) of previous reports for AGE PUB and LEN1 (Eliasson et al., 1991; Rydhmer et al., 1994; Knauer et al., 2010a). The difference in the genetic correlation between AGE PUB with LEN2 compared to LEN1 (0.09) perhaps can be attributed to significant variation in first estrous symptoms, which were previously discussed by Rydhmer et al. (1994) and Knauer et al. (2010a). Yet the

relationship between AGE PUB and LEN1 perhaps explains the favorable associations between age at puberty and sow reproductive lifetime (Holder et al., 1995; Yazdi et al., 2000; Knauer et al., 2010b). Sows showing stronger visual estrous symptoms are more likely to be bred and remain in the herd longer. Conversely, genetic relationships between AGE PUB with VW1 and VW2 were positive (0.25 and 0.19, respectively), implying that animals reaching puberty later in life have a greater vulva width during standing estrus, in agreement with previous reports (Knauer et al., 2010a). Combined results suggest females who reach puberty at a younger age have an increased ability to exhibit the standing reflex, yet will have a decreased vulva width. Vulva width at first estrus and VW2 is perhaps related to PUBWT, since larger animals could be predisposed to have a larger vulva, yet the genetic and phenotypic relationships between PUBWT with VW1 (0.06 and 0.24, respectively) and VW2 (0.15 and 0.18, respectively) from this experiment were not different from zero.

Genetic and phenotypic correlations between age at puberty with growth traits are in agreement with previous estimates of Rydhmer et al. (1992) and to the average of literature values (Eliasson et al., 1991; Rydhmer et al., 1994; Bidanel et al., 1996; Knauer et al., 2010a). Negative genetic relationships were found between AGE PUB with WT178 and BF (-0.43 and -0.21 , respectively), implying that gilts reaching puberty at a young age are heavier at 178 d of age and will deposit more body condition. Hutchens et al. (1981) reported similar estimates of the relationship between AGE PUB and growth rate (-0.38), defined as average daily gain, in agreement with associations more recently reported (Rydhmer et al., 1992). Estimates from the present study for the genetic relationship between AGE PUB and BF (-0.21) are in agreement with those previously reported (Eliasson et al., 1991; Bidanel et al., 1996). Conversely, AGE PUB showed genetic and phenotypic relationships with LEA (0.15 and 0.14, respectively), meaning that as gilts reach puberty at older ages they will scan a larger loin eye. The authors speculate that the increase is due to adjusting to a common weight in the prior correlation, removing physiological advantages in growth from early puberty animals that drives the increase in muscle development. Previous literature and results from the current study suggest that a minimum level of growth and body condition is required for pubertal development.

Table 5. Summary statistics and variance components¹ for puberty, growth, and compositional traits

Trait	No.	Mean	Minimum	Maximum	σ_p^2	c^2	h^2	SE
Puberty								
Age at puberty	1,166	183	124	281	719	0.08	0.40	0.07
Probability of puberty	1,778	0.7	0	1	4.23	0.14	0.07	0.03
Puberty weight, kg	1,051	110.3	69.4	162.8	1,268	0.03	0.39	0.08
Length of estrus 1, d	1,048	1.6	1	5	0.43	0.00	0.19	0.05
Length of estrus 2, d	756	1.9	1	5	0.47	0.01	0.17	0.06
Vulva width 1, cm	1,051	38.4	25	59	22.4	0.05	0.36	0.08
Vulva width 2, cm	753	39.3	28	57	22.3	0.00	0.48	0.08
Growth								
Birth weight, kg	4,941	1.1	0.4	2.6	0.31	0.03	0.20	0.05
Weaning weight, kg	3,988	5.4	1.7	11.2	5.1	0.29	0.12	0.05
Loin eye area, cm ²	2,095	42.9	24.9	62.7	3.10	0.02	0.42	0.06
Backfat, cm	2,095	1.7	0.7	3.9	0.03	0.10	0.43	0.06
Weight at 178 d, kg	2,107	113.6	54.4	164.4	820	0.11	0.37	0.06

¹ σ_p^2 = phenotypic variance; c^2 = proportion of variance explained by common litter environment; h^2 = proportion of variance explained by additive genetic effects.

Table 6. Phenotypic and genetic correlations¹ between gilt puberty, growth, and compositional traits

Trait	AGEPUB	PUB	PUBWT	LEN1	LEN2	VW1	VW2	BWT	WWT	LEA	BF	WT178
Age at puberty (AGEPUB)		–	0.83	–0.22	–0.31	0.25	0.19	–0.08	–0.29	0.15	–0.21	–0.43
Probability of puberty (PUB)	–		–0.62	0.07	0.43	0.01	0.16	0.06	0.64	0.20	0.45	0.69
Weight at puberty (PUBWT)	0.80	–0.18		–0.27	–0.33	0.06	0.15	0.25	0.14	–0.07	–0.19	0.41
Length of estrus 1 (LEN1)	–0.03	0.03	0.01		0.80	0.14	0.20	–0.06	–0.11	–0.12	–0.04	–0.30
Length of estrus 2 (LEN2)	–0.11	0.02	–0.02	0.22		0.25	0.20	–0.04	–0.01	–0.21	–0.09	0.03
Vulva width 1 (VW1)	0.30	–0.04	0.24	0.10	0.10		0.97	–0.01	0.10	–0.34	–0.22	0.04
Vulva width 2 (VW2)	0.20	0.03	0.18	0.07	0.16	0.61		–0.05	0.47	–0.19	–0.04	0.27
Birth weight (BWT)	–0.01	0.01	0.34	–0.01	0.02	0.07	0.03		0.90	0.04	–0.48	0.30
Weaning weight (WWT)	–0.02	0.08	0.25	–0.02	0.03	0.09	0.04	0.60		–0.04	–0.35	0.60
Loin eye area (LEA)	0.14	0.01	0.07	–0.08	–0.06	–0.10	–0.12	0.07	0.02		–0.26	0.05
Backfat (BF)	–0.21	0.13	–0.19	0.06	0.04	–0.02	–0.02	–0.19	–0.12	–0.23		–0.07
Weight at 178 d (WT178)	–0.26	0.37	0.44	0.01	0.07	0.05	0.11	0.34	0.39	–0.03	–0.15	

¹Phenotypic and genetic correlations are below and above the diagonal, respectively.

Implications

Age at puberty is a moderately heritable trait that can be improved through selection in swine. A correlated increase in PUB and decrease in PUBWT can be expected with selection for reduced AGE PUB. Potential decreases in economic inputs can result from selection for decreased age at puberty. Nonproductive days during gilt development can be reduced with earlier pubertal animals whom reach a critical weight sooner in life. Decreases in sow maintenance costs could also be expected due to decreased mature sow size and reduced feed intake during gestation. Previous reports from literature reports suggest that AGE PUB is a useful and effective indicator trait for sow lifetime productivity and retention. However, further work with these genetic lines is needed to determine the long-term

effects of selection on sow lifetime productivity and longevity measures.

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