Abstract

SEE, GARRETT MURPHY. Correlated Responses to Selection for Age at Puberty in Swine. (Under the direction of Dr. Mark Knauer.)

The objective of the study was to evaluate the performance of a population of swine after 4 generations (GEN) of divergent selection for age at puberty. Analyses includes, estimates of genetic parameters of age at puberty and the correlated response to selection in sow and boar performance. Composite Landrace $\times$ Large White animals (n=4,941) were divided into genetic lines (GL), young age at puberty (YNG) and old age at puberty (OLD). At 130 d of age, gilts were exposed to 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. Traits utilized in genetic parameter estimation included: age at puberty (AGEPUB), probability of a gilt reaching puberty (PUB), puberty weight (PUBWT), length of estrus at puberty (LEN1), estrous length at first estrus after puberty (LEN2), vulva width at puberty (VW1), vulva width at first estrus after puberty (VW2), piglet birth weight (BWT), piglet weaning weight (WWT), loin eye area (LEA), backfat depth (BF), and weight at 178 d of age (WT). Sow reproductive performance traits included: total number born (TNB), litter BWT (LBW), average BWT (ABW), BWT CV (BWT_CV), litter WWT (LWW), average WWT (AWW), WWT CV, (WWT_CV), and litter size weaned (LSW). Boar traits included: backfat depth (BF), loin eye area (LEA), ADG, testis width (TW), testis length (TL), testis volume (TV), ejaculate volume (VOL), number of sperm cells per ml (NO_CELL), progressive sperm motility (MOT), total sperm cells per ejaculate (TOT_CELL), projected semen doses per boar (DOSE), libido score (LIB) and testosterone concentration (TEST). Collection of testis traits and TEST were captured at 215 d (C1) and 293 d (C2) of age. All other reproductive traits included in the boar analysis were collected at C2 only. Variance components were estimated using ASReml with an animal model. Models

included GEN and sex as fixed effects, a random common litter effect and animal genetic effect. Covariates were fit for reproductive traits (age at boar exposure), LEA and BF (WT) and WT (age). Sow traits were analyzed in SAS using PROC MIXED. Fixed effects included GEN, GL, and GEN $\times$ GL interaction. Covariates of TNB and LSW were included. Statistical analysis for boar performance was performed in R using lm and lmer. Fixed effects of GEN, GL, collection period, inbreeding percentage (used as a covariate), random effect of animal and two way interaction terms when (P<0.05). In GEN four, YNG and OLD gilts had a PUB of 85 and 50%, respectively, and AGEPUB of 163 and 183 d, respectively. Heritability estimates for AGEPUB, PUB, PUBWT, LEN1, LEN2, VW1, VW2, BWT, WWT, LEA, BF and WT were 0.40, 0.11, 0.39, 0.19, 0.17, 0.36, 0.48, 0.20, 0.12, 0.42, 0.43 and 0.37, respectively. Overall, TNB tended (P=0.07) to be greater for OLD compared to YNG (11.73 vs. 11.03). Yet, in GEN 4 YNG had greater (P<0.01) ABW than OLD (1.09 vs. 1.00 kg). Genetic line did not influence (P<0.05) BF, LEA, VOL, NO_CELL, MOT, TOT_CELL or DOSE. Yet, interactions between GL and collection period favored (P<0.05) YNG boars for TW, TL, TV and TEST. Boars from YNG had greater (P<0.05) ADG and LIB when compared to OLD. Results suggest selection for reduced AGEPUB effectively decreased AGEPUB and improved PUB in gilts. In boar, results suggest selection increased ADG, LIB, testicular development and TEST in boars. Selection for reduced AGEPUB appeared to generate faster growing gilts that were lighter weight at maturity, while farrowing litters with improved piglet quality.

Correlated Responses to Selection for Age at Puberty in Swine

by
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Dedication

First to my parents for teaching me the value of hard work and education. Also, to my grandparents for their continued support in my academic endevors. Lastly, but most certianly not least, to my fiancé, Marisa, for her never ending support and for pushing me to reach my dreams.

Biography

Garrett See, son of Todd and Leslie See, grew up with one younger sister, Emma in Raleigh, North Carolina. He grew up raising and showing pigs on his small family farm. He was an active member of 4-H, FFA and the National Junior Swine Association. His early years developed his passion for the swine industry and led him to peruse graduate and undergraduate degrees to apply his ability for the industry.

During his undergraduate career, he studied Animal Science at North Carolina State University. During his studies he worked with the State 4-H Livestock Specialist, Brent Jennings, on providing youth outreach programs across the state. While working on his B.S, Garrett was a member of the NC State 4-H livestock judging team, where he represented his state at the national livestock judging contest in Louisville, Kentucky where they placed 9^{th}.

Following graduation, Garrett was an intern with The Maschhoffs in Carlyle, Illinois, the third largest pork producer in the US. During his internship, he worked within the genetics department improving data collection strategies that were being implemented at genetic test farms. This experience led him to start a Master's degree program at North Carolina State University where he worked on estimating genetic parameters of age at puberty in swine.

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My fellow graduate students and now friends, without whom I would have a great number of unanswered questions also deserve to be acknowledged. In particular I would like to thank Jeremy Howard, Jeff Wiegert, Matthew Morrison, and Ben Lemmer, for their frequent assistance to my studies. I would also like to acknowledge the help from Dr. Francesco Tiezzi, who always kept his door open and never failed to have an answer or path to solve a problem.

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Chapter 1

Literature Review

This literature review is comprised of five sections, covering the importance, genetic influences, physiological impacts and associated male reproductive traits relating to age at puberty in gilts. The first section covers definitions and the importance of age at puberty. The second and third sections will cover age at puberty in relation to economics and genetics, respectively. The fourth and fifth sections will cover factors affecting gilt pubertal development and the association between gilt puberty and male reproductive traits, respectively.

1.1 Definitions of age at puberty

Onset of puberty can be defined by physiological events which occur as a gilt matures. Age at puberty is commonly referred to as the age at first observed estrus or the age at first ovulation. First observed estrus is often detected by reaction to the back-pressure test in the presence of a boar (Hemsworth and Barnett, 1989). First ovulation is detected by analysis of progesterone levels through repeated sampling to determine the presence of corpa lutea on the ovary, which develop following ovulation (Esbenshade et al., 1983).

Rarely is age at puberty a recorded trait on nucleus, multiplier or commercial farms. However, there are other commonly measuered traits that are strongly correlated to age at puberty. Age at first service, age at first farrowing, and age at puberty are similar traits used in experiments to measure early gilt reproductive performance (Knauer et al., 2010b). Age at first service is the age of a gilt when she is first bred. Age at first farrowing is the age of a gilt when the she first farrows a litter.

Using age at first service and age at first farrowing in place of age at puberty presents possible problems. Le Cozler et al. (1998) reported that differences between herds for age at first farrowing can be large due to differing management strategies. For example, initial boar exposure to gilts of differing ages could reduce the correlation between age at first service and age at first farrowing with age at puberty. Age at puberty, and related traits, are greatly influenced by management and genetics (Rydhmer, 2000). Perhaps strong environmental and genetic interactions among these traits have limited their use in genetic evaluations.

1.2 Economic impacts

1.2.1 Non-productive days

Reducing nonproductive days can be achieved by reducing the period between birth and first service, the interval between weaning and mating, and the interval between weaning and culling (Le Cozler et al., 1998). Onset of puberty can directly influence the interval before first service when replacement gilts are being developed. The positive correlation between onset of puberty and the period before first service allows for manipulation of pubertal development to be a viable way to diminish nonproductive days.

In an Australian study, Amer et al. (2014) developed a simple model to ascertain economic

values of single maternal breeding traits. Increasing time until puberty lengthens the period before a first service event resulting in amplified maintenance and operating costs for replacement gilts. The model was built to predict the economic value of age at puberty by summing operating costs per gilt per day and feed costs required to maintain gilt energy requirements until first service. A scenario was developed based on dietary requirements needed by a developing gilt. In the scenario the energy required by a gilt taking one day longer to reach puberty was calculated. The cost of energy utilized was assumed $0.024/MJ ME resulting in an economic value of $2.28 for an animal taking one day longer to reach puberty. This study demonstrates that animals reaching puberty sooner decreases the cost of raising replacement gilts.

There is a deficient number of studies researching the economic impact of age at puberty in swine. While economic models for sow longevity measures are more plentiful, models focused on age at puberty are limited. Hence, more work is needed on a global scale to determine a more holistic economic effect of age at puberty on the production of replacement gilts.

1.2.2 Sow longevity

Economic measures of sow longevity are important when discussing age at puberty in that a young age at puberty or first farrowing is correlated with improved sow longevity (Holder et al., 1995; Koketsu et al., 1999; Yazdi et al., 2000; Serenius and Stalder, 2004; Serenius et al., 2008; Knauer et al., 2010b; Hoge and Bates, 2011). Hence age at puberty has an economic impact beyond that of replacement gilts, which was discussed previously, in that it impacts sow lifetime productivity.

Improved sow longevity can reduce economic inputs in several ways on commercial swine farms. Replacement gilt pools can be reduced if sows remain in the herd longer decreasing genetic input and gilt rearing costs. Sows typically don't reach a positive net present value until

the third parity (Stalder et al., 2003), therefore, sows remaining in the breeding herd past three parities increase profit margins. Greater parity sows often bring higher premiums when culled since older sows typically weigh more than young sows.

Amer et al. (2014) developed an economic model to determine the value of sow longevity. The economic value was defined as the marginal benefit of a sow reaching an extra parity. Net returns were calculated based on weaned pig sales. Gilt development, piglet disposal, and energy requirement costs were removed from net returns. It was assumed that 90% of the sows were sold as cull animals. The remaining 10% of the sows were assumed to have died on the farm. Cull revenues and disposal fees were respectively included in the net returns. After base survival estimates were calculated, the model was reevaluated with a 1% increase in survival past parity one resulting in a 0.8% decrease in replacement costs. This survival increase attributed to a $3.07 profit increase per parity by decreasing replacement rate of females. This demonstrates that sows whom remain in the herd longer are more profitable. Age at puberty thus effects the survival of sows in the long term picture due to the correlations between age at puberty with sow longevity mentioned previously, ultimately increasing net returns.

Stalder et al. (2003) reported which factors impact the net present value (NPV) of sows in production farms. The authors developed software to calculate the NPV of sows with customizable input costs. Records were gathered from PigCHAMP swine data management software to set baseline production numbers for live pigs born per litter, pre-weaning mortality, breeding herd mortality, litters per mated female, and average parity. Other investment costs were accounted for per pig sold. Net present value sensitivity was analyzed in relation to number born alive, segregated early weaning (SEW) pig price, and replacement gilt price. Segregated early weaning pig price influenced which parity the NPV would be positive, a $2 decline in SEW increased positive NPV from parity three to four. Net present value was least sensitive to replacement gilt costs in that a larger percent change in cost is needed to change the parity which

a positive NPV is achieved. Due to the unpredictability in SEW prices it becomes increasingly important to retain high quality females past parity three to see returns on initial investment.

1.3 Genetics

Holder et al. (1995) evaluated genetic selection lines attempting to draw connections between sow longevity and age at puberty. Using the Nebraska Gene Pool population two genetic lines were developed, age at puberty (PUB) and a randomly mated control (C). Animals (n=96) from the PUB line were selected for a decreased age at puberty and compared against females (n=47) from the C line. Selection was continued for eight generations with a final selection differential between lines of 15.7 d. Gilts from both lines were then selected from each line for a longevity assessment. Measures of longevity used include; total number born alive per sow (TP1), total number born alive per sow which achieved parity five (TP2), productivity per day of life until culling using TP1 (PDL1), and productivity per day of life till culling using TP2 (PDL2). None of the longevity measures above statistically differed by line. Mean accumulative productivity was assessed by comparing the slopes produced in a linear regression analysis of animals born alive and sow age. Figure 1.1 depicts linear regressions of this relationship by genetic line. A significant increase in productivity of gilts from the PUB line can be seen pasted 24 months of age. This suggests that animals who reach puberty earlier will be higher performing at an increased age.

1.3.1 Heritability

Estimates of heritability for age at puberty are summarized in Table 1.1. Age at puberty has been reported to be moderately heritable with estimates ranging from 0.19 to 0.53. When compared to other reproductive traits, age at puberty is generally more heritable (Rothschild and Ruvinsky,

2001). Since age at puberty as a phenotype is an observation based on one animal, it tends to have higher heritability estimates and genetic correlations. Thus, age at puberty is more readily influenced by selection when compared to other reproductive traits which involve complex relationships (i.e. number born alive and number weaned).

Hutchens et al. (1981) used Henderson's Method 3 to estimate the heritability of age at puberty by separating ancestral records by paternal and maternal half-sibs using 33 sire and 131 dam groups. Data were collected on cross and purebred gilts under normal management conditions. Initiation of estrous detection ranged from 163.5 to 172.9 days, on average, for the different breeding groups. Gilts were left with boars for 15 to 30 minutes. Estrous detection continued until the youngest animal was 219 days. Average age at puberty during the experiment was 190.9 days. Heritability estimates were 0.19 and 0.40 for sire and dam half sib regressions, respectively. The difference in heritability between the two estimates raises questions of a possible maternal effect. The heritability generated from the maternal half sibs is in agreement with the average (0.37) reported in Table 1.1. The heritability estimate calculated using the paternal pedigree is relatively smaller, perhaps sampling error due to the limited number of sire groups used is influencing the estimate.

With the advent of new estimation practices such as restricted maximum likelihood (Reml) there was an increase in the number of heritability estimates for age at puberty being published, as seen in Table 1.1. With the improvement of computing machines and new statistical machinery, such as Reml, realized heritability estimates are more easily calculated. This ease in calculation has increased the number of estimates being published in large pedigreed groups of animals when heritability estimates were not the aim of the research objectives.

The average heritability calculated from the reported estimates found in Table 1.1 is 0.37 which is considered relatively high for a reproductive trait as previously mentioned. Since the heritability is relatively high, successfully decreasing age at puberty can be expected, and

has been shown through selection (Hixon et al., 1987; Lamberson et al., 1991). Nucleus or multiplier farms should be cautious of selecting replacements expressing late puberty to prevent unintended selection for greater age at puberty and increased associated costs.

Sterning et al. (1998) reported heritability estimates using Reml estimation for 452 Swedish Yorkshire gilt records compiled from a seven generation selection experiment. Estrous detection began at 160 days of age. Mean age at puberty was 206 days and ranged from 164 to 259 days. Included in the animal model were the effects of batch, diet, and the random effects of animal and residual error. The authors reported a heritability of 0.40, which is in agreement with other studies using similar model structures (Rydhmer et al., 1994; Kuehn et al., 2009).

Other studies reported considerably lower heritability estimates using the same estimation practice. Knauer et al. (2010b) and Bidanel et al. (1996) both reported heritability estimates for age at puberty of 0.29. Both studies included random effects of birth litter, animal and residual error. With the addition of the common litter effect to the animal model, heritability estimates further separate genetic and environmental effects. It has been shown that colostrum intake and preweaning average daily gain have significant impacts upon age at puberty (Vallet et al., 2016). Thus, accounting for the common litter environment becomes essential in reducing the environmental noise that may lead to inflated heritability estimates.

1.3.2 Genetic and phenotypic correlations

Favorable, negative genetic correlations have been reported amongst age at puberty and growth rate (Young et al., 1978; Bidanel et al., 1996) suggesting that higher performing gilts reach puberty at an earlier age. Hutchens et al. (1981) reported the genetic correlation between average daily gain and age at puberty was -0.38, which is in agreement with associations reported by Rydhmer et al. (1992). More recent estimates reported the genetic relationship between the

onset of puberty and average daily gain are slightly lower, -0.18 (Bidanel et al., 1996). Genetic correlations reported by Bidanel et al. (1996) are notably lower than those produced by Young et al. (1978) and Hutchens et al. (1981). This decrease could be attributed to the use of crossbred animals in the earlier reports as opposed to the purebred population used by Bidanel et al. (1996). Phenotypic correlations between average daily gain and age at puberty are also reported to be moderate and negative on the same magnitude of previously discussed genetic correlations (Hutchens et al., 1981; Bidanel et al., 1996). These reports suggest that as the industry selects for faster growing females that they will reach puberty at a younger age.

Backfat thickness and lean percentage exhibit unfavorable correlations with age a puberty (Eliasson et al., 1991; Rydhmer, 2000). Bidanel et al. (1996) reported a negative, moderate genetic correlation, -0.24, between age at puberty and backfat thickness on a group of Large White gilts. In a lean growth selection experiment, the phenotypic correlation between backfat thickness and age at puberty was -0.19 (Eliasson et al., 1991). In agreement, age at puberty and lean percentage have a similar reported genetic correlation of 0.20 (Rydhmer et al., 1992), further suggesting that a minimum level of growth and body condition is needed for puberty attainment.

Relationships between age at puberty and estrous symptoms are relatively smaller than other reproductive correlations (Rydhmer et al., 1994; Sterning et al., 1998; Knauer et al., 2010b). Rydhmer et al. (1994) reported genetic correlations between age at puberty with the length of proestrus and the length of standing estrus of 0.15 and -0.12, respectively, on a group of 610 Yorkshire gilts. This report implies that gilts reaching puberty earlier have a decreased proestrus phase but lengthened estrous phase and increased period of sexual receptivity. However, large standard errors suggest that further research with larger sample sizes is needed to determine more accurate measures of this relationship. Sterning et al. (1998) reported relationships with reproductive traits focused on returns to estrus. A study involving 464 first parity Swedish

Yorkshire females showed that there was a relationship between age at puberty with weaning-to-estrus interval (WEI) and exhibiting estrus within 10 days after weaning. Both traits were moderately correlated with age at puberty, 0.45 and -0.50 respectively. These relationships suggest that selecting early pubertal gilts will decrease the number of irregular WEI's in primiparous sows, in agreement with findings by Holder et al. (1993). Knauer et al. (2010b) evaluated puberty and its relationship with observable standing estrus in a group of 1,225 Landrace-Large White gilts. Estrus was observed with and without a boar present every 12 hours. Results showed that age at puberty had moderate genetic correlations with length of estrus and vulva width, -0.23 and 0.16, respectively. These traits were further analyzed by looking at the maximum strength of the standing reflex with a boar present (MAX BR STD) and the strength of vulva reddening (VISVULV). Stronger genetic correlations were found between age at puberty with MAX BR STD and VISVULV, -0.32 and 0.25, respectively, in comparison with the phenotypes previously mentioned (i.e. length of estrus and vulva width). Collectively, these results suggest that gilts which reach puberty earlier will have a longer length of estrus, exhibit a stronger standing reflex, possess a smaller vulva size, and have less noticeable vulvar symptoms.

Age at puberty has been shown to have limited, yet small, relationships with reproductive maternal traits. Relationships reported between age at puberty with subsequent litter traits are small in number. Rydhmer et al. (1992) reported genetic correlations between age at puberty with litter size and piglet birth weight of 0.20 and -0.11, respectively. These results suggest that gilts which reach puberty later have larger litters with smaller piglets at birth. Stronger genetic relationships were exhibited between sow weight loss during first lactation (weaning weight minus farrowing weight) and age at puberty, 0.33 (Rydhmer et al., 1992). Age at puberty has reportedly low correlations with ovulation rate, number of embryos, and embryo survival rate (Bidanel et al., 1996). Bidanel et al. (1996) reported genetic correlations between age at puberty

with ovulation rate and embryo survival, 0.01 and -0.04 respectively. These results suggest that there is a limited weak relationship between age at puberty and litter traits yet responses in litter size and piglet birth weight are seen in selection for age at puberty.

Schinckel et al. (1983); Young et al. (1986); Johnson et al. (1994) have studied relationships between the onset of puberty in gilts and male reproductive performance. Schinckel et al. (1983) reported significant residual correlations between testes weight and dams age at puberty from a selection experiment for ovulation rate. Residual correlations for testes weights ranged from -0.06 to -0.48, depending on year of experiment and number of observations. Granted, most significant correlations were reported with smaller number of animals observed. The relationship between testes size and age at puberty was further explored by Young et al. (1986). In an experiment using multiple breeds, Young et al. (1986) reported high genetic correlations between early testes volume measurements and age at puberty using a sib analysis, -0.94. However, results from the daughters on sire analysis reported the opposite relationship, 0.74, further clouding the correlation between male and female reproductive performance. Johnson et al. (1994) conducted an index selection experiment for predicted testes size. The genetic correlation between age at puberty of the dams and predicted testes weight of their offspring was -0.16, suggesting that a relationship might exist but indirect selection would not be very effective. Thus, further research on male reproductive performance and age at puberty is needed on a larger scale to determine the true sign and size of the association.

1.3.3 Breed

Differences in average age at puberty have been reported between breeds. Bidanel et al. (1996) noted crossbred gilts reaching puberty sooner compared to purebred females in a genetic study. Improved crossbred performance can be attributed to the effects of heterosis (Cassady et al.,

2002). Large White females have lower average age at puberty compared to French Landrace (Bidanel et al., 1996). Hutchens et al. (1982) reported Duroc females having greater age at puberty than Yorkshire, Spots and Landrace. However, limited sample size hindered the ability to detect differences between Yorkshire, Spot and Landrace females. While common commercial breeds may differ in average age at puberty, it is often disregarded due to the high influence of management factors. Variance in age at puberty within breed is large and likely negates most differences observed between continental breeds of swine (Evans and O'Doherty, 2001).

Hutchens et al. (1982) investigated the effect of breed on puberty and pubertal weight in swine. Animals from a Diallel mating plan composed of Yorkshire, Landrace, Spotted and Duroc animals were used. Animals tested were composed of 16 breed groups with differing combinations of sire and dam breeds used, with approximately 50 animals per group. Across purebred groups Landrace gilts were the earliest to reach puberty while Durocs were the latest. Overall, crossbred animals reach puberty earlier than their purebred counterparts. Heterosis effects for age at puberty were estimated and it was found that there were significant impacts for heterosis in Spot-Duroc, Duroc-Landrace, Spot-Landrace and crossbred-purebred animals. There were no significant effects of heterosis in Yorkshire-Landrace, Yorkshire-Duroc or Yorkshire-Spot crosses. The largest overall heterosis advantage was to the Duroc-Landrace cross with a 7.2% decrease in age at puberty. Only the Yorkshire-Landrace cross exhibited a significant heterosis effect for weight at puberty, 4.9% heavier than their purebred counterparts. These results suggest that there are differing breed effects in terms of age at puberty and pubertal weight. Furthermore, these results suggest that heterosis can give an advantage to pubertal traits in specific crosses.

1.4 Factors influencing age at puberty

1.4.1 Boar exposure

Exposing gilts to a boar has been shown to decrease the age at which puberty is reached (Mavrogenis and Robison, 1976). Furthermore, Kirkwood and Hughes (1979) reported differing pubertal responses depending on the age at which boar exposure begins. Previous reports suggest that boar exposure should begin when gilts are 160 days of age (Eastham et al., 1986). However, more recent reports suggest that early age at puberty isn't the only factor to consider when determining the initiation of boar exposure.

In an Australian study, van Wettere et al. (2006) examined a group of 192 Large White $\times$ Landrace crossbred gilts which began boar exposure at 161, 182, or 203 days of age. Females were kept in groups of six and taken to a separate pen where they were exposed to a boar for 20 minutes daily. The number of days to puberty and the age at puberty for the three treatments can be seen in Table 1.2. Age at which gilts were first exposed to a mature boar had a significant impact on age at puberty. Females first exposed at 161 and 203 days of age reached puberty at 179.5 and 210.6 days, respectively. Gilts exposed at a younger age (161 days) required more days of boar exposure until puberty was reached, in comparison to the intermediate (182 days) and late group (203 days). These results suggest animals exposed at 160 days of age attain puberty earlier yet require more total stimulus from the boar, increasing labor and other associated costs. However, the delayed reaction to boar contact seen at younger ages suggests that other biological factors control the initiation of estrus.

Kummer et al. (2009) purposed that weight may be a more important biological factor than age, when initiating boar exposure in gilts. Camborough 22 gilts (n=120) of the same age were allocated into two groups, G1 and G2, with mean growth rates of 577 and 727 g/d, respectively. Both groups of gilts began boar exposure at 144 days and were inseminated approximately 50

days after the initiation of boar exposure. Animals in G2 were heavier, on average, throughout the testing period. Gilts from G2 achieved puberty on average nine days earlier than those in G1. This equated to a significantly shorter interval from boar exposure to puberty for G2 gilts. These results suggest that growth rate to 144 days of age, or the initiation of boar exposure, greatly impacts a female's ability to exhibit puberty.

Patterson et al. (2002b) analyzed the effect of boar exposure method on the induction of first estrus in Large White gilts. It has been shown that direct contact between boars and gilts is a more effective stimulus in the induction of puberty than indirect contact (Pearce and Hughes, 1985). Patterson et al. (2002b) evaluated 89 gilts, penned in groups of 6, using one of three boar exposure methods: direct contact with group pens of gilts (DP), direct contact in gilt home pens (HP), or fence line contract with gilts in individual stalls. Boar exposure began at day 160 and lasted for 10 to 15 minutes each day. Both methods of direct boar exposure, HP and DP, significantly lowered the number of days until first estrus compared to fence line testing (21.8 and 24.0 vs. 32.0 days, respectively). Direct boar contact reduced age at puberty compared to indirect contact, in agreement with Zimmerman et al. (1996). However, in Patterson et al. (2002b) the method of direct boar contact (HP vs DP) didn't significantly impact the age of first estrus. Collectively, these results suggest that direct boar exposure effectively decreases age at puberty, compared to indirect boar exposure, and the method of direct exposure, exposing gilts to a boar in their home pen vs. a different pen, doesn't impact the onset of puberty.

Kirkwood and Hughes (1981) studied the impacts of boar age on the ability to prompt puberty in gilts. Four groups of Large White $\times$ (Landrace $\times$ Large White) gilts (n=24) were exposed to one of three different ages of boars (two years, 11 months, or six to five months of age) at 165 d while the fourth group was not exposed to a boar. Gilts were exposed to boars daily for 30 minutes. Average age at first estrus did not differ between gilts exposed to two year or 11 month old boars (182 vs. 181 days). Gilts exposed to no boar or to boars of five to six months of

age didn't differ in average age at puberty (203 vs. 206 days). However, there was a statistical difference between groups of gilts exposed to boars $\geq$ 11 months of age when compared to five to six months of age. This suggests that there is a developmental curve in which the effect of boar exposure begins to impact female animals.

There is a deficient number of studies examining the effect of boar age on inducing puberty in the gilt. While there are numerous studies examining the biological responses of the gilt and its relationship to boar exposure, aspects of the boar have received far less attention. Physiological effects of the boar have largely focused on boar related odors and their impact on puberty in gilts (Kirkwood and Hughes, 1983). More research is needed to determine the importance of boar age, breed, and season on stimulation and induction of puberty.

1.4.2 Season

Several authors have reported variation in the induction of puberty due to seasonal effects in livestock species. Early findings suggested that the initiation of puberty is delayed in females born in early spring months compared to animals born during other seasons of the year (Wiggins et al., 1950; Mavrogenis and Robison, 1976). Others have speculated what environmental factors cause delayed puberty in spring born animals. Flowers et al. (1989) implied elevated ambient temperatures could cause a delay in pubertal development. Photoperiod has also been implicated a characteristic of spring born animals that could impact age at puberty (Paterson and Pearce, 1990).

Tummaruk et al. (2000) gathered records (n=14,761) from Swedish Landrace and Yorkshire gilts born across 22 nucleus farms. Gilts were mated no earlier than second observed estrus, 7 to 9 months of age and 120 kg. Effects of herd-year were fit to all models to account for management differences. Effects of birth month on growth rate, age at first mating, and adjusted

age at first mating can be seen in Figure 1.2. Age at first mating was greater in animals born in early spring months. Growth rate was also lower for animals born in early spring. This is in agreement with results published by Paterson et al. (1991), which found that gilts whom were 165 days of age in late summer showed delayed puberty. Paterson et al. (1991) went further to discuss effects of photoperiod on prepubescent gilts. Taken together, these results suggest that there is a significant effect of season on puberty in gilts (Tummaruk et al., 2000) that is likely caused by underlying characteristics of that season (Paterson et al., 1991).

Paterson and Pearce (1990) conducted four experiments to determine the effect of photoperiod on age at puberty. Experiments one (n=32) and two (n=26) focused on the effect of photoperiod and boar stimulation on age at puberty. Gilts were kept in controlled environment rooms at a constant 23°C where the light dark ratio was initially 12 hours (h) light:12 h dark. The ratio was increased to 16 h light:8 h dark or 8 h light:16 h dark with increases of 10 to 15 minutes per week. Gilts completed the test at an average age of 230 days. Experiments three (n=35) and four (n=36) used the same protocol as first two experiments, but without boar exposure and increased the ratio to 14.5 h light:9.5 h dark or 9.5 h light:14.5 h dark. With boar exposure, photoperiod had no effect on the induction of puberty in gilts. Yet without boar exposure, gilts not exposed to boars were significantly impacted by photoperiod. Gilts reared in long day environments showed delayed puberty compared to those under short day lengths. This suggests that photoperiod, regardless of heat stress, is a major factor in the seasonal dip in reproductive development in gilts, however, this effect can be countered with the use of boar exposure.

Temperature during the developmental phase is also a characteristic of interest in determining the cause of seasonal effect on puberty in gilts. Flowers et al. (1989) studied the effects of elevated temperatures on crossbred gilts born in March and September. Gilts were assigned one of two treatments. Control animals were housed in rooms at 15.6°C, 35% relative humidity and

normal 12 h light:12 h dark photoperiods. Heat stressed animals were housed in rooms at 33.3°C, 35% relative humidity and normal 12 h light:12 h dark photoperiods. Boar exposure started at 180 and continued until 230 days of age. No statistical differences were observed due to the season of birth. Fewer gilts reached puberty by 230 days in the heat stressed group compared to the control and those that did reach puberty at a significantly older age. These results suggest that temperature drives seasonal differences in age at puberty observed by Wiggins et al. (1950) and Mavrogenis and Robison (1976), implying that increased ambient temperature delays the onset of puberty.

1.4.3 Growth

Growth rate and reproductive performance have long been a focus of swine genetic experiments (Bidanel et al., 1996; Rozeboom et al., 1995; Knauer et al., 2011; Vallet et al., 2016). Increased growth rate has been shown to accelerate the induction of puberty by effecting major developmental points in the growth cycle. Growth rate and puberty can be analyzed as the correlation of prenatal, preweaning and lifetime growth rates with age at puberty.

Prenatal growth rate, often measured as birth weight, has been shown to effect puberty in gilts (Flowers, 2012). During the prenatal growth period many reproductive tissues and organs begin development as early as day 50 of gestation. This development continues through the gestation period and consequently adds to the weight of animal prior to birth. Thus, birthweight can subsequently be used as one of the first measures of reproductive potential. Data presented by Flowers (2012) showed a negative trend between birth weight and age at puberty. Animals weighing 3.5 pounds or higher and 2.0 to 2.8 pounds reached puberty at an average age of 170 and 188 days, respectively. Animals with higher birth weights had greater ovulation rate and embryonic survival percentage (Bidanel et al., 1996). This suggests that prenatal environment

impacts pubertal development in that higher birth weight animals are better suited to reach puberty sooner.

Vallet et al. (2016) examined the effects of litter of origin traits, mainly preweaning litter environment, and how it can affect the subsequent reproductive development in gilts. Growth measures were gathered on maternal line gilts (n=1,200). Boar exposure began at 160 days of age and gilts were observed for estrous behavior daily. Age at puberty was significantly impacted by preweaning growth rate. Both linear and quadratic effects of preweaning growth were found to be associated with age at puberty. The relationship between preweaning growth and age at puberty was optimized at a growth rate of 0.26 kg/day. The difference in age at puberty from the optimum growth rate to the slowest growth rate impacted age at puberty by 22.5 days. While the model only accounted for 2.0% of the variance in age at puberty, the drastic difference driven by preweaning growth rate suggests that adjusted weaning weight could have a significant effect in the time needed for gilt development.

Lifetime growth rate and its relationship with reproductive traits has been the subject of numerous experiments (Amaral Filha et al., 2009). In a Thai study conducted by Tummaruk et al. (2007), Landrace $\times$ Yorkshire replacement gilts (n=696) were observed to determine the impact of body weight and lifetime growth rate on subsequent reproductive performance. Gilts were housed in groups and were not sorted by growth rate. Body weight was measured at birth, entry into the gilt pool (24 weeks of age), and first and second estrus. The interval from age at entry to first estrus was positively correlated with age and body weight at puberty, 0.59 and 0.52, respectively, suggesting that weight and age have similar relationships with age at puberty. When examining growth rate in later life, stronger relationships between growth and age at puberty are observed. Weight gain from gilt pool entry to first estrus was strongly related with the interval from entry to the gilt pool until first observed estrus, 0.77, yet ADG from entry to the gilt pool until puberty was only slightly negatively correlated, -0.19. Stronger relationships were

reported with lifetime growth traits such as body weight and late life weight gain as opposed to ADG during boar exposure. Thus, suggesting that removal of early life growth factors results in ADG having a weaker relationship with age at puberty. This suggests that growth prior to 24 weeks of age controls age at puberty to a greater degree than growth later in life.

The association between lifetime growth rate with age at puberty was further examined by Tummaruk et al. (2009). Three measures of growth rate; growth rate from birth to 90kg (GRe), from 91kg to 134kg (GRi), and birth to 134kg (GRs), were calculated on a population of crossbred Landrace $\times$ Yorkshire gilts (n=6,946). Growth rate measures were significantly correlated with each other. Growth rate from birth to 134kg (GRs) was positively related to GRi and GRe, 0.46 and 0.25 respectively. However, GRi was negatively correlated with GRe, -0.20. Age at first estrus was significantly influenced by GRs and GRe, r = -0.40 and -0.20 respectively. Age at puberty was not significantly impacted by GRi. This further suggests that increased lifetime growth rate decreases age at first estrus. Yet within GRs, GRe has a greater impact than GRi. This suggests that factors effecting growth early in life impact age at puberty to a greater extent than factors influencing growth later in life. Speculation could be made that the factor driving the relationship between lifetime growth rate and age at puberty is preweaning growth.

Rozeboom et al. (1995) also examined the relationships between lifetime growth rate and puberty. The relationship between lifetime average daily gain and age at puberty was examined on a group of Yorkshire $\times$ Landrace gilts (n=93) in five groups. Gilts were initially exposed to boars at 120 d of age and were mixed with new pen mates every 20 to 25 days. Lifetime growth rate (ADGt) was defined as weight at puberty minus birth weight divided by age at puberty. Late life growth rate (ADGl) was defined as weight at puberty minus weight at 63 days of age divided by age at puberty. Results showed a limited relationship between average daily gain and age at puberty. Linear models were fit showing that ADGt and ADGl explained 2 and 9 percent of the variation in age at puberty. The linear regression term for ADGt was not statistically

different from zero. This suggests that there is a weak relationship between average daily gain and age at puberty, in disagreement with findings from Tummaruk et al. (2007) and Tummaruk et al. (2009). Significant relationships many be weaker in the current study due to sampling bias associated with fewer observations.

1.4.4 Nutrition

Due to the close association between growth rate and age at puberty, it stands to reason that nutrition also plays a major role in the induction of puberty in the gilt. Nutritional requirements change throughout gilt development but can largely be broken down into two distinctive phases, preweaning and postweaning nutrition. Preweaning nutrition has been the focus of few experiments in terms of reproductive development (Vallet et al., 2016). Post-weaning nutrition, however, has been frequently studied during traditional gilt development phases (Cunningham et al., 1974; Miller et al., 2011; Calderón Díaz et al., 2015).

Birth weight and colostrum consumption have been shown to be influential factors in preweaning growth performance (Vallet et al., 2013) yet limited conclusions have been drawn between these traits and reproductive performance. Preweaning nutrition and its relationship with pubertal development was examined by Vallet et al. (2015). Approximately 1200 gilts were observed for estrous, production, and early life traits, with the goal being to identify early life traits that best predict future reproductive performance. Gilts were exposed to boars for 10 minutes daily beginning at 160 days and continued until 260 days of age. Age at puberty was not related with birth weight. Increase colostrum consumption, however, was shown to decrease age at puberty. Improved colostrum consumption was associated with increased preweaning growth rate. Furthermore, gilts with higher preweaning growth rates exhibited puberty earlier in life. These results suggest that age at puberty can be improved through improving preweaning

growth rate which is largely controlled by colostrum consumption and lactation performance.

Stocking density prior to weaning has been identified as a key period in the development of the gilt which has been shown to impact the ability to express puberty (Flowers, 2009). A factorial experiment was conducted on 3,180 gilts involving treatments of season of birth, neonatal litter size, and method of estrous stimulation. Two levels of neonatal litter size were evaluated, ≤ 7 and ≥ 10 piglets. Regardless of age at boar exposure or season of birth, neonatal litter size was shown to significantly impact pubertal development. The proportion of gilts to reach estrus within the first 28 days of boar exposure was 82 and 60% for gilts raised in small litters (≤ 7) and large litters (≥ 10), respectively. It's possible that neonatal litter size is a large driver of preweaning growth, which has been previously shown to have a relationship with age at puberty (Vallet et al., 2016). If the relationship between neonatal litter size and preweaning growth is true, neonatal litter size could be the force that is driving an earlier pubertal response in gilts when in the presence of a boar. The effects of neonatal litter size and preweaning growth rate, are not yet fully understood and require more investigation to be able to separate their effects pubertal development in swine (Flowers, 2012). Recent findings further suggest that preweaning effects such as cross fostering, weaning age, and preweaning growth rate drive reproductive efficiency later in life (Knauer, 2016).

Miller et al. (2011) studied the effects of reduced energy content and its effect on pubertal development on gilts post-weaning. Females (n=661) were split into two groups and fed different diets. One group was feed ad libitum from weaning to breeding (AL) and the other was restricted fed 75% of the ad libitum group (RES) starting at 123 days of age. Nutrition of the RES diet matched those of the AL diet with the exception of energy and selenium. Sires of females used were from a maternal line supplied by industry. Dams of females used were either industry Large White $\times$ Landrace or from the Nebraska selection Line 45. Estrous detection began at 140 days and age at puberty was recorded. Body composition traits were measured every 14 days.

Females, regardless of dam group, from AL reached puberty sooner than those fed RES diets, 174 and 177 days, respectively. Gilts fed the AL diet had increased rate of backfat deposition compared to gilts fed the RES diet. These results suggests that backfat and pubertal development are perhaps linked. Results also suggest that gilts fed post-weaning diets restricting energy by 25% have delayed puberty relative to those fed ad libitum, in contrast to results found by Knauer et al. (2010b). Differences between Miller et al. (2011) and Knauer et al. (2010b) could be due to the differences in reduction of nutrient requirements or feeding amounts. Reductions made by Miller et al. (2011) are far below those made by Knauer et al. (2010b) which could be responsible for greater physiological delay of pubertal traits. Further investigating is needed to determine the effects of body condition and puberty.

Calderón Díaz et al. (2015) examined the effects of diet composition in relation to pubertal development, expanding work done by Miller et al. (2011). Large White $\times$ Landrace gilts (n=1,221) were fed ad libitum diets with three different levels of metabolizable energy (ME) and two levels of standard ileal digestible (SID) lysine. Levels of dietary components were decided based on a poll of U.S. commercial swine producers. Grower diets from the poll had an average SID lysine and ME of 1.02% and 3.25 Mcal per ME/kg, respectively. Finisher diets reported by the poll had an average SID lysine and ME of 0.85% and 3.26 Mcal per ME/kg, respectively. The three experimental levels of ME utilized were 90, 100, and 110% of the polled industry average. The two experimental levels of SID lysine were 85 and 100% of the polled industry average. Gilts were fed two diet phases starting at 100 d of age, changing to phase two at 90 kg. Experimental diets ended at 260 days of age. Boar exposure began at 160 days of age. Average age at puberty was 193 days with a minimum of 160 and maximum of 265 days and 91% of gilts reached puberty by day 260. Results showed no impact of diet on age at puberty. The lack of difference suggests that puberty is not altered with differing levels of SID lysine and ME which are near NRC suggested requirements.

1.4.5 Body composition

Body composition, mainly fat deposition and muscle development, has been the focus of many reproductive experiments noting differences in the initiation of puberty. Body composition of females at puberty has been discussed by Rozeboom et al. (1995) and selection for lean tissue growth rate and its relationship with age at puberty has been reported by Rydhmer et al. (1994).

Many have speculated that the induction of puberty will not be achieved until the gilt has reached specific state in physiological maturity, which has been related to measures of lean carcass gain (Bidanel et al., 1996; Hanenberg et al., 2001). Rozeboom et al. (1995) studied body composition traits on 91 Landrace $\times$ Yorkshire prepubertal gilts. Measures of lean body composition included; fat to lean ratio (FLR), lean pounds of growth per day from birth to puberty (GPD), and lean pounds of carcass per day from purchase to puberty (LCD). There was a negative relationship between age at puberty with FLR, GPD, and LCD. The growth measure relationship which explained the most variation in age at puberty was LCD, which when added into the model accounted for 43% of the variation in age at puberty. The quadratic relationship between pounds of lean carcass per day and age at puberty can be seen in Figure 1.3. It is noted that the range in lean growth rate at the onset of puberty is large and highly variable. Patterson et al. (2002a) also evaluated lean growth rate and puberty in gilts. Lean growth rate is largely driven by protein accretion rates which begin to decline around 65kg of body weight, thus, some animals are predisposed to have higher lean growth rates due to initial differences in sexual maturation. After removing the highly variable period, in terms of lean tissue gain, from initiation of boar stimulation to puberty, the relationship between lean tissue growth and age at puberty is nonexistent which is in disagreement to the findings by Rydhmer et al. (1992). The findings by Patterson et al. (2002a) suggest that lean tissue growth rate after 65kg of body weight does not impact age at puberty. However, this does imply that growth rate and earlier life

performance greatly impact reproductive development later in life.

Rydhmer et al. (1994) investigated age at puberty and estrous symptoms on a population of Yorkshire gilts (n=740) selected for lean growth, as describe in previous sections. Weak relationships were found between lean percentage with the standing reflex, length of standing estrus and reddening and swelling of the vulva. This further implies that lean growth rate doesn't greatly impact the onset of puberty. In terms of body composition, early puberty gilts appear to place greater importance on backfat deposition than lean muscle growth (Gaughan et al., 1997; Miller et al., 2011) although this relationship is controversial (Rozeboom et al., 1995).

1.4.6 Housing

Effective numbers of gilts per development pen have been retroactively observed, suggesting that gilts raised in groups of 50 to 60 animals have a delayed pubertal response (Levis, 2000). Mavrogenis and Robison (1976) experienced an effect of socialization on the induction of puberty. Gilts penned individually reached puberty later than those in a more social environment in pes of 30, in agreement with observational findings from Levis (2000). Furthermore, observational remarks have been noted about the effect of floor type used during rearing of replacement females. Producers have noted increased pubertal development in groups of gilts raised on partial slatted flooring compared to total slatted floors (Levis, 2000).

Young et al. (2008) examined the effects of space allowance per pig and its relationship to pubertal development on 1,257 Pig Improvement Company (PIC USA, Franklin, KY) gilts. Gilts were divided into two treatments being placed in pens of 15 or 22 gilts per pen allowing each animal 1.13 and 0.77m^2 per gilt, respectively. Boar exposure began at 140 days of age and continued to approximately 200 days of age. Two boars were used where the first boar was exposed to five pens of gilts then allowed to rest for 40 minutes before moving to the next group

of pens. The second boar was exposed to four pens of gilts then also allowed to rest for 40 minutes before moving to the next group of pens. Space allowance per animal did significantly impact the average age at puberty in gilts. Animals with 1.13 m^2 per gilt reached puberty sooner that those with 0.77m^2 per gilt (182 vs. 184 days), in agreement with results published by Clark et al. (1985). This suggests that gilts with at least 1.13 m^2 of individual pen space will reach first estrus sooner compared to those in more confined conditions with only 0.77m^2. The decrease in average age at puberty, however, doesn't drastically change between the two treatments discussed above. Thus, suggesting that this method might not be an economically effective way to decrease age at puberty.

Housing method and its relationship to induction of puberty in gilts has been the focus of few authors. Methods of housing gilts prior to breeding have not been of great interest in recent years, few studies have investigated impacts of the number of females per pen or social interactions among pen mates and their relationships with puberty in recent history. Stocking density or socialization aspects during rearing may not be of great interest in the commercial swine industry due to vertical integration resulting in more standardized methods of replacement gilt management.

1.5 Associated male reproductive factors

Populations selected for reproductive performance have often included measures quantifying the response to selection in the opposite sex. Eisen and Johnson (1981) measured the response to selection in male counterparts reproductive performance which were produced from lines of mice selected for litter size and body weight. After selection for litter size, male mice exhibited positive correlations with testis weight but no differences were found in basal hormone levels. Similar results were presented by Toelle and Robison (1985b) demonstrating the correlation

between male and female reproductive performance in cattle. Results suggesting that selection for increased testis size in bulls improves female reproductions, namely decreased age at first breeding and increased calving rate. Martínez-Velázquez et al. (2003) found moderate genetic correlations between yearling scrotal circumference with age at first calving and age at puberty in heifers, -0.91 and -0.63 respectively. In swine, male reproductive traits, i.e. testis size, libido, and semen quality, are under significant amounts of genetic control compared to other species (Rothschild, 1996). Thus, possibilities of favorable relationships exist between female reproductive performance, age at puberty, and male reproductive traits in swine.

1.5.1 Libido

In a Chinese study, Ren et al. (2009) investigated the libido in 411 White Duroc $\times$ Chinese Erhualian cross boars and its relationships with other male reproductive traits. Semen characteristics, testes measurements, libido, and testosterone levels were observed in White Duroc $\times$ Chinese Erhualian Cross boars produced from a four generation intercross population. Libido was evaluated using an 18 point scoring system seen in Table 1.3 with boars having no prior mating experience. Serum testosterone concentration was measured by taking blood samples when the boars were 300 days of age using AutoDELFIA Testosterone kits. Libido score was found to have no significant correlations with any of the reproductive traits except for serum testosterone level, r = 0.35. Testosterone levels were significantly correlated with epididymis weight, but not testes weight, r = 0.30 and 0.08, respectively. Epididymis weight was, not surprisingly, significantly correlated with testes weight, r = 0.58. This suggest that while libido is lowly heritable (Rothschild and Ruvinsky, 2001) it could possibly be indirectly impacted by selection for testes weight. However, improvement in libido traits through indirect selection is not commonly practiced and has not been formally explored.

Overall, there are few reports about selection or correlation between boar libido and other reproductive traits beyond biological theory. One might assume that increased testosterone could increase libido and therefore selection for testes size could be utilized to impact libido, but this theory lacks experimental evidence (Flowers, 2008). To be able to draw more concise conclusions about the relationships between libido with male or female reproductive traits more research is needed.

1.5.2 Testis development

Measures of testis traits have been well documented in swine and are of great importance in quantifying other, harder to evaluate, male reproductive traits (Rothschild and Ruvinsky, 2001). Large variation in testes size between populations and between breeds has been documented and linked to other male reproductive factors such as hormone secretion and semen quality traits (Toelle et al., 1984; Borg et al., 1993). Selection for testes volume in swine has been discussed by numerous authors (Schinckel et al., 1984; Johnson et al., 1994; Harder et al., 1995) and has been shown to have a moderate response to selection. Few authors have looked at the correlation in swine testes size and female reproductive traits (Toelle and Robison, 1985a; Young et al., 1986; Johnson et al., 1994) possibly due to the difficulty in collecting testes measurements making implementation into breeding programs less desirable.

Toelle et al. (1984) examined the variation and genetic relationships with testes traits in swine. Data collection and variance component estimation was performed on 1,245 Duroc and 527 Yorkshire boars for a number of different reproductive traits. Both in situ and excised testis measurements were collected and found to have a moderate relationship between measurements, suggesting in situ measurement are a good representative of the true measurement. Variation between continental breeds was limited. Average testes volume at 168 days of age was 392

and 380 cm^3 for Duroc and Yorkshire boars, respectively. Paired testis volume was found to have strong to moderate relationships with other reproductive measures. Moderate genetic relationships between sperm per gram of testes with excised testes width and excised testis length were found 0.11 and 0.56, respectively. Suggesting that testes traits are reasonable predictor of semen production. The authors further reported excised testes length had the largest genetic relationship with sperm production.

In a selection experiment, Johnson et al. (1994) selected on predicted testes weight in Landrace $\times$ Large White boars for ten generations and calculated the correlated response to selection in the reproductive performance of female offspring produced. Two genetic lines were formed, a random control line (C) and a line selected for increased predicted testes weight (TS). In each generation 40 to 45 litters were produced per line. In generation ten the cumulative selection differential of sires was 19.4 and 670.2 g, for the C and TS lines, respectively. Predicted testes weight was found to be moderate to highly heritable, 0.39, suggesting testes weight is expected to be under more additive genetic control than other reproductive measures. In addition to selection for testes weight, female reproductive measures were also observed between the two lines i.e. age at puberty and ovulation rate. In generation ten females from the C and TS lines reached puberty on average at 181.7 and 175.0 d of age, respectively. Genetic correlations were calculated between predicted testes weight and age at puberty using REML procedures. Low, negative genetic correlations were found between predicted testes weight and age at puberty, -0.16, which is in agreement with results found by Toelle and Robison (1985a). While genetic relationships between testes traits and age at puberty are not high and shouldn't be used for indirect selection, they do suggest there is a complex connection between male and reproductive performance in swine.

Schinckel et al. (1983) preformed a selection experiment where female reproduction traits were selected and the response in related males was calculated. Boars observed were from a

line selected for increased ovulation rate (OR), lean growth, and a randomly mated control (C). Selection for OR in maternal line gilts occurred for six generations. In the sixth generation comparisons were made in the testicular development in boars between the OR and C lines. In situ testes width and length, as well as excised testes measurements, were captured on 377 boars. In comparison, boars from the OR line had 10.5% heavier testes than the C line at 90 kg. These results further build upon the possibilities of a complex genetic relationship between male and female reproductive performance.

Selection for testes size in boars has also been reported to effect semen traits (Huang and Johnson, 1996). Two lines of boars were developed, a line selected for increased testes size at 150 days of age (TS) and a randomly mated control line (C). From the TS and C lines 25 and 18 boars, respectively, had semen collected three times per week for three weeks and then daily for four weeks beginning at 276 days of age. The TS line had a greater number and concentration of cells per ejaculate. However, the motility between lines did not differ. These results suggest that while increased testes size may increase the number of sperm cells produced it does not necessarily improve semen quality.

1.5.3 Semen characteristics

Little selection pressure is placed on semen characteristics within the swine industry, however, it can be argued that ability to efficiently produce gametes is the most important trait. Sperm production characteristics differ greatly between populations (Flowers, 2009), and are considered highly variable traits. Thus, it is important to insure selection doesn't negatively impact the production or quality of sperm cells by indirect selective pressures. Selection for increased testes size has resulted in greater numbers of cells produced (Harder et al., 1995; Huang and Johnson, 1996). Other populations selected for increased ovulation rate have shown a higher

percentage of active sperm cells in the seminiferous tubules compared to a randomly mated control line, 44.1 vs 21.2% (Schinckel et al., 1983) suggesting a possible link between male and female gamete production and reproductive performance.

Borg et al. (1993) investigated the variability in semen production traits between populations of purebred boars. In an attempt to quantify the difference between commercial terminal breeds and highly prolific Chinese breeds, mature Duroc, Meishan, Fengjing, and Minzhu boars (n=8, 9, 8, and 7, respectively) had semen samples collected during four different seasons of the year, where each boar had two samples collected per season. Using ejaculates collected, semen characteristics were evaluated across breeds and seasons. Duroc and Minzhu boars produced significantly more total sperm that Fengjing and Meishan boars. However, there was a significant range in total number of sperm produced within breeds and between seasons. Duroc boars produced a significantly larger ejaculate than any of the Chinese breeds. When comparing progressive motility across breeds no significant differences were observed, yet there was an impact of season of collection. Suggesting that while semen quality traits may not differ between common populations of swine, but there is a considerable amount of variation between other semen traits between Chinese and Duroc boars. While differences in ejaculate and sperm cell volume can largely be attributed to testes size, these results do raise questions on the impacts of selection for higher reproductive performance between sexes and within breeds.

More recently, Freking et al. (2012) compared semen quality in boars produced from genetic lines selected for either ovulation rate (OR) or uterine capacity (UC). Selection for ovulation rate and urine capacity was practiced for eleven generations and was compared against an unselected randomly mated control (C) line. Boars from all three lines (n=60), over two farrowing seasons, were collected twice, retaining the sperm-rich fraction for analysis. Sperm quality traits were evaluated by computer-assisted sperm analysis and investigated quantity, quality and morphological traits. Results showed that the C line boars produced a lower volume

of ejaculate compared to the OR line. Similarly, the OR line boars showed a significantly higher total number of sperm production, compared to the C line, 54.9 vs. 40.5 ($\times 10^9$ cells). To account for differences due to processing of sperm cells, each ejaculate was evaluated at three different processing points (fresh, extended, or thawed after freezing). No significant differences were found between semen quality traits in fresh or post-thawed ejaculates. However, significant differences in motility %, progressive motility %, velocity straight line, velocity curved line, and velocity average path were found in extended ejaculates that favored C line boars (Table 1.4). These results suggest that boars produced from sows selected for increased ovulation rate or uterine capacity produce more sperm cells comparted to randomly selected control boars. While differences were found in sperm quality traits favoring C line boars, these results were not consistent across processing points. More information will be needed to concussively determine effects of selection on female reproductive performance with subsistent male sperm quality traits.

1.5.4 Endocrinology

It is largely known that endocrinology drives reproductive development and provides the pathways for the reproductive performance traits mentioned above. Many reports that evaluate both male and female reproductive performance include measures of pivotal hormone response traits to better understand the physiological changes that occur biased upon selection or observed phenotypic differences (Lubritz et al., 1991; Borg et al., 1993; Ren et al., 2009). Hormones which have been evaluated previously include testosterone, follicle stimulating hormone, and luteinizing hormone. Successful selection for testosterone production has been previously discussed by Robison et al. (1994) and Walker et al. (2004). Response to selection for testes size and testosterone and luteinizing hormone levels have been evaluated by Schinckel et al. (1984).

Numerous authors have commented on the variation in hormone levels due to selection and breed, attempting to draw conclusions on the relationships with other reproductive measures (Borg et al., 1993; Ford et al., 1997; Zanella, 1999; Ren et al., 2009).

Borg et al. (1993) investigated the variability in serum hormone levels between populations of pure bred Duroc and Chinese bred boars. Chinese breeds of swine are often considered more prolific than their continental counterparts. Thus, in an attempt to quantify the difference between these distinct populations mature Duroc, Meishan, Fengjing, and Minzhu boars (n=8, 9, 8, and 7, respectively) had blood samples collected during four different seasons of the year. Hormone profiles that were evaluated include follicle stimulating hormone (FSH), testosterone, and inhibin. No significant differences were found in serum testosterone level between the different breeds. However, there was a significantly greater level of serum testosterone in the Fall season compared to Winter, Spring, and Summer. Limited differences in testosterone levels between breeds is in agreement with findings by Ren et al. (2009). Potential reasons for increase in testosterone in the Fall are not yet clear, but it is possible that there is a limited breeding seasonality effect in swine. Furthermore, Duroc boars had significantly higher levels of inhibin compared to the Chinese breeds. Fenging and Meishan boars showed significantly higher levels of FSH than Duroc of Minzhu boars, regardless of season. The authors speculate that this could be due to increase numbers of Sertoli cells, driving the differences in reproductive performance. Ford et al. (1997) reported a negative relationship with testes size and FSH levels in Meishan and White composite boars further clouding the causative action for increased FSH levels. Possibilities however, do exist for a weak relationship with Sertoli cells and testicular mass. Since FSH is crucial in early development of the testis (Griswold, 1998), higher levels of FSH could result increased overall reproductive performance via Sertoli cells, however, more research is needed before such conclusions could be drawn.

In a selection experiment Walker et al. (2004) divergently selected for testosterone produc-

tion in Duroc boars. Selection for high testosterone levels (HTL) and low testosterone levels (LTL) occurred over 10 generations preceding a Gonadotropin Releasing hormone challenge. Generations 11 through 21 were randomly mated within line while samples were collected. In generation 21 boars from the HTL and LTL line averaged 49.0 and 27.8 ng/mL of testosterone, respectively. Follicle stimulating hormone levels nor sperm quality traits differed between lines. Sertoli cells measured in biopsy samples showed no difference between the lines. Biopsy samples did show the HTL line had a significantly larger number of Leydig cells than counter parts from the LTL line. Boars from the HTL line had heavier epididymal weights yet lighter total testes weights compared to the LTL line, 126 vs. 93 g and 417 vs. 457 g, respectively, after accounting for body weight and age. These results suggest that selection for increased testosterone levels is possible, yet it will not result in increased sperm quality or boar fertility.

1.6 Tables

Table 1.1: Reported heritability estimates of age at puberty with method of estimation and breeds evaluated.

Source	Method	Breed[a]	Obs.	h^2	SE
Knauer et al. (2010b)	AIReml	L × LW	1225	0.29	0.08
Kuehn et al. (2009)	MTDReml	4 way cross	924	0.46	0.08
Sterning et al. (1998)	Reml	Swedish Y	452	0.40	_
Bidanel et al. (1996)	Reml	LW	1393	0.29	0.02
Johnson et al. (1994)	DFReml	L & LW composite	1194	0.55	_
Rydhmer et al. (1994)	Reml	Y	740	0.32	0.08
Rydhmer et al. (1992)	Multivariate Reml	Swedish Y	393	0.51	_
Lamberson et al. (1991)	Psudo expect. approx.	14 breed composite	1784	0.25	0.05
Hixon et al. (1987)	_	Composite	1784	0.24	0.28
Hutchens et al. (1981)	Hendersons method 3[b]	Diallel cross D, Y, S, L	819	0.19	_
Hutchens et al. (1981)	Hendersons method 3[c]	Diallel cross D, Y, S, L	819	0.40	_
Young et al. (1978)	Hierarchical ANOVA	14 breed composite	2095	0.53	0.13
Average				0.37	

[a]L = Landrace, LW = Large White, Y = Yorksire, D = Duroc, S = Spot.
[b]based upon sire half-sib regression.
[c]based upon dam half-sib regression.

Table 1.2: Days from start of boar exposure to puberty attainment, age, liveweight and P2 backfat at puberty for gilts that started boar exposure at either 161, 182, or 203 days of age (Adapted from van Wettere et al. (2006)).

Age at start of boar exposure	Days-to-puberty[a,b]	Age at puberty[b] # (days)	Liveweight at puberty (kg)	P2 backfat at puberty (mm)
161 Days of age (n=60)	18.9a	179.5a	109.2a	15.1ab
182 Days of age (n=54)	10.6b	191.9b	122.1b	14.1a
203 Days of age (n=54)	8.3b	210.6c	138.8c	16.4b
Polled S.E.M.	1.2	1.2	1.4	0.4

Means (a-c) in column are significantly different (P<0.01).
[a]Interval from initial exposure to a boar until exhibition of a standing reflex.
[b]Gilts not attaining puberty by day 35 of boar exposure were ascribed to nominal days-to-puberty of 40 days.

Table 1.3: Scoring system to asses libido levels during semen collection. (Adapted from Ren et al. (2009)).

Sexual behavior	Scores		
Excitability on the way to the semen collection pen	Poor	Intermediate	High
	0	1	2
Uttering short series of grunts	No		Yes
	0		1
Champing of jaws producing saliva	No		Yes
	0		1
Tried to climb the door and bars of collection pen	No		Yes
	0		1
Sniffing anal-genital region or head of dummy sow	No		Yes
	0		1
Nudging or nosing flanks of the dummy sow	No		Yes
	0		1
Mounting of dummy sow	No		Yes
	0		1
Reaction time	$\geq$6 min	2-6 min	> 2 min
	0	2	4
Duroation of ejaculation	< 4 min	4-7 min	$\geq$7 min
	0	2	4
Trainers impression on the libido level of measured boar	Poor	Intermediate	High
	0	1	2

Table 1.4: Boar selection line least-squares means, SE, and levels of significance for sperm motility, velocity, and velocity ratio measures on fresh semen extended and post thaw processing points. (Adapted from Freking et al. (2012)).

	Selection line				Variance componet estimates	
Trait	Control	Ovulation rate	Uterine capacity	P-Value for line	Between boar	Within boar
Motility, %						
Fresh	88.3	87.3	80.3	0.1	122.5	55.9
Extended	85.1[a]	76.2[b]	74.4[b]	0.0001	19.3	70.4
Postthaw	39.6	30.5	34.2	0.11	105.4	147.8
Progressive Motility, %						
Fresh	81.1	79.8	71.3	0.07	42.2	62.3
Extended	44.4[a]	41.7[a,b]	37.2[b]	0.05	31.3	78.4
Postthaw	18.7	13.6	17.7	0.16	37.3	72.9
Velocity straight line (VSL), m/s						
Fresh	57.5	57.3	51.7	0.07	42.2	62.3
Extended	55.5[a]	41.7[a,b]	50.0[b]	0.05	19.9	45.6
Postthaw	55.0	13.6	56.7	0.72	18.8	42.2
Velocity curved line (VCL, m/s						
Fresh	152	57.3	199.8	0.3	300.3	255.9
Extended	220[a]	52.6[ab]	190.9[b]	0.0001	243.4	464.6
Postthaw	144.5	55.4	142.7	0.86	154.9	259.4
Velocity average path (VAP), m/s						
Fresh	71.3	129.8	66.0	0.14	71.7	81.3
Extended	106.0[a]	191.6[b]	88.8[b]	0.0001	67.7	147.8
Postthaw	74.6	141.5	74.3	0.82	39.5	60.4

[a,b]Within a row, means without a common superscript differ (P<0.05).

Table 1.4 Continued.

	Selection line				Variance componet estimates	
Trait	Control	Ovulation rate	Uterine capacity	P-Value for line	Between boar	Within boar
Linearity, VSL/VCL						
Fresh	0.45	0.44	0.43	0.18	0.0009	0.0009
Extended	0.29	0.28	0.27	0.06	0.0004	0.0003
Postthaw	0.39	0.40	0.40	0.39	0.0003	0.0016
Straightness, VSL/VAP						
Fresh	0.80	0.76	0.78	0.11	0.0005	0.001
Extended	0.53[a]	0.57[b]	0.57[b]	0.002	0.0012	0.0012
Postthaw	0.72	0.74	0.74	0.3	0.0006	0.0019

[a,b]Within a row, means without a common superscript differ (P<0.05).

1.7 Figures

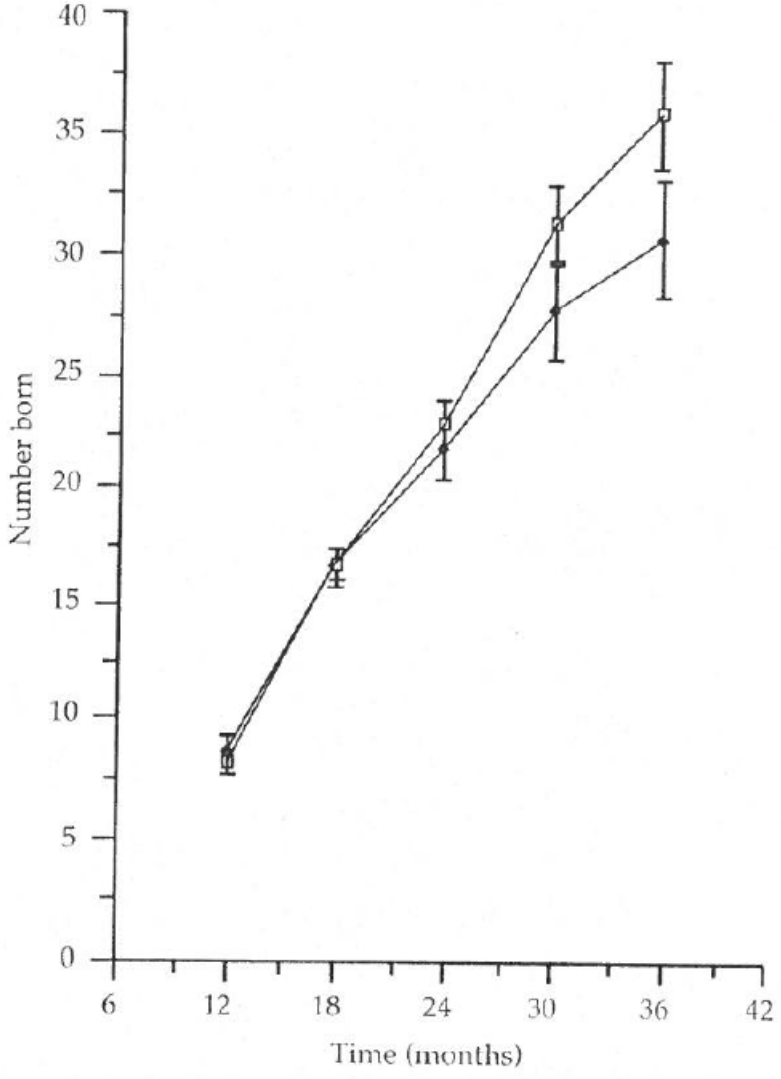

Figure 1.1: Mean accumulative productivity of age at puberty and randomly selected gilts over time. (Adapted from Holder et al. (1995)).

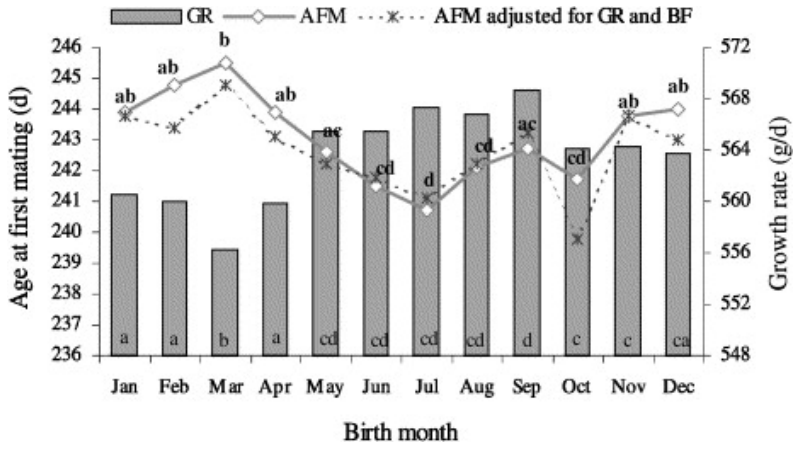

Figure 1.2: The influence of birth month of gilts on age at first mating and growth rate. Valuest with different letter on the same line differ significantly (P<0.05). (Adapted from Tummaruk et al. (2000)).

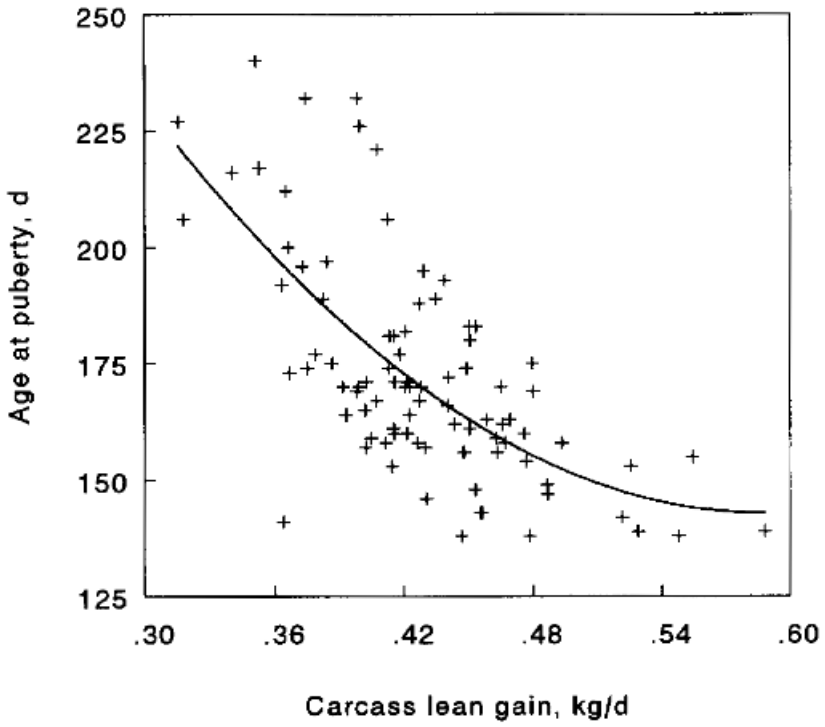

Figure 1.3: Relationship between age at puberty ($\hat{y}$) and carcass lean gain from purchase to puberty (x, kg/day). (Adapted from Rozeboom et al. (1995)).

Chapter 2

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

2.1 Abstract

The objective was to evaluate 4 generations (GEN) of divergent selection for age at puberty in swine. Composite Landrace × Large White animals (n = 4,941) were divided into genetic lines (GL), young age at puberty (YNG) and old age at puberty (OLD). Animals were reared at the North Carolina Department of Agriculture Tidewater Research Station. At 130 d of age, gilts were exposed to 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 (PUB), puberty weight (PUBWT), length of estrus at puberty (LEN1), estrous length at second estrus (LEN2), vulva width at puberty (VW1), vulva width at second estrus (VW2), piglet birth weight (BWT),

piglet weaning weight (WWT), loin eye area (LEA), backfat depth (BF), and weight at 178 d of age (WT). Sow traits included: total number born (TNB), litter BWT (LBW), average BWT (ABW), BWT CV (BWT_CV), litter WWT (LWW), average WWT (AWW), WWT CV, (WWT_CV), and litter size weaned (LSW). Variance components were estimated using ASReml with an animal model. Models included GEN and sex as fixed effects, a random common litter effect and a random animal genetic effect. Covariates were fit for reproductive traits (age at boar exposure), LEA and BF (WT) and WT (age). Sow traits were analyzed in SAS using PROC MIXED. Fixed effects included GEN, GL, and GEN $\times$ GL interaction. Covariates of TNB and LSW were included for applicable weight traits. In GEN 4, YNG and OLD gilts had a PUB of 85 and 50%, respectively, and AGEPUB of 162 and 181 d, respectively. Heritability estimates for AGEPUB, PUB, PUBWT, LEN1, LEN2, VW1, VW2, BWT, WWT, LEA, BF and WT were 0.40, 0.11, 0.39, 0.19, 0.17, 0.36, 0.48, 0.20, 0.12, 0.42, 0.43 and 0.37, respectively. Genetic correlations between AGEPUB with PUB, PUBWT, LEN1, LEN2, VW1, VW2, BWT, WWT, LEA, BF and WT were -0.82, 0.83, -0.22, -0.31, 0.25, 0.19, -0.08, -0.29, 0.15, -0.21 and -0.43, respectively. Overall, TNB tended (P = 0.07) to be greater for OLD compared to YNG (11.73 vs. 11.03). Yet, in GEN 4 YNG had greater (P <0.01) ABW than OLD (1.09 vs. 1.00 kg). Results show selection for reduced AGEPUB in swine decreased AGEPUB and improved PUB. Selection for reduced AGEPUB would generate gilts that are faster growing yet lighter weight at mating and farrow litters with improved piglet quality.

2.2 Introduction

Maximizing salable pigs per female per year at the least cost is the goal of the modern swine industry. Recent improvements in sow reproduction efficiency have resulted from improved litter size (Knauer and Hostetler, 2013). Problems still exist for other economic sow farm measures

such as gilt and sow retention. Reproductive failure continues as the number one reason for early removal from the herd (Stalder et al., 2003). Perhaps genetic improvement of gilt and sow retention will require the incorporation of new precursor phenotypic metrics into genetic evaluations. Typically 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. Perhaps further quantification on the importance of early puberty is needed to ensure proper economic weighting is calculated.

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 three 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. Hence the objective of this study was to evaluate associated responses to four generations of divergent selection for age at puberty in swine. Variance component estimates and correlated responses to selection with age at puberty are reported for swine estrous, growth, composition and litter traits.

2.3 Materials and methods

Experimental protocols used in this study were approved by the North Carolina State University Institutional Animal Care and Use Committee.

2.3.1 Animals

Composite Landrace × Large White pigs (n=4,941) were reared at the North Carolina Department of Agriculture Tidewater Research Station (Plymouth, NC) from 2012 to 2016. 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 activated at 27°C. Stocking density allowed for 0.84 m^2 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 2.1, were formulated to meet or exceed NRC requirements (National Research Council, 2012).

Estrous detection was performed from mid-May through August. Gilts were first exposed to mature boars at 130 d of age and estrous detection continued for 90 d. Estrous was defined using the back-pressure test in the presence of a mature boar (Willemse and Boender, 1966). Boars, greater than 12 months of age, were used once daily to check gilts for expressions of estrus. Estrous detection was carried out by bringing a pen of gilts to a harnessed boar and penning them together for 7 min. During that period, two 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. Fence-line boar exposure consisted of two boars 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 of age (PUB) was coded as a binary trait (1 = yes, 0 = no). Estrous length 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 body weight, backfat, and LM area 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. Natural mating was utilized for all matings. Gilts were bred once daily by the same boar each day they exhibited the standing reflex. Matings were randomly assigned within genetic line while avoiding full-sib and half-sib matings to minimize inbreeding. Males used as sires were housed in pens. After pregnancy was confirmed, bred 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 caliper (Knauer and Baitinger, 2015). At day 108 of gestation, females were moved to environmentally controlled farrowing rooms.

Litter performance traits were captured for sows (n=332). Total number born (TNB) was calculated as the number of piglets born alive plus stillborns. Within 24 hours of birth, piglets were processed and individually weighed (BWT). Litter BWT (LBW), average piglet BWT (ABW), and BWT CV (BWT_CV) were calculated. Cross-fostering was performed, within and between lines, to equalize the number of piglets nursed per sow. At 21 d of age piglets were individually weighed (WWT). Litter WWT (LWT), average piglet WWT (AWW), WWT CV (WWT_CV) were calculated. Litter size weaned (LSW) was the number of piglets weaned by the biological dam. At weaning piglets were sorted by sex, and moved to environmentally controlled nursery rooms. At 70 d of age gilts and boars were moved to their respective finishing buildings.

2.3.2 Divergent selection for age at puberty

Divergent selection for age at puberty created two genetic lines, young and old age at puberty (YNG and OLD, respectively). In 2012, 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 YNG and OLD. The youngest AGEPUB gilts were selected to create the YNG line and the 20 oldest AGEPUB gilts and 45 gilts that had not cycled by 220 days of age were selected to create the OLD line. Both YNG and OLD gilts were randomly mated to the same 22 boars (13 sire families), avoiding full-sib and half-sib matings. Hence, generation 1 progeny from YNG and OLD were a half sib population. This strategy was used to speed up the creation of the selection lines and ensure balanced allele frequencies across genetic lines. 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 YNG 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, again avoiding full-sib and half-sib matings. Number of mated sires, dams and offspring produced by generation are presented in Table 2.2.

2.3.3 Statistical methods

Variance components were estimated using restricted maximum likelihood mixed model approach in 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 is a vector of observed traits (AGEPUB, PUB, PUBWT, LEN1, LEN2, VW1, VW2,

BWT, WWT, LEA, BF and WT); b is a vector of fixed effects including generation, sex, and covariates when applicable (Table 2.3); a is a vector of additive genetic effects of the animal; l is a vector of random common litter effects; e is a vector of random residuals; X, Z, and W are design matrices associating b, a, l, and e with y, respectively. Probability of puberty (PUB) was fit as a binary trait using the logit link function. The effects estimated are 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 to the residual variance estimates in all PUB models fit (Gilmour et al., 2015). Gilt age at boar exposure was included as a covariate (Table 2.3). The model fit assumes that random effects have

$$var\begin{bmatrix} u \\ l \\ e \end{bmatrix} \sim N\left(\begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} A\sigma_a^2 & 0 & 0 \\ 0 & I_l\sigma_l^2 & 0 \\ 0 & 0 & I_e\sigma_e^2 \end{bmatrix}\right),$$

where σ_a^2 is the additive genetic variance; σ_l^2 is the variance due to the common litter effect; σ_e^2 is the variance associated with the residuals; A is the additive genetic relationship matrix; I_l is an identity matrix with dimensions equal to the number of litters; and I_e is an identity matrix with dimensions equal to the number of observations. Covariance's between σ_a^2, σ_l^2, and σ_e^2 were assumed to be zero. The pedigree used to create A utilized five generations and contained 5,105 individuals, 420 dams and 105 sires.

Reported heritability estimates (h^2) and standard errors of prediction were averaged across one univariate model and eleven 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 maternal environment (c^2) was defined as $c^2 = \sigma_l^2/\sigma_p^2$. Common maternal environment effects were fit in all univariate and bivariate mixed models.

Bivariate models used to calculate genetic correlations allowed for covariance between traits for random additive genetic, common litter, and residual effects. To allow convergence, variance and/or covariance estimation of common litter was fixed to zero in bivariate models containing LEN1, LEN2, and VW2. Random common litter variance, however, was estimated for the second trait of bivariate models whom contained LEN1, LEN2 and VW2. Bivariate models including PUB and AGEPUB were not calculated. Instead, estimated breeding values, produced from univariate models, from sires who produced greater than 5 daughters observed for PUB and AGEPUB were used to determine potential relationships between traits.

Genetic trends were computed using Best Linear Unbiased Predictions (BLUP) generated from univariate and bivariate linear mixed models. Genetic trends for AGEPUB and PUB were produced from univariate linear mixed models. Yet, trends for all other traits were produced from bivariate linear mixed models, with AGEPUB 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 AGEPUB. genetic line differences were calculated by separating BLUP's by generation and then dividing by the SD of BLUP's within each line to standardize all traits.

Statistical analysis to evaluate sow reproductive performance trends across generations was performed in SAS using PROC MIXED. Fixed effects for all models included genetic line, generation and genetic line $\times$ generation interaction. Covariates of TNB and LSW were included for LBW, ABW and BWT_CV and LWW, AWW and WWT_CV, respectively.

2.4 Results and discussion

2.4.1 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 2.4 and Figures 2.1 and 2.2, respectively. In generation four, YNG and OLD gilts were 85 and 50% pubertal, respectively. Average AGEPUB in generation four for YNG and OLD gilts was 163 and 183 d, respectively. In agreement, Lamberson et al. (1991) reported response to selection for decreased AGEPUB of 15.7 d after nine 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, AGEPUB 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 four between YNG and OLD for AGEPUB was 1.95 genetic SD units. Similarly, PUB in generation four differed between YNG and OLD lines by 2.70 genetic SD units. Genetic trends suggest that selection for decreased AGEPUB produces greater additive genetic change in PUB than in AGEPUB (1.93 vs. -0.68 genetic SD units). To our knowledge, few prior studies have quantified the response in PUB by selecting for decrease AGEPUB.

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

costs.

Marginal differences in phenotypic or genetic trends exist in generation 4 between YNG and OLD for VW1 and LEN1. In generation four YNG and OLD gilts differed by 0.20 and 0.91 genetic SD units for VW1 and LEN1, respectively. Length of estrus at puberty differed (P<0.05) between genetic lines in generation four, favoring YNG (0.24 d). Yet, no clear trends resulted between genetic line for LEN1 or LEN2. Furthermore, phenotypic estimates between YNG and OLD gilts for VW1 and VW2 showed no trend and did not differ (P>0.05) between lines in generation four.

Divergent selection for AGEPUB affected measures of sow reproductive performance (Table 2.5). At generation four, TNB and LSW did not differ (P>0.05) when comparing OLD and YNG sows. However, it is important to note that the genetic line $\times$ generation interaction was not significant (P>0.05). After removal of the interaction TNB tended (P=0.07) to be greater for OLD when compared to YNG sows (11.73 vs. 11.03) and LSW tended (P=0.06) to be greater for OLD when compared to YNG sows (9.68 vs. 8.96). These results are in agreement with genetic correlations between AGEPUB and litter size (0.20) reported by Rydhmer et al. (1992). Combined, results suggest associations between litter size and AGEPUB are not large. Differences in TNB and LSW in the current study could be exaggerated due to other genetic forces (i.e. Mendelian sampling or genetic drift) or lack of genetic relationship between AGEPUB and litter size.

In generation 4, LBW and LWW differed (P<0.05) between genetic lines, favoring YNG. In generation 1, ABW did not differ (P>0.05) between YNG and OLD but in generation 4, YNG had greater (P<0.05) ABW than OLD (1.09 vs. 1.00 kg). These trends suggest that selection for decreased AGEPUB resulted in increased ABW. Similar to ABW, in generation 1, AWW did not differ (P>0.05) between YNG and OLD (5.18 vs. 5.11 kg, respectively) but in generation 4, YNG had greater (P<0.05) AWW than OLD (5.15 vs. 4.66 kg). Furthermore, ABW_CV and

LWW_CV were not different (P>0.05) between genetic lines in generation 4. However, the genetic line × generation interaction was not significant (P>0.05) for ABW_CV and AWW_CV. After removal of the interaction, BW_CV was greater (P<0.01) for YNG when compared to OLD (17.7 vs. 15.8%) yet AWW_CV was lower (P=0.05) for YNG when compared to OLD (14.0 vs. 15.5%). Collectively, results suggest selection for decreased AGEPUB may enhance piglet size and litter quality at weaning.

2.4.2 Estimates of genetic parameters

Descriptive statistics and estimates of genetic parameters are shown in Table 2.6. Variance component analysis resulted in a heritability of 0.40 for AGEPUB, similar to a composite of literature estimates (0.37) reported by Rothschild and Ruvinsky (2001). Variation between heritability estimates between models including AGEPUB was low (CV=7.2%). Effects from a common maternal environment on AGEPUB were found to be limited (0.08). Yet, results from the current study are consistent with estimates previously reported by Bidanel et al. (1996) and Knauer et al. (2010b) (0.08 and 0.09, respectively). Combined results suggest maternal environment effects impact subsequent reproductive phenotypes such as AGEPUB. Flowers (2012) reported that gilts whom were born at heavier weights (>3.5 lbs.) 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 AGEPUB to prevent falsely inflated estimates.

In contrast to AGEPUB, PUB had a lower heritability of 0.11 and a lower CV between heritability estimates between models (6.66%). Common maternal environmental variance

explained a larger proportion of the total variance in PUB compared to additive genetic effects (0.14 vs. 0.11 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. Collectively, results suggest PUB is controlled to a greater degree by maternal environment than additive genetic effects.

Since genetic and phenotypic relationships between AGEPUB and PUB were not estimable due to confoundment, the relationship has been displayed as a correlation between sire EBV's in Figure 2.3. The correlation between sires EBV's for AGEPUB and PUB was -0.78, suggesting that AGEPUB 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 AGEPUB and PUB. Results from the current study suggest that direct selection for AGEPUB would result in significant genetic progress in AGEPUB and PUB via indirect selection. Direct selection for PUB would be ineffective in furthering genetic progress in either trait.

Genetic and phenotypic correlations between AGEPUB with reproduction, growth and compositional traits are shown in Table 2.7. Positive genetic and phenotypic relationships were found between AGEPUB 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, strong positive correlations between AGEPUB and PUBWT are reported by Eliasson et al. (1991), Rydhmer et al. (1994), Bidanel et al. (1996) and Knauer et al. (2010b). Utilization of this relationship could benefit producers selecting for decreased age at puberty thought the development of smaller gilts at first breeding.

Estimates of genetic relationships between AGEPUB and estrous traits are similar to those reported by Eliasson et al. (1991) and Knauer et al. (2010b). Moderate genetic correlations

between AGEPUB with LEN1 and LEN2 (-0.22 and -0.31, respectively) were found, 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 AGEPUB and LEN1 (Eliasson et al., 1991; Rydhmer et al., 1994; Knauer et al., 2010b). The difference in the genetic correlation between AGEPUB with LEN2 compared to LEN1 (0.09) could be attributed to significant variation in first estrus symptoms, which were previously discussed by Rydhmer et al. (1994) and Knauer et al. (2010b). Increases in this relationship however, could also explain the favorable associations between age at puberty and sow reproductive lifetime (Knauer et al., 2010a). Sows showing stronger visual estrus symptoms are more likely to be bred and remain in the herd longer. Conversely, genetic relationships between AGEPUB with VW1 and VW2 were low in magnitude and 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., 2010b). 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 could be driven more by PUBWT, since larger animals could be predisposition 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 are not different from zero.

Genetic and phenotypic correlations between age at puberty and growth traits are close to 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., 2010b). Negative genetic relationships were found between AGEPUB with WT 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 AGEPUB 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 AGEPUB and BF (-0.21) are in agreement with those previously reported (Eliasson et al., 1991; Bidanel et al., 1996). Conversely, AGEPUB showed favorable 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. Knauer et al. (2010b) reported similar genetic correlations between AGEPUB and LEA adjusted to 114kg (0.17), yet, a strong favorable phenotypic correlation with LEA and AGEPUB (0.66). 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.

2.4.3 Implications

Age at puberty is a moderately heritable, yet variable trait, that can be improved though selection in swine. Correlated increases in PUB, PUBWT and BF can be expected. 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 the literature suggest that AGEPUB is a useful and effective indicator trait for sow lifetime productivity and retention. In this experiment, significant increases in piglet birth weight were found in sows selected for decreased age at puberty. However, further work with these lines is needed to determine the long term effects of selection on sow lifetime productivity and longevity measures. Further work has been done with boars produced from these lines to determine

whether selection has impacted boar reproductive traits.

2.5 Tables

Table 2.1: Feeding regimen and formulated diets[1] (as-fed basis) of net energy (NE), crude protein (CP), Calcium (Ca), and Phosphorus (P) for each production phase[2].

Phase	NE, kcal/kg	CP, %	Lysine %	Ca, %	P, %
Nursery					
Day 1 to 7		21.88	1.59	0.78	0.71
Day 8 to 14		20.70	1.52	0.68	0.57
Day 14 to 11 kg		20.55	1.51	0.67	0.55
Grower					
11 to 23 kg	2337	18.97	1.43	0.68	0.52
23 to 41 kg	2427	15.67	1.16	0.54	0.42
41 to 59 kg	2496	13.13	0.97	0.52	0.40
59 to 82 kg	2544	11.31	0.82	0.50	0.38
82 to 105 kg	2566	10.42	0.72	0.49	0.36
105 kg to mating	2566	10.39	0.69	0.49	0.36
Gestation	2277	10.98	0.68	0.85	0.61
Lactation	2352	16.04	1.10	0.89	0.69

[1]Corn and soybean meal were the base ingredients for all diets. Diets were supplemented with Renaissance Nutrition Base mix additives to meet vitamin an dmineral requirements suggested by NRC (2012).
[2]All animals were fed adlibitum from nursery till 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.

Table 2.2: Number of sows to farrow and sires used by line[1] and by generation.

	Sows Farrowed		Sires		Offspring Produced		F, %[2]	
Generation	YNG	OLD	YNG	OLD	YNG	OLD	YNG	OLD
0	87		22		1215			
1	45	32	10	13	492	366	0.00	0.00
2	55	36	16	11	576	458	1.81	1.00
3	60	23	10	7	701	251	1.56	2.84
4	60	27	16	15	635	314	3.71	4.74

[1]YNG = young age at puberty line; OLD = old age at puberty line.
[2]F = inbreeding percentage.

Table 2.3: Covariates included in mixed model analysis to estimate genetic parameters by specific trait.

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

[1]AGEPUB = age at puberty, PUBWT = weight at puberty, PUB = probability of reaching puberty, BWT = birth weight, WWT = weaning weight, LEA = loin eye area, BF = backfat depth, WT = weight at 178 d.
[2]Age of the animal at first exposure to a boar.
[3]Age of the animal when WT, LEA and BF were recorded.

Table 2.4: Least squares means[1] by line[2] and generation for reproductive, growth and compositional traits[3] in response to selection for age at puberty.

	Generation				
Trait	0	1	2	3	4
AGEPUB, d					
YNG	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	NA	<0.01	<0.01	<0.01	<0.01
PUBWT, kg					
YNG	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	NA	0.27	0.12	0.26	<0.01
LEN1, d					
YNG	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	NA	0.10	0.04	0.03	<0.01
LEN2, d					
YNG	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	NA	0.60	0.87	0.16	<0.01
VW1, cm					
YNG	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	NA	0.02	0.45	0.14	0.28
VW2, cm					
YNG	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	NA	0.20	0.43	0.72	0.53
PUB					
YNG	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	NA	0.86	0.19	0.44	<0.01

[1]Model included generation, line, generation × line interaction and covariate effects.
[2]YNG = line selected for young age at puberty; OLD = line selected for old age at puberty.
[3]AP = age at puberty; PUBWT = weight at puberty; LEN1 = length of first estrus; LEN2 = length of second estrus; VW1 = vulva width at first estrus; VW2 = vulva width at second estrus; PUB= probability of reaching puberty; BWT = birth wight; WWT = weight at 22.3 d; LEA = loin eye area; BF = backfat depth; WT = weight at 178 d.

Table 2.4 Continued.

	Generation				
Trait	0	1	2	3	4
BWT, kg					
YNG	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	NA	0.22	0.29	<0.01	<0.01
WWT, kg					
YNG	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	NA	0.12	0.07	<0.01	<0.01
LEA, cm^2					
YNG	16.6 ± 0.18	17.2 ± 0.19	16.1 ± 0.2	15.9 ± 0.19	16.0 ± 0.19
OLD		17.7 ± 0.21	16.2 ± 0.2	16.3 ± 0.22	16.2 ± 0.20
P-Value	NA	<0.01	0.56	0.05	0.23
BF, cm					
YNG	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	NA	0.20	0.08	0.24	<0.01
WT, kg					
YNG	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	NA	0.05	<0.01	<0.01	0.75

[1]Model included generation, line, generation × line interaction and covariate effects.
[2]YNG = line selected for young age at puberty; OLD = line selected for old age at puberty.
[3]AP = age at puberty; PUBWT = weight at puberty; LEN1 = length of first estrus; LEN2 = length of second estrus; VW1 = vulva width at first estrus; VW2 = vulva width at second estrus; PUB= probability of reaching puberty; BWT = birth wight; WWT = weight at 22.3 d; LEA = loin eye area; BF = backfat depth; WT = weight at 178 d.

Table 2.5: Least squares means[1] by line[2] and generation for sow reproductive performance traits[3] in response to selection for age at puberty.

	Generation			
Trait	1	2	3	4
TNB				
YNG	11.09 ± 0.49	10.57 ± 0.44	11.83 ± 0.42	10.64 ± 0.42
OLD	11.47 ± 0.59	12.64 ± 0.54	11.27 ± 0.69	11.56 ± 0.63
P-Value	0.63	<0.01	0.49	0.23
LBW				
YNG	12.90 ± 0.26	12.41 ± 0.24	12.25 ± 0.23	12.16 ± 0.23
OLD	12.75 ± 0.32	12.60 ± 0.29	10.90 ± 0.37	11.19 ± 0.34
P-Value	0.72	0.62	<0.01	0.02
ABW				
YNG	1.17 ± 0.026	1.11 ± 0.023	1.09 ± 0.022	1.09 ± 0.022
OLD	1.16 ± 0.031	1.13 ± 0.029	1.00 ± 0.036	1.00 ± 0.033
P-Value	0.79	0.45	0.03	0.02
ABW CV, %				
YNG	18.05 ± 0.90	17.56 ± 0.82	18.37 ± 0.78	16.98 ± 0.79
OLD	14.98 ± 1.09	14.23 ± 1.00	17.03 ± 1.27	17.04 ± 1.15
P-Value	0.03	0.01	0.37	0.97
LWW				
YNG	47.22 ± 1.30	56.65 ± 1.18	57.29 ± 1.15	47.25 ± 1.15
OLD	46.06 ± 1.57	56.72 ± 1.46	50.38 ± 1.83	42.74 ± 1.66
P-Value	0.57	0.97	<0.01	0.03
AWW				
YNG	5.18 ± 0.14	6.40 ± 0.128	6.17 ± 0.124	5.15 ± 0.124
OLD	5.11 ± 0.17	6.13 ± 0.157	5.46 ± 0.198	4.66 ± 0.179
P-Value	0.76	0.2	<0.01	0.03

[1]Model included generation, line, generation × line interaction and covariate effects.
[2]YNG = line selected for young age at puberty; OLD = line selected for old age at puberty.
[3]TNB = total number born; LBW = litter birth weight; ABW = average birth weight; LWW = litter weaning weight; AWW = average weaning weight; LSW = litter size weaned.

Table 2.5 Continued.

	Generation			
Trait	1	2	3	4
AWW CV, %				
YNG	13.30 ± 0.94	15.26 ± 0.87	13.68 ± 0.84	13.75 ± 0.85
OLD	14.66 ± 1.15	18.16 ± 1.06	14.44 ± 1.33	15.26 ± 1.21
P-Value	0.36	0.04	0.63	0.31
LSW				
YNG	9.34 ± 0.48	8.19 ± 0.43	9.46 ± 0.42	8.82 ± 0.42
OLD	10.00 ± 0.58	9.86 ± 0.54	9.27 ± 0.68	9.67 ± 0.61
P-Value	0.38	0.02	0.81	0.26

[1]Model included generation, line, generation × line interaction and covariate effects.
[2]YNG = line selected for young age at puberty; OLD = line selected for old age at puberty.
[3]TNB = total number born; LBW = litter birth weight; ABW = average birth weight; LWW = litter weaning weight; AWW = average weaning weight; LSW = litter size weaned.

Table 2.6: Summary statistics and variance components[1] for puberty, growth, and compositional traits.

Trait	No.	Mean	Minimum	Maximum	σ_p^2	c^2	h^2	SE
Puberty								
Age at Puberty, d	1166	183	124	281	719	0.08	0.40	0.07
Probability of Puberty	1778	0.7	0	1	4.23	0.14	0.11	0.03
Puberty Weight, kg	1051	110.3	69.4	162.8	1268	0.03	0.39	0.08
Length of Estrus 1, d	1048	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	1051	38.4	25	59	22.4	0.05	0.36	0.08
Vulva Width 2	753	39.3	26	57	22.3	0.00	0.48	0.08
Growth								
Birth Wight, kg	4941	1.1	0.4	2.6	0.31	0.03	0.20	0.05
Weaning Weight, kg	3988	5.4	1.7	11.2	5.1	0.29	0.12	0.05
Loin Eye Area, cm^2	2095	16.9	9.8	24.7	0.48	0.02	0.42	0.06
Backfat, cm	2095	1.7	0.7	3.9	0.03	0.10	0.43	0.06
Weight at 178 d	2107	113.6	54.4	164.7	820	0.11	0.37	0.06

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

Table 2.7: Phenotypic and genetic correlations[1] between gilt puberty, growth and compositional traits.

Trait	AGEPUB	PUB	PUBWT	LEN1	LEN2	VW1	VW2	BWT	WWT	LEA	BF	WT
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 (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 (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 (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 (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 (WT)	−0.26	0.37	0.44	0.01	0.07	0.05	0.11	0.34	0.39	−0.03	−0.15	

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

2.6 Figures

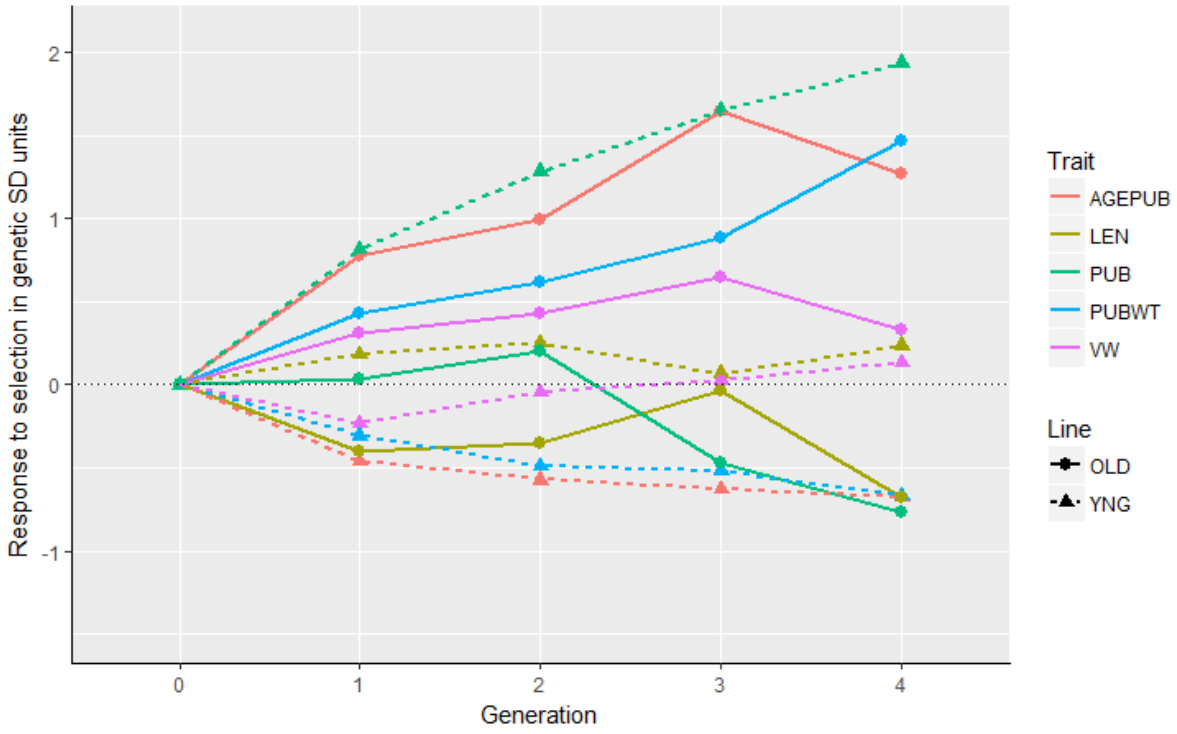

Figure 2.1: Direct and correlated response to selection on age at puberty and associated reproductive traits biased on average EBV. Average EBVs only include those gilts with phenotypes; OLD = old age at puberty line; YNG = young age at puberty line; AGEPUB = age at puberty; LEN = length of pubertal estrus; PUB = probability of reaching puberty (0 or 1); PUBWT = weight at puberty; VW1 = vulva width at pubertal estrus.

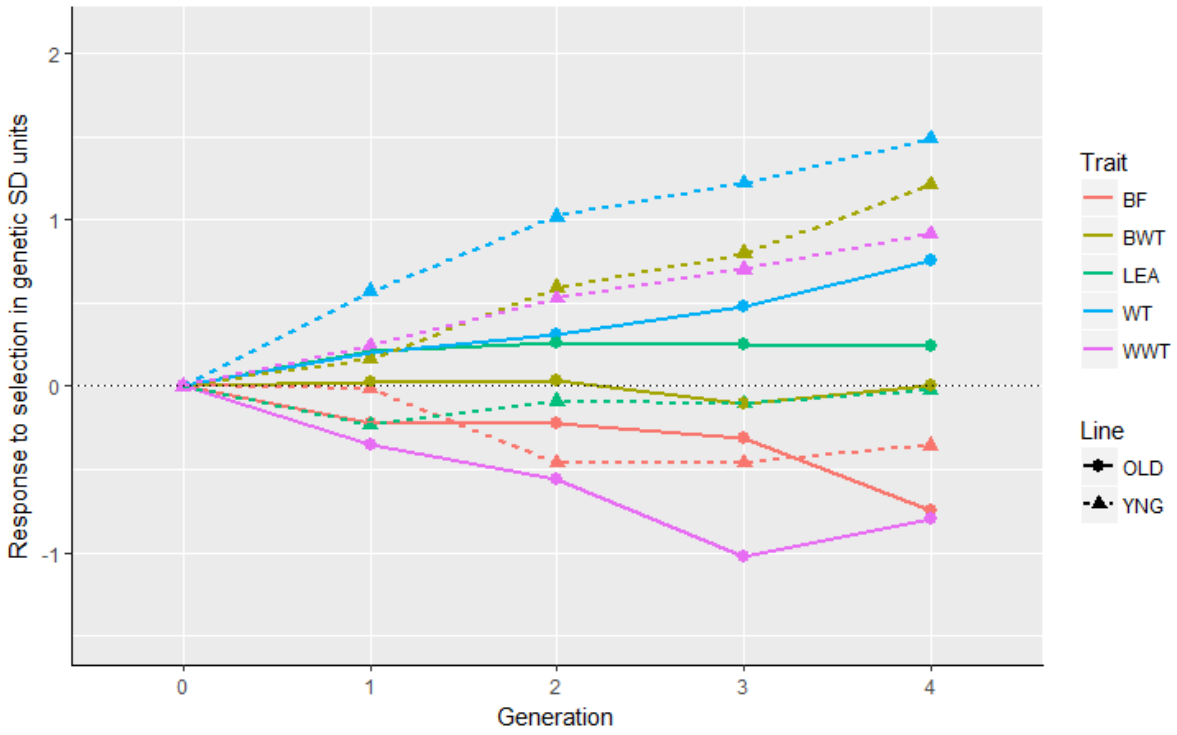

Figure 2.2: Direct and correlated response to selection on age at puberty and associated production traits biased on average EBV. Average EBVs only include those gilts with phenotypes; OLD = old age at puberty line; YNG = young age at puberty line; BF = backfat depth at 178 d; BWT = birth weight; LEA = loin eye area at 178 d; WT = body weight at 178 d; WWT = weaning weight at 22 d.

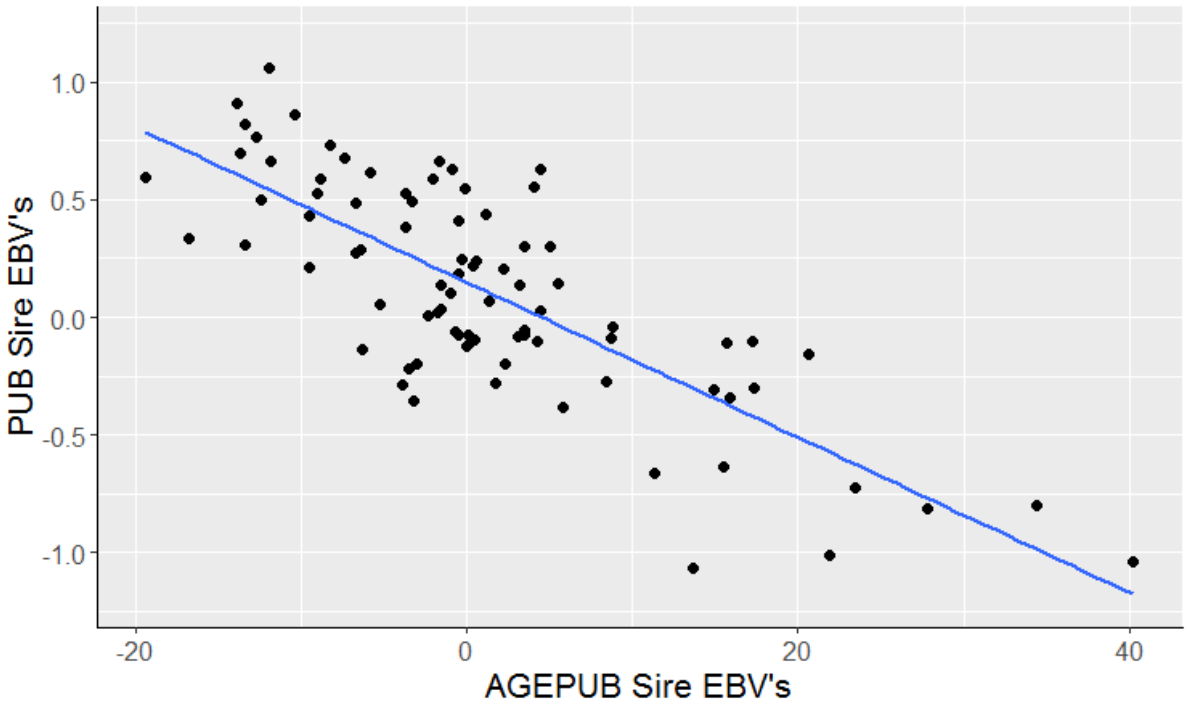

Figure 2.3: Correlation between sire estimated breeding values for age at puberty (AGEPUB) and the probability of reaching puberty by 220 d of age (PUB).

Chapter 3

Response to selection for age at puberty in female swine: male performance

3.1 Abstract

The objective was to examine the response to selection in boar characteristics from genetic lines selected for female age at puberty. Composite Landrace × Large White females were divergently selected for young age at puberty (YNG) and old age at puberty (OLD) across four generations. Age at puberty was defined as first observed standing reflex in the presence of a boar. In generation 4, YNG and OLD gilts obtained puberty at 163 and 183 d of age, respectively, and 85 and 50%, respectively, exhibited puberty. Boar data utilized was from generation 3 (n=35) and 4 (n=113). Animals were produced at the North Carolina Department of Agriculture Tidewater Research Station. Boars were group housed on partial slatted floors in environmentally controlled buildings. Sprinklers were manually activated when temperature reached 27°C. Growth and composition traits measured at 178 d of age included: backfat depth (BF), loin eye area (LEA) and ADG. Reproductive traits included: testis width (TW),

testis length (TL), testis volume (TV), ejaculate volume (VOL), number of sperm cells per ml (NO_CELL), progressive sperm motility (MOT), total sperm cells per ejaculate (TOT_CELL), projected semen doses per boar (DOSE), libido score (LIB) and testosterone concentration (TEST). Collection of testis traits and TEST were captured at 215 d (C1) and 293 d (C2) of age. All other reproductive traits were collected at C2 only. Semen collection was performed using parity two sows. Statistical analysis was performed in R using the *lm* and *lmer* functions. Fixed effects of generation, genetic line, collection period, inbreeding percentage (used as a covariate) and random effects of animal and two way interaction terms when ($P<0.05$). Genetic line did not influence ($P>0.05$) BF, LEA, VOL, NO_CELL, MOT, TOT_CELL or DOSE. Yet, interactions between genetic line and collection period favored ($P<0.05$) YNG boars for TW, TL, TV and TEST. Boars from YNG had greater ($P<0.05$) ADG and LIB when compared to OLD. Results suggest divergent selection for early puberty in females increased growth rate, libido, testicular development and testosterone concentration in boars.

3.2 Introduction

Improved sow reproductive efficiency is imperative for increased system performance within the swine industry. Age at puberty has been suggested as a potential selection candidate to achieve improved sow lifetime performance. A younger age at puberty has favorable associations with both 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. Before selection for decreased age at puberty is incorporated into breeding schemes, perhaps understanding the response on male reproductive performance and biology is needed.

Few studies in swine have examined the impact of selection for female reproductive perfor-

mance on correlated male performance. Correlations between male gonads and related female performance have been reported in sheep (Fossceco and Notter, 1995), cattle (van Melis et al., 2010) and mice (Eisen and Johnson, 1981) suggest genetic links between male and female reproduction traits exist. In swine, Johnson et al. (1994) reported hastened female puberty after 10 generations of selection for increased testes weight. Schinckel et al. (1983) and Toelle and Robison (1985a) also examined female reproductive characteristics in swine from genetic lines selected based on male traits. Yet no studies have evaluated the impact of selection for early puberty in swine on male characteristics. Hence the purpose of this study was to quantify the impact of selection for age at puberty in female swine on the phenotypic reproductive performance of their male counterparts. Analysis of phenotypic responses in growth, testes, semen quality, libido, and basal testosterone traits after four generations of divergent selection for age at puberty are reported.

3.3 Materials and methods

Experimental methods and protocols for this experiment were approved by the North Carolina State University Institutional Animal Care and Use Committee.

3.3.1 Animals

Composite Landrace $\times$ Large White boars (n=148) were used from a selection experiment for divergent age at puberty in gilts. Line development was previously reported in See et al. (2017). In short, divergent selection for four generations resulted in two genetic lines, young age at puberty (YNG) and old age at puberty (OLD). Boars observed in the present study were from generations three (n=35) and four (n=113). Animals were reared at the North Carolina Department of Agriculture Tidewater Research Station (Plymouth, NC). Boars were group

housed on partial slatted floors in an environmentally controlled building separate from females. Sprinklers were manually activated when temperatures reached 27°C. Animals were fed a corn and soybean meal based ration, ad libitum, formulated to meet or exceed NRC requirements (National Research Council, 2012).

Boars were at 178 d of age when body weight, backfat (BF) and loin muscle area (LEA) were measured. Average daily gian (ADG) was calculated as weight at 178 d of age divided by age. Composition traits were measured from a cross-sectional 10^{th} rib image obtained by using an Aloka 500V SSD ultrasound machine (Corometrics Medical Systems Inc., Wallingford, CT).

Male reproductive performance was measured at two age points. Collection point 1 (C1) and collection point 2 (C2) were recorded at 215 and 293 d of age, respectively. Repeated collections were recorded during generation four. Boars measured at C1 included all males available to be selected as sires for the next generation of the selection experiment. Boars evaluated at C2 included those males selected as sires. Collection of testis traits and testosterone (TEST) were captured at both C1 and C2. All other reproductive traits were collected at C2 only. Descriptive statistics of male traits are reported in Table 3.1.

Testis length (TL) and width (TW) of the right testes were measured using a caliper (Grand Rapids Industrial Products Inc., Wayland, MI). Paired testes volume (TV) was calculated as,

$$TV = \frac{4}{3}\pi \times (\frac{1}{2}TL) \times (\frac{1}{2}TW)^2 \times 2$$

as described by Young et al. (1986).

Semen samples were collected from YNG (n=35) and OLD (n=23) boars at C2. Semen was collected using the gloved hand technique with vinyl semen collection gloves (Minitube of America, Verona, WI) by a single technician. Boars were collected off of weaned sows in standing estrus. Boars who failed to have a successful collection were allowed a second attempt with a different weaned sow in standing estrus. During collection semen was filtered using the Blue Bag (Minitube of America, Verona, WI) to remove the gel fraction after which only the

sperm rich fraction was retained. Ejaculates were weighed to calculate semen volume (VOL) and extended to a 1:2 ratio using B.T.S® extender (Mini-tube of America, Verona, WI). Extended samples were allowed to cool to room temperature before transfer to the semen processing lab.

Progressive sperm motility (MOT) and number of cells (NO_CELL) per ml were measured using computer assisted semen analysis system (CASA, SpermVision®, Minitube of America, Verona, WI). During overnight storage, samples were stored in a climate controlled semen storage unit keeping a constant temperature of 18°C. Prior to analysis, extended semen samples were slowly heated to 37°C in a water bath over 30 min. Software settings used were those recommended by the manufacturer for analysis of boar semen. Prior to analyses, one milliliter of extended ejaculate was placed into a Leja slide (Minitube of America, Verona, WI) and analyzed on an Olympus (BX41) equipped with a heated stage maintained at 37°C. Five different fields were analyzed.

Sperm concentration was used to calculate the total number of spermatozoa per ejaculate (TOT_CELL). The estimated number of semen doses (DOSE) produced per boar were calculated in accordance with recommendations from Rozeboom (2000). The number of doses produced from each ejaculate was found using the following equation,

$$DOSE = ((VOL \times MOT \times SpermConcentration))/(2 \times 10^6)$$

Ejaculates with <62% progressive motility were considered not viable and resulted in zero doses produced. Boars whom failed to mount the weaned sow for collection also resulted in zero doses.

The proportion of abnormal heads (HEAD), tails (TAIL), and acrosomes (ACRO) were observed and calculated from all extended ejaculates. One milliliter of extended semen used for motility analyses was placed in a test tube (12 × 75 mm) and 100 µl of 10% formalin solution was added. All microscopic analyses were conducted with a phase contrast microscope (ZeissB071, Berlin, West Germany). Spermatozoa were initially located using the 25 × objective.

Once located, a drop of immersion oil (Fisher Scientific, Atlanta, GA) was placed on the slide and the 100× oil immersion objective was used to visualize and evaluate sperm cells. A random sample of 100 spermatozoa was counted and the head, tail and acrosome classification schemes were based on the evaluation guidelines of Pursel et al. (1972).

Libido was visually evaluated during semen collection. Libido evaluation was performed using a 15 point scoring system adapted from Ren et al. (2009). A single observer recorded libido behaviors. Libido score (LIB) was calculated as the sum of behavioral traits defined in Table 3.2.

Blood samples were collected at both C1 and C2. Ten mL of blood was collected from each animal (n=121) via the jugular vein with 10-mL serum separator vacutainer tubes (Becton Dickinson and Company, Franklin Lakes, NJ). Post-collection, samples were allowed to clot for 15 minutes at room temperature before being placed on ice for transport. Following 12 h storage at -20°C, samples were centrifuged at 4°C for 15 minutes at 1,000 × g. Serum samples were poured off and split into two microcentrifuge tubes and stored at -80°C.

Serum samples were assayed for Testosterone concentration (TEST). Testosterone concentration was measured using double antibody testosterone radioimmunoassay kits with 125I-marked Testosterone (MP Biomedicals LLC, Santa Ana, CA) in accordance with instructions of the manufacturer. Intra- and interassay CV for TEST assays were 8.1 and 9.2%, respectively.

3.3.2 Statistical methods

Data were analyzed in R using the *lmer* function from the lme4 package (Bates et al., 2014) for models with random effects and the *lm* function, from base R, for fixed effect models. Effect of genetic line was analyzed for all traits using the following models:

$$ModelI : Y_{ijkl} = \mu + L_i + G_j + I_k + \beta(u_l - \bar{u}) + e_{ijkl}$$

$$ModelII : Y_{ijklm} = \mu + L_i + G_j + C_k + (L \times C)_{ik} + (L \times G)_{ij} + I_l + A_m + e_{ijklm}$$

$$ModelIII : Y_{ijk} = \mu + L_i + G_j + I_k + e_{ijk}$$

$$ModelIV : Y_{ijklm} = \mu + L_i + G_j + C_k + (L \times C)_{ik} + I_l + A_m + e_{ijklm}$$

Where L = genetic line, G = generation, u = weight at 178 d, C = collection group, I = inbreeding percentage, and A = random effect of boar. Model I was used to test the effects of BF, LEA and ADG. Model II was used to determine differences in TL, TW and TV. Model III was used to analyze sperm production traits and differences in LIB. Model IV was used to evaluate levels of TEST between YNG and OLD boars. In Model II age or weight at collection of testes measurements was not included as a covariate. Yet collection group was included in Model II which accounted for age differences between C1 and C2 as age differences could influence testes development (Schinckel et al., 1983; Toelle and Robison, 1985a). Genetic line $\times$ generation and genetic line $\times$ collection effects were tested in all models when applicable yet removed if P>0.05.

Inbreeding coefficients for all animals in the pedigree were calculated using the INBUPGF90 program (Aguilar and Misztal, 2012). The pedigree used was traced back 5 generations and consisted of 5,105 individuals, 420 dams, and 105 sires. INBUPGF90 uses a recursive algorithm assuming nonzero inbreeding values for known parents. For the analysis inbreeding coefficients for only boars utilized in the current study were retained.

Least squares means were estimated using R. Estimated means from fixed effect models were produced using the *lsmeans* function from the LSMeans package (Lenth, 2016). Least squares means from mixed effect models were produced using the *lsmeanLT* function from the lmerTest package (Kuznetsova et al., 2016), utilizing Satterthwaite's approximation in the denominator degrees of freedom.

Principal components analysis were conducted to determine multivariate population differences between YNG and OLD lines in R. Principal components were calculated using the

princomp function from base R. Boars (n=39) with complete records were used. All variates (BF, LEA, ADG, TW, TL, TV, VOL, NO_CELL, TOT_CELL, MOT, DOSE, HEAD, TAIL, ACRO and TEST) were centered and scaled prior to the analysis.

3.4 Results

Divergent selection for age at puberty resulted in 85 and 50% of YNG and OLD gilts, respectively, obtaining puberty by 220 d of age in generation four. In YNG and OLD, age at puberty in generation four was 163 and 183 d of age, respectively. Average rate of inbreeding due to selection was 1.6 and 3.7% for YNG and 2.8 and 4.7% for OLD, in generations 3 and 4, respectively.

Least squares means estimates for growth and compositional traits are represented in Table 3. Least squares estimates for OLD and YNG lines were similar (P>0.05) for BF (1.72 vs 1.69 cm, respectively) and LEA (16.83 vs 16.82 cm^2, respectively). In contrast, ADG was lower (P<0.05) for OLD when compared to YNG (0.696 and 0.720 kg/d, respectively).

Phenotypic differences between genetic lines for semen quality traits and LIB are shown in Table 3.4. No differences (P>0.05) were found between OLD and YNG genetic lines for VOL (185 vs 211 ml, respectively), TOT_CELL (57.6 vs 54.4 billion, respectively), DOSE (17.5 vs 19.3, respectively), HEAD (6.51 vs 6.42%, respectively), and TAIL (13.2 vs 12.8%, respectively). Contrasts between OLD and YNG lines for NO_CELL tended (P=0.13) to favor OLD boars (191 vs. 160 cells/ml, respectively). Numerically, MOT tended (P=0.17) to be higher for OLD boars when compared to YNG (85.5 vs. 80.5, respectively). The percentage of abnormal acrosomes was numerically higher for OLD boars in comparison to YNG (2.22 vs. 1.72%, respectively). In contrast, estimates for ACRO favored YNG boars. Composite libido score was lower (P<0.05) for OLD when compared to YNG (7.4 vs 8.9, respectively).

Least squares means for genetic line × collection period interactions (P<0.05) for TV and TEST are presented in Figure 3.1 and Figure 3.2, respectively. Testicle volume was greatest for YNG boars at C2 (546 cm^3). In contrast, TV was lowest OLD boars at C1 (240 cm^3). Across genetic lines, TV increased (P<0.01) from C1 to C2. Interaction effects for YNG and OLD at C1 were significant (P<0.01). Estimates showed YNG boars had greater (p<0.01) TV at C1 when compared to OLD (358.1 and 239.8 cm^3, respectively) yet this difference deteriorated (P>0.05) at C2 (546.8 and 516.0 cm^3, respectively). These results suggest that earlier in life animals from YNG have a larger TV than OLD, yet as animals develop this relationship doesn't hold. Similarly, there was an interaction (P<0.05) between genetic line × collection period for TEST. Testosterone concentration was greatest for YNG boars at C2 (9.5 ng/ml). In contrast, TEST was lowest for OLD boars at C1 (2.2 ng/ml). Within YNG boars, TEST increased (P<0.01) from C1 to C2 (2.3 to 4.2 ng/ml, respectively). Yet TEST levels in OLD boars did not differ (P>0.05) between C1 and C2 (2.18 and 2.63 ng/ml, respectively). Pairwise contrasts between simple interaction effect for genetic line at C2 when modeling TEST were significant (P<0.05) and favored YNG boars. Contrast estimates of least squares means produced suggest that YNG boars had 1.6 ng/ml greater TEST, compared to OLD boars at C2. These contrast estimates suggest that during C1 genetic lines do not differ in TEST levels, yet, at C2 YNG boars have a higher TEST compared to OLD boars at C2.

Pearson correlation coefficients between all traits measures are presented in Table 3.5. A covariate of individual inbreeding percentage (INB) was included in all models as an experimental design term, thus, it was also included in the correlation matrix. Inbreeding percentage showed unfavorable correlation (P<0.01) with LEA, ADG, and ACRO (-0.22, -0.29 and -0.39, respectively). In contrast, INB was favorably correlated (P<0.05) with TAIL (0.27). Growth and compositional traits showed moderated to strong favorable correlations (P<0.01). Backfat was positively correlated (P<0.05) with TOT_CELL (0.26). Average daily gain was estimated to

have a correlation (P<0.05) with TOT_CELL and MOT (0.37 and -0.30, respectively). Testis measurement traits were correlated (P<0.05) with several sperm morphology traits. Testis width was correlated (P<0.05) with HEAD and ACRO (0.29 and -0.34, respectively). Similarly, TV was associated (P<0.05) with HEAD (0.30). Testis length, however, showed a strong favorable correlation (P<0.01) with ACRO (0.43). Testis length was correlated (P<0.01) with TEST (-0.38). Libido score was positively related (P<0.05) with TL, TV, and DOSE (0.38, 0.28, and 0.71, respectively). Few relationships were found among sperm morphology traits. However, ACRO was unfavorably related (P<0.05) to MOT and TAIL (-0.50 and -0.27, respectively).

Principal component analysis yielded 18 components, where the first six cumulatively explained 75% of the variance. Multivariate analysis was used to investigate clustering of raw phenotypic variation across OLD and YNG boars for all traits measured in the current study. Phenotypic variation captured by the first two principle components is graphically displayed in Figure 3.3. After the effect of genetic line is overlaid upon the records utilized, no clear clustering structure formed.

3.5 Discussion

Few studies have comprehensively evaluated reproductive characteristics of boars from different genetic lines. Borg et al. (1993) reported differences in testes volume, ejaculate parameters and basal hormone levels between Durocs and Chinese breeds of boars. The authors concluded that large differences exist between Chinese and U.S. breeds. American breeds had larger testes, yet, produced a smaller ejaculate volume. The breeds further differed in follicle stimulating hormone (FSH), which plays a major role in the early development of the testis. Johnson et al. (1994) selected for increased predicted testes weight at 150 d of age for 10 generations. Response to selection per generation was a 19 g increases in testes weight. Following selection the impact of

selection on female reproductive measures, age at puberty and ovulation rate, were quantified between the selection and control lines. No significant differences were detected between lines for age at puberty, yet females from the increased predicted testis weight line were pubertal 6 d earlier than controls. Females from the testis weight line had greater ovulation rate by 0.73 eggs when compared to the control genetic line. Collectively, results suggest variation exists in male reproductive performance between genetic lines and selection for reproductive performance in one gender can impact traits in the other gender.

Hormone production from the anterior pituitary is critical for reproductive capabilities in both males and females. In females, FSH is required for the recruitment and early development of ovarian follicles. Following follicle selection, Luteinizing hormone (LH) is responsible for dominant follicle development, ovulation and maintenance of the corpora lutea (Knox, 2005). In males, LH is responsible for testosterone production via a feedback regulation loop between leydig cells and the anterior pituitary (Aldrich et al., 1982). Testosterone acts upon the hypothalamus to regulate GnRH pulse frequency, releasing LH which stimulates the Leydig cells completing the feedback loop (van Straaten and Wensing, 1978). Follicle stimulating hormone acts upon Sertoli cells and early testicular formation which aids in early spermatogenesis. Testosterone is required for complete maturation of sperm cells (Griswold, 1998). In both sexes, LH and FSH are responsible for the onset of puberty, thus, selection for age at puberty in either sex could affect hormone production and ultimately reproductive performance. Divergent selection for age at puberty would be expected to change developmental differences in hormone production and ultimately reproductive phenotypes stimulated by testosterone and FSH. In the current study, divergent selection for age at puberty in female swine resulted in phenotypic differentiation between lines in TEST. As hypothesized, developmental differences were observed between YNG and OLD boars for TEST. At C1 TEST didn't differ ($P>0.05$) between lines yet at C2 TEST was greater ($P<0.05$) for YNG boars (Figure 3.2). Increases in TEST later in life

could be driven by a greater prevalence of Leydig cells in YNG boars. Walker et al. (2004) evaluated the effect of divergent selection for testosterone production on testes morphology. The authors reported Leydig cell density was greater in the high TEST line increasing the capacity for testosterone production, despite testes size being smaller. Quantification of Leydig cells in the current study was not included.

Testis length was moderately correlated with TEST suggesting a positive relationship between testis size and TEST. In agreement, Lubritz et al. (1991) reported a positive genetic correlation between TV and TEST (0.31). Developmental differences in TV between YNG and OLD boars resulted a difference 118 cm^3, favoring the YNG boars at 215 d of age. Yet, this difference was no longer present when boars were 293 d of age. Taken together, results suggest that selection for decreased age at puberty in gilts accelerates testes development in boars but does not increase mature testis size. Since the underlying mechanisms are the same for both boars and gilts, selection for age at puberty should effect age at puberty in both sexes (Schinckel et al., 1983). Since puberty attainment is difficult to measure in boars, testes size could be used as a measure of reproductive activity. Sertoli cell development stops after pubertal attainment suggesting rapid growth of the testes slows after puberty (Petersen and Söder, 2006). Johnson et al. (1994) selected for increased predicted testes weight in swine and noted a difference in age at puberty, yet, this result was not statistically different. Perhaps, a greater response to selection for male and female reproductive performance would occur if selection was practiced in females. Age at puberty has been reported to have a heritability of 0.37 (Rothschild and Ruvinsky, 2001) while the heritability of testes volume at 168 d, adjusted for age is considerably lower, 0.28 (Toelle et al., 1984). These results suggest that selection for decreased age at puberty in gilts would result in a more rapid response than selection in boars if the genetic correlation between the two sexes is high.

Genetic links have been reported between semen traits and testis size. Huang and Johnson

(1996) evaluated semen quality on a group of boars whom were selected for increased testis size. Selection effectively increased testis size, ejaculate volume and sperm cells produced. Yet differences between genetic lines for percentage of abnormal sperm did not differ. Similarly, Walker et al. (2004) evaluated sperm quality traits on boars divergently selected for testosterone production. The authors reported at 211 d of age boars from the high and low testosterone production lines differed in paired testes weight, favoring low testosterone boars. The same authors reported a difference in epididymal weight between genetic lines favoring high testosterone boars. Given differences in paired testes and epididymal size between boars selected for high and low testosterone semen traits did not differ (Walker et al., 2004). Taken together, results add complexity between the genetic relationships between physiological factors of the boar affecting semen quality and production. Despite differences and associations previously reported between semen quality and testis size, semen quality traits were not found to differ between genetic lines in the present study. Ejaculate volume and motility were found to numerically favor OLD while percentages of abnormal sperm numerically favored YNG. Yet considerable variation was observed between semen traits suggesting other factors contribute to the differentiation in semen quality traits besides genetic line. Hence further work is needed to help reduce variation between semen quality measurements to understand the potential differences between selected lines.

Libido is important in semen collection and impregnation, being impacted by multiple environmental and genetic factors (Hemsworth and Tilbrook, 2007). Genetic line impacted LIB. Perhaps differences in libido between YNG and OLD were due to the accelerated development of the testes of boars within YNG. Libido was not associated with TEST. In contrast, Ren et al. (2009) reported LIB was positively correlated with TEST. The same authors suggested that the regulation hormones estradiol or its precursor, testosterone, are associated with libido levels in boars. However, a prior literature report found no associations between TEST and LIB (Louis

et al., 1994). Other regulatory hormones, including prostaglandin and oestrodiol-17β, have been reported to be associated with LIB (Louis et al., 1994; Estienne et al., 2007). Collectively, results suggest further investigation is needed to determine if cellular structure or acceleration of sexual maturation effects libido in boars.

Selection for age at puberty in female swine effected phenotypic characteristics in related males. Despite differences between genetic lines in testis size, TEST and LIB, principal component analysis suggests that divergent selection for age at puberty resulted in minimal population divergence in male animals. Phenotypic change between average daily gain, backfat and loin eye area can be expected. Selection did not result in a correlated response in semen quality traits. Increases in abnormal or lowly motile sperm are not expected to result from increase age at puberty in related females. However in this experiment, males differed in testes size earlier in life and testosterone concentration later in life. Selection for decreased age at puberty could result in increased libido levels in related males. Perhaps more generations of selection are needed to develop physiological changes in semen traits. Further work is needed to determine the biological drivers behind increases in testis size and testosterone levels between boars related to gilts divergently selected for age at puberty.

3.6 Tables

Table 3.1: Descriptive statistics and number of observations for growth, composition and reproductive traits.

Trait	Animals	Obs.	Mean	Minimum	Maximum	SD
Growth & Composition						
Backfat, cm	181	181	1.72	0.99	2.84	0.38
Loin muscle area, cm^2	181	181	16.8	11.0	22.9	2.15
Average daily gain, kg	181	181	0.71	0.46	0.88	0.07
Reproduction						
Testis volume, cm^3	149	192	423	209	848	155
Testis length, cm	149	192	12.5	8	18	2.3
Testis width, cm	149	192	5.8	4.5	8.0	0.74
Ejaculate volume, ml	58	58	201	80	412	71.6
No. cells, /ml	58	58	172	56	375	71.8
Total cells, billions	58	58	55.6	18	129	19.2
Progressive motility, %	58	58	82.5	41	96	13.8
Dose	58	58	18.30	0	60	13.7
Abnormal heads, %	58	58	6.46	1	12	2.9
Abnormal tails, %	58	58	12.9	0	48	10.6
Abnormal acrosomes, %	58	58	1.95	0	8	2.1
Libido score	79	79	8.13	1	13	3.3
Testosterone, ng/ml	105	131	3.20	0.3	11.3	2.3

Table 3.2: Libido scoring system adapted from Ren et al. (2009).

Sexual behaviour			Scores	
Excitability on the way to the semen collection pen		Poor 0	Intermediate 1	High 2
Uttering short series of grunts		No 0		Yes 1
Champing of jaws producing saliva		No 0		Yes 1
Sniffing anal-genital region or head of dummy sow		No 0		Yes 1
Nudging or nosing flanks of the dummy sow		No 0		Yes 1
Mounting of dummy sow		No 0		Yes 1
Trainers impression on the libido level of measured boar		Poor 0	Intermediate 1	High 2
Times				
Reaction time	>176 Sec. 0	>60 Sec. 1	<60 Sec. 2	<35 Sec. 3
Duration of ejaculation	<165 Sec. 0	<228 Sec. 1	>228 Sec. 2	>283 Sec. 3

Table 3.3: Least squares means for growth and compositional traits with associated P-values for differences between young and old age at puberty lines.

	Young age at puberty		Old age at puberty		
Trait	Estimate	SE	Estimate	SE	P-value
Backfat depth, cm	1.69	0.03	1.72	0.04	0.70
Loin muscle area, cm^2	16.82	0.16	16.83	0.20	0.98
Average daily gain, kg	0.720	0.01	0.696	0.01	0.01

Table 3.4: Least squares means for semen quality and libido traits with associated P-values for differences between young and old age at puberty lines.

	Young age at puberty		Old age at puberty		
Trait	Estimate	SE	Estimate	SE	P-value
Ejaculate volume, ml	211	12.6	185	15.7	0.22
No. cells, /ml	160	12	191	15	0.13
Total cells, billions	54.4	3.36	57.6	4.20	0.57
Progressive motility, %	80.5	2.15	85.5	2.68	0.17
Dose	19.3	2.09	17.5	2.38	0.56
Abnormal heads, %	6.42	0.52	6.51	0.65	0.91
Abnormal tails, %	12.8	1.72	13.2	2.12	0.88
Abnormal acrosomes, %	1.72	0.23	2.22	0.28	0.19
Libido score	8.86	0.48	7.40	0.54	0.05

Table 3.5: Correlations between male growth, composition, and reproductive traits[1].

Trait	INB	BF	LEA	ADG	TW	TL	TV	VOL	NO_CELL	TOT_CELL	MOT	DOSE	HEAD	TAIL	ACRO	LIB
BF	−0.11															
LEA	−0.22**	0.21**														
ADG	−0.29**	0.33**	0.60**													
TW	0.02	0.21	0.11	0.09												
TL	−0.19	−0.18	0.24*	0.31**	−0.05											
TV	−0.06	0.12	0.20	0.22	0.90**	0.38**										
VOL	0.08	0.17	−0.23	0.08	0.23	−0.05	0.19									
NO_CELL	−0.06	0.07	0.18	−0.02	0.08	−0.20	0.01	−0.37**								
TOT_CELL	−0.19	0.26*	0.06	0.37**	0.17	0.08	0.18	0.39**	0.34**							
MOT	0.17	−0.19	−0.06	−0.30*	0.21	−0.32*	0.05	−0.30*	0.41**	0.03						
DOSE	−0.05	0.05	0.07	0.24*	0.11	0.27*	0.22	0.28*	0.44**	0.96**	0.28*					
HEAD	−0.24	0.10	0.02	0.07	0.29*	0.10	0.30*	0.15	−0.09	0.08	0.02	0.09				
TAIL	0.27*	0.23	−0.14	−0.01	0.24	−0.28*	0.12	0.04	−0.10	−0.11	−0.06	−0.17	0.06			
ACRO	−0.39**	−0.05	0.14	0.26	−0.34*	0.43**	−0.14	−0.06	−0.21	−0.02	−0.50**	−0.12	0.08	−0.27*		
LIB	−0.03	−0.11	0.09	0.18	0.11	0.38**	0.28*	0.20	−0.11	0.06	−0.17	0.71**	−0.01	−0.32*	0.05	
TEST	−0.02	0.23	0.01	−0.03	0.19	−0.38**	0.02	−0.03	0.16	0.12	−0.14	−0.10	0.05	0.18	−0.20	−0.03

** = $P < 0.01$; * = $P < 0.05$.

[1]INB = inbreeding percentage; BF = backfat depth; LEA = loin muscle area; ADG = average daily gain; TW = testis width; TL = testis length; TV = testes volume; NO_CELL = number of cells per ml of ejaculate; TOT_CELL = total cells per ejaculate; MOT = progressive motility; DOSE = predicted doses produced; HEAD = percent of abnormal heads; TAIL = percent of abnormal tails; ACRO = percent of abnormal acrosomes; TEST = testosterone concentration; LIB = libido score.

3.7 Figures

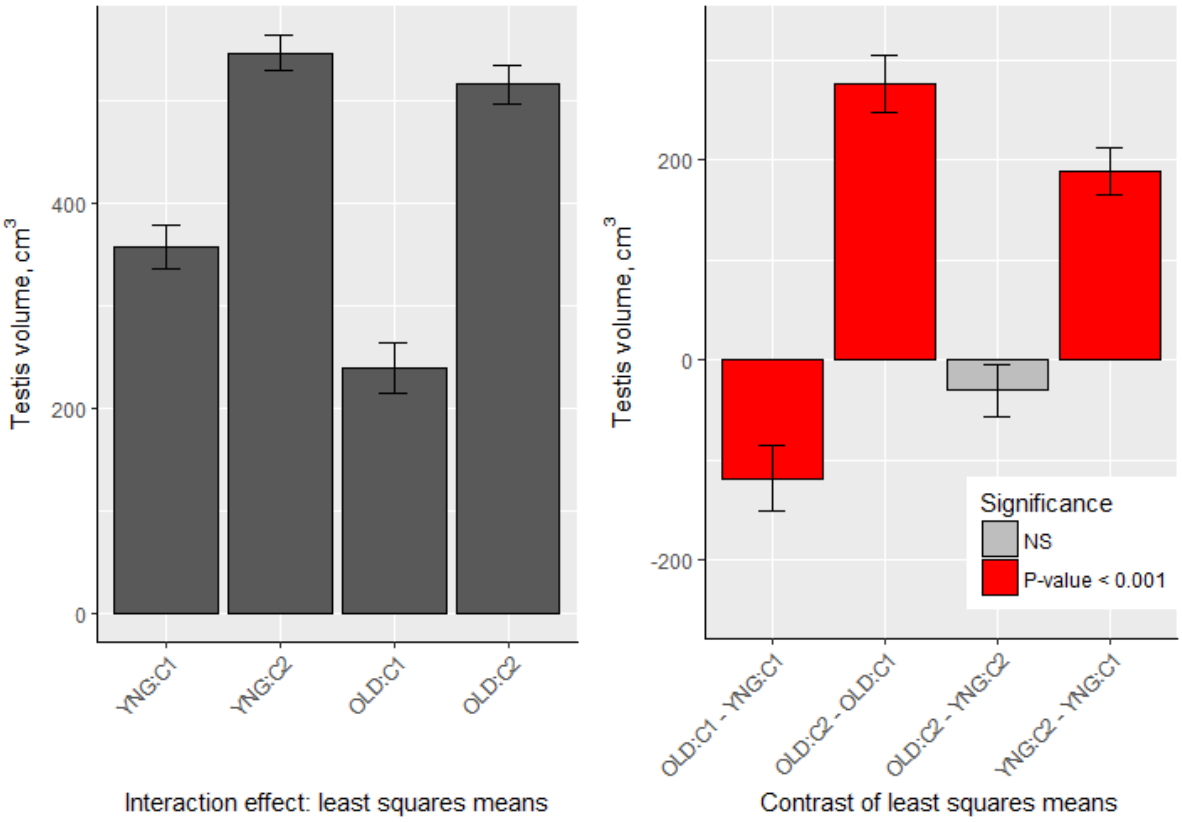

Figure 3.1: Least squares means estimates for simple effects of genetic line (young age at puberty = YNG, old age at puberty = OLD) $\times$ collection period (C1 and C2) interaction effect on testis volume.

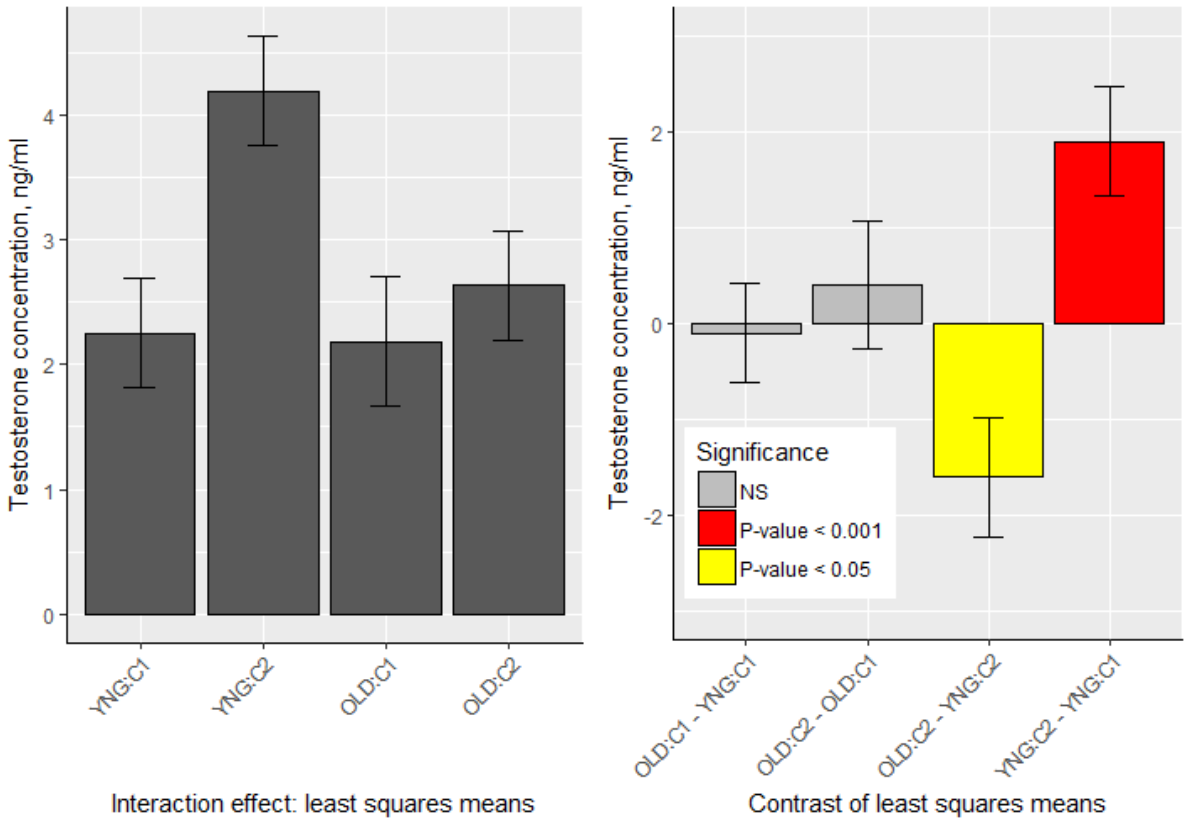

Figure 3.2: Least squares means estimates for simple effects of genetic line (young age at puberty = YNG, old age at puberty = OLD) $\times$ collection period (C1 and C2) interaction effect on testosterone concentration.

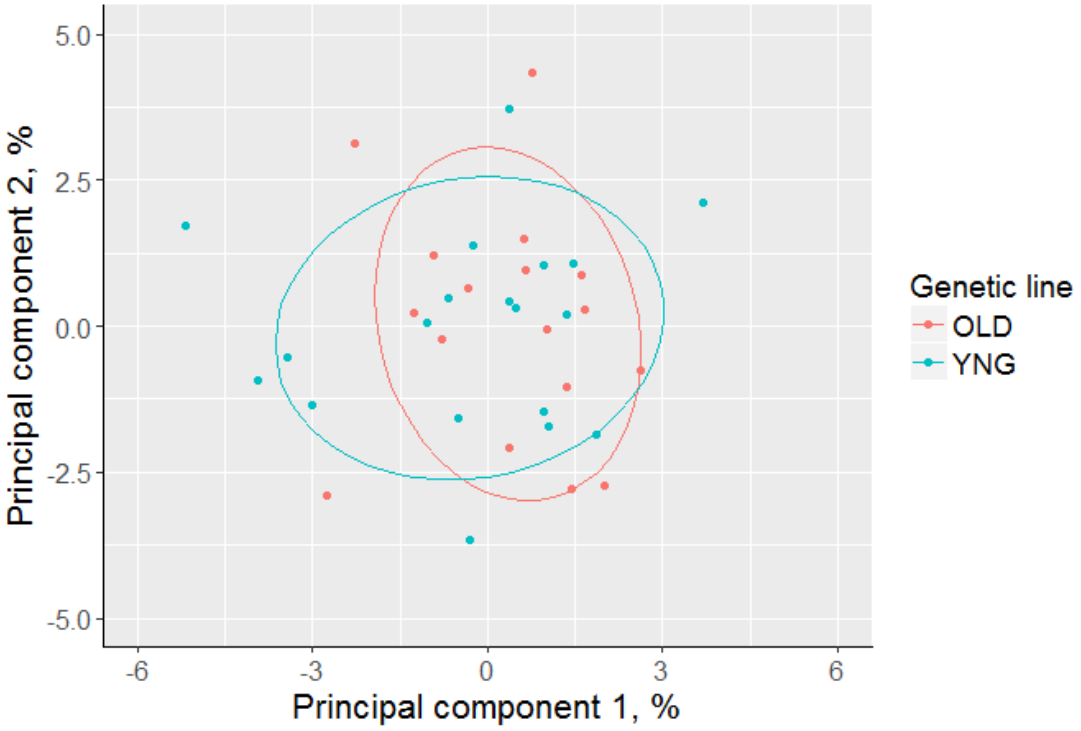

Figure 3.3: Multivariate boar trends associated with principal components 1 and 2, overlaid with the effect of either Young Age at Puberty (YNG) or Old Age at Puberty (OLD) genetic line.

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Appendix

Appendix A

Supplemental tables and figures

A.1 Tables

Table A.1: Standard errors (SE) assocaited with reported common litter effects by trait.

Trait	SE
Age at puberty (AGEPUB)	0.029
Probability of puberty (PUB)	0.034
Puberty weight (PUBWT)	0.031
Length of pubertal estrus (LEN1)	0.000
Length of second estrus (LEN2)	0.037
Pubertal vulva width (VW1)	0.032
Second estrus vulva width (VW2)	0.000
Birth weight (BWT)	0.025
Weaning weight (WWT)	0.025
Loin muscle area (LEA)	0.017
Backfat depth (BF)	0.022
Weight at 178 d (WT)	0.022

Table A.2: Individual heritability estimates for all traits[1] from both univarite and bivariate models.

	Trait											
Second Variate	AGEPUB	PUB	PUBWT	LEN1	LEN2	VW1	VW2	BWT	WWT	LEA	BF	WT
Univariate	0.41	0.06	0.40	0.19	0.17	0.36	0.48	0.20	0.12	0.41	0.50	0.42
AGEPUB			0.40	0.18	0.16	0.37	0.49	0.20	0.10	0.42	0.50	0.39
PUB	0.34		0.41	0.19	0.17	0.37	0.48	0.21	0.11	0.42	0.42	0.31
PUBWT	0.47	0.12		0.18	0.16	0.28	0.49	0.21	0.12	0.42	0.41	0.39
LEN1	0.41	0.11	0.39		0.16	0.36	0.48	0.19	0.12	0.44	0.41	0.38
LEN2	0.40	0.11	0.38	0.18		0.36	0.49	0.21	0.12	0.41	0.42	0.38
VW1	0.40	0.11	0.39	0.19	0.17		0.47	0.21	0.12	0.44	0.43	0.39
VW2	0.40	0.11	0.41	0.18	0.17	0.41		0.21	0.11	0.41	0.42	0.38
BWT	0.39	0.11	0.36	0.20	0.17	0.37	0.49		0.12	0.44	0.42	0.37
WWT	0.39	0.11	0.38	0.19	0.17	0.36	0.47	0.21		0.44	0.43	0.38
LEA	0.40	0.11	0.40	0.19	0.17	0.39	0.48	0.20	0.12		0.42	0.33
BF	0.40	0.12	0.39	0.19	0.17	0.38	0.49	0.20	0.12	0.41		0.34
WT	0.43	0.13	0.33	0.18	0.18	0.36	0.48	0.21	0.12	0.41	0.43	
Average	0.40	0.11	0.39	0.19	0.17	0.36	0.48	0.20	0.12	0.42	0.43	0.37
SD	0.03	0.01	0.01	0.01	0.01	0.03	0.01	0.01	0.01	0.01	0.03	0.03
CV, %	7.16	6.66	5.95	3.35	2.37	8.68	1.51	3.32	4.66	3.08	7.34	8.52

[1]AGEPUB = age at puberty; PUB = probability of reaching puberty; PUBWT = puberty weight; LEN1 = length of pubertal estrus; LEN2 = length of second estrus; VW1 = pubertal vulva width; VW1 = vulva width at second estrus; BWT = birth weight; WWT = weaning weight; LEA = loin muscle area; BF = backfat depth; WT = weight at 178 d of age.

Table A.3: Genetic[1] and phenotypic[2] correlation errors for reproduction, growth and composition traits[3].

	AGEPUB	PUBWT	LEN1	LEN2	VW1	VW2	PUB	BWT	WWT	LEA	BF	WT
AGEPUB		0.053	0.180	0.198	0.149	0.143	NE[4]	0.167	0.216	0.130	0.110	0.110
PUBWT	0.014		0.180	0.208	0.167	0.180	0.213	0.169	0.214	0.140	0.142	0.139
LEN1	0.038	0.035		0.190	0.186	0.189	0.312	0.205	0.242	0.159	0.172	0.176
LEN2	0.047	0.042	0.035		0.203	0.192	0.326	0.219	0.261	0.191	0.191	0.197
VW1	0.037	0.035	0.034	0.038		0.034	0.278	0.179	0.219	0.119	0.138	0.155
VW2	0.048	0.043	0.039	0.038	0.025		0.261	0.165	0.196	0.129	0.136	0.139
PUB	NE	0.041	0.036	0.038	0.042	0.045		0.296	0.378	0.241	0.207	0.182
BWT	0.035	0.032	0.033	0.037	0.036	0.039	0.031		0.098	0.152	0.136	0.158
WWT	0.034	0.033	0.032	0.036	0.035	0.038	0.028	0.016		0.190	0.191	0.169
LEA	0.035	0.037	0.034	0.040	0.036	0.042	0.034	0.030	0.029		0.110	0.141
BF	0.033	0.035	0.034	0.038	0.036	0.041	0.033	0.029	0.029	0.028		0.140
WT	0.035	0.031	0.036	0.041	0.038	0.043	0.030	0.029	0.026	0.038	0.038	

[1]Genetic correlation errors above the diagonal.
[2]Phenotypic correlation errors below the diagonal.
[3]AGEPUB = age at puberty; PUB = probability of reaching puberty; PUBWT = puberty weight; LEN1 = length of pubertal estrus; LEN2 = length of second estrus; VW1 = pubertal vulva width; VW1 = vulva width at second estrus; BWT = birth weight; WWT = weaning weight; LEA = loin muscle area; BF = backfat depth; WT = weight at 178 d of age.
[4]NE = not estimatable.

A.2 Figures

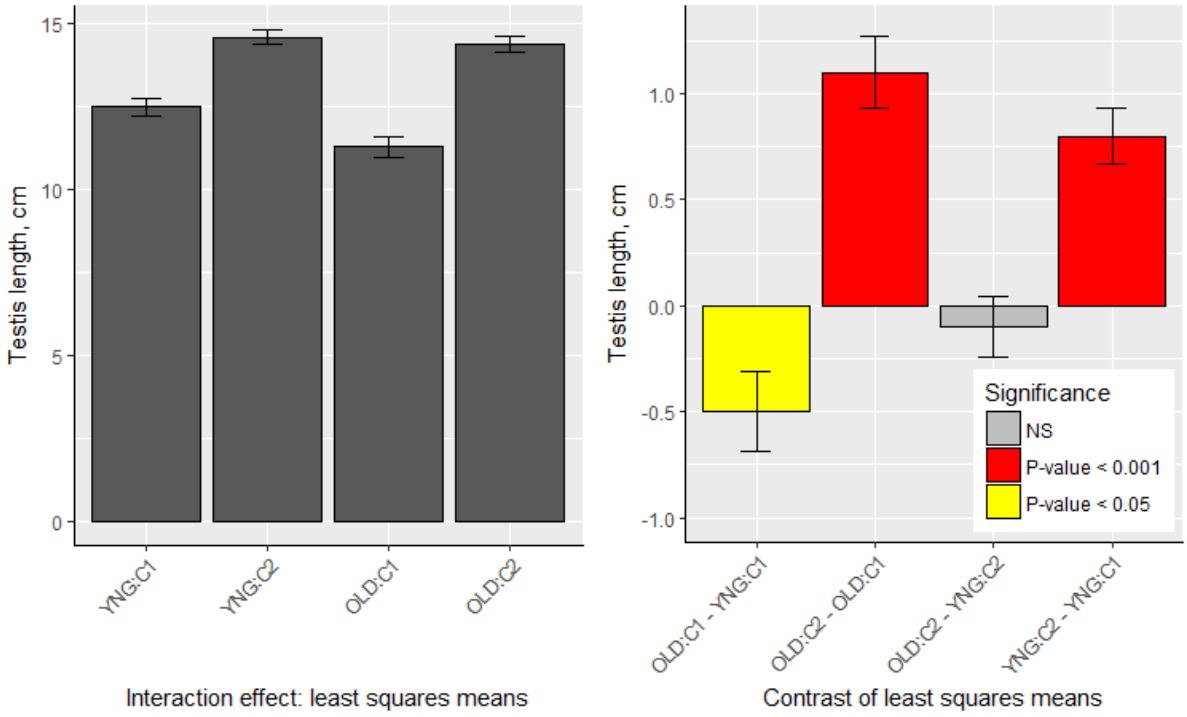

Figure A.1: Least squares means estimates for simple effects of genetic line (young age at puberty = YNG, old age at puberty = OLD) × collection period (collection period 1 = C1, collection period 2 = C2) interaction effect on testis length.

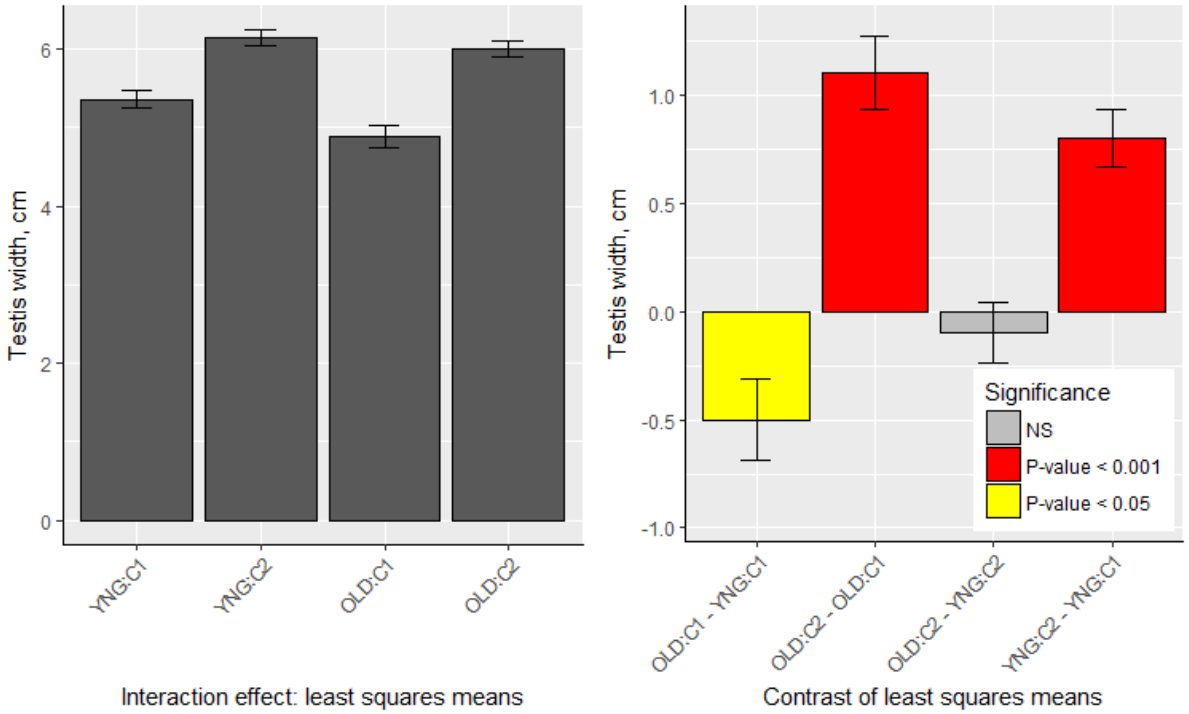

Figure A.2: Least squares means estimates for simple effects of genetic line (young age at puberty = YNG, old age at puberty = OLD) $\times$ collection period (collection period 1 = C1, collection period 2 = C2) interaction effect on testis width.