

ABSTRACT

PEPPMEIER, ZACK CAMERON. Estimates of Variance Components for Genetic Correlations among Growth and Gilt Service Traits. (Under the direction of Dr. Mark Knauer).

The objective of this study was to associate swine growth traits, at different phases, with subsequent gilt service traits. Landrace (n=62,208) and Large White (n=61,743) pigs were reared in three Smithfield Premium Genetics nucleus farms located in eastern North Carolina. Weights were collected at birth, weaning (25 days of age), nursery exit (67 days of age) and finishing exit (162 days of age) in both Landrace and Large White. Growth traits evaluated were pre-weaning average daily gain (PWADG; 0 to 25 days of age), nursery average daily gain (NADG; 25 to 67 days of age), finishing average daily gain (FADG; 67 to 162 days of age) and weight per day of age (WDA; 0 to 162 days of age). Weights at birth, weaning and finishing exit were collected January 2013 to January 2020 while weights at the end of nursery began collection January 2018. After editing, growth traits for PWADG, NADG, FADG and WDA were 61,895, 13,807, 10,267 and 51,234 records, respectively, for Landrace and 61,435, 12,458, 7,671 and 40,331 records, respectively, for Large White. Gilts were reared with the rest of the herd during preweaning, nursery and finishing. Gilts were selected within a week following the capture of finishing exit data. After finishing, males and non-selected females were sold to slaughter. Selected gilts entered the herd at 171.7 ± 7.2 and 172.5 ± 9.3 days for Landrace and Large White, respectively. After three weeks of management protocols, gilts were observed daily for signs of estrus. The following service traits were extracted: age at first service (AFS); entry to the gilt pool to first service interval (ENTRY_FSI); whether a gilt was serviced (SERV); and whether a gilt was serviced within 60 days of entry to the gilt pool (SERV60). Age at first service was 231 ± 18 and 240 ± 27 days for Landrace and Large White, respectively. Gilts with service records and PWADG, NADG, FADG and WDA growth traits were 5,056, 682, 687 and 5,079, respectively,

for Landrace and 4,575, 557, 557 and 4,581, respectively, for Large White. Pre-weaning average daily gain, NADG, FADG, WDA, ASF and ENTRY_FSI were treated as continuous traits while SERV and SERV60 were treated as categorical traits. Variance components were estimated with GIBBS3F90 and THRGIBBS1F90 using an animal model for continuous and categorical traits, respectively. Estimated heritability for direct effects of PWADG, NADG, FADG, WDA, AFS, ENTRY_FSI, SERV and SERV60 were 0.03, 0.12, 0.31, 0.21, 0.15, 0.14, 0.15 and 0.14, respectively, for Landrace and 0.011, 0.06, 0.031, 0.23, 0.08, 0.08, 0.17 and 0.17, respectively, for Large White. Estimated maternal heritability for PWADG, NADG, FADG and WDA were 0.141, 0.068, 0.026 and 0.029, respectively for Landrace and 0.115, 0.044, 0.001 and 0.019, respectively, for Large White. In general, genetic correlations between growth and service traits were favorable for Landrace and unfavorable for Large White. The strongest genetic correlations, whether favorable or unfavorable, typically occurred during PWADG and FADG. Results suggest genetic progress for market throughput can be increased by selection for FADG vs. WDA. Early and late growth appear to have the greatest impact on gilt service traits.

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Estimates of Variance Components for Genetic Correlations among Growth and Gilt Service
Traits

by
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DEDICATION

To my parents. They showed me the value of hard work and provided me with the opportunity to be where I am today.

BIOGRAPHY

Zack Peppmeier was born in Creston, Iowa on March 17th, 1996, to Ken and Lori Peppmeier. He grew up with two older sisters, Brooke and Ayla, both of which helped foster is passion for agriculture. Growing up, Zack helped his father run the family farm. They raised cattle, pigs, sheep, goats, and horses along with a few hundred acres of row crops and hay ground. Following graduation from Creston High School in May of 2014, he attended Southwest Community College in Creston, Iowa where he received an associate of arts degree in May of 2015. After which he began his Bachelors of Science degree as an animal science student at Iowa State University. In May of 2018, he graduated with a B.S. in animal science.

As an undergraduate, Zack further expanded his experience in the swine industry through various internships, intercollegiate judging teams, and jobs. He interned with Iowa Select Farms on a sow farm and Tyson Foods in swine procurement. Hoping to broaden his understanding of the industry as a whole, he joined the Iowa State Meat Judging and Meat Animal Evaluation teams. His last semester, he joined a breeding and genetics lab where his research concerned the accuracy of using photos to measure gilt vulva sizes. After graduation, he was a research contractor with swine genetics company and pharmaceutical company where he was exposed to stratification methods and data collection. These experiences confirmed his desire to focus on a career in the swine industry and further explore research. He began his career at North Carolina State University as Master's student in August of 2018. During the summer of 2019, he interned with Smithfield Premium Genetics (SPG) where he began his thesis project. His project centered on identifying selection strategies to help maximize throughput as well as correlating early growth periods with swine reproductive and service traits.

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I would like to thank my advisor Dr. Mark Knauer and North Carolina State University Department of Animal Science for providing me with the opportunity to continue my education. Growing up on a diversified livestock farm in southern Iowa, I never thought I would move halfway across the country to a state I had never visited previously. I am extremely grateful for the guidance and encouragement Dr. Mark Knauer has provided me during my graduate career. I would also like to thank my committee Dr. Jeremy Howard and Dr. Francesco Tiezzi. Both of which have been an essential part of my graduate education and research experience. Furthermore, I would like to thank the Smithfield Premium Genetics group for the funding of this project.

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TABLE OF CONTENTS

LIST OF TABLES	vii
LIST OF FIGURES	viii
Chapter 1: Literature review	1
Introduction.....	1
Section 1. Growth	2
1.1. Definitions.....	2
1.1.1. Throughput.....	2
1.2. Economic Impacts.....	3
1.2.1. Throughput.....	3
1.3. Genetics of Growth.....	4
1.3.1. Growth rate	4
1.3.2. Impact of maternal and direct effects over time	8
1.3.3. Genetic associations between direct and maternal effects	9
1.4. Environmental Factors Influencing Growth Rate	10
1.4.1. Health status.....	10
1.4.2. Air quality	12
Section 2. Reproduction.....	13
2.1. Definitions.....	13
2.1.1. Age at puberty.....	13
2.2. Economic Impacts	14
2.2.1. Non-productive days.....	14
2.2.2. Gilt retention	15
2.2.3. Sow longevity	16
2.3 Genetics of Reproduction	18
2.3.1. Puberty	18
2.3.2. Gilt retention	18
2.4. Environmental Factors Influencing Reproduction.....	20
2.4.1. Boar exposure	20
2.4.2. Season	22
2.4.3. Growth rate	23
2.4.4. Nutrition.....	28
2.4.5. Housing.....	31
Literature Cited	33
Chapter 2: Estimates of variance components for genetic correlations among growth and gilt service traits	42
Abstract.....	42
Introduction.....	44
Materials and Methods.....	46
Animals	46
Birth to Finishing Exit.....	46
Gilt Selection to First Service	47
Gilts with Growth Data	48
Data editing	48

Statistical analysis	49
Results and Discussion	51
Birth to Finishing Exit.....	51
Gilt Selection to First Service	55
Associations Between Growth with Gilt Service Traits.....	59
Implications.....	60
Literature Cited.....	62

LIST OF TABLES

Table 2.1	Descriptive statistics for growth traits for Landrace and Large White	68
Table 2.2	Number of pigs with growth records by trait for Landrace and Large White.....	68
Table 2.3	Descriptive statistics for service traits for Landrace and Large White	69
Table 2.4	Number of selected gilts with growth records (by respective trait) for Landrace and Large White	69
Table 2.5	Covariates, fixed effects and random effects by trait for Landrace and Large White.....	70
Table 2.6	Landrace Variance Components	71
Table 2.7	Large White Variance Components	72
Table 2.8	Landrace estimates of direct heritability (h^2) (diagonal), genetic correlations (r_g) (above diagonal) and phenotypic correlations (below diagonal)	73
Table 2.9	Landrace estimates of maternal heritability (m^2) (diagonal), genetic correlations (r_g) (above diagonal)	73
Table 2.10	Large White estimates of direct heritability (h^2) (diagonal), genetic correlations (r_g) (above diagonal) and phenotypic correlations (below diagonal)	74
Table 2.11	Large White estimates of maternal heritability (m^2) (diagonal), genetic correlations (r_g) (above diagonal)	74
Table 2.12	Correlations between direct and maternal additive effects (by respective trait) for Landrace and Large White.....	75
Table 2.13	Correlations between maternal effects of growth traits (rows) and direct effects of gilt traits (columns) in Landrace	76
Table 2.14	Correlations between maternal effects of growth traits (rows) and direct effects of gilt traits (columns) in Large White.....	76

LIST OF FIGURES

Figure 2.1 Additive direct (h^2) and maternal (m^2) heritability for ADG by growth phase for Landrace and Large White.	67
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CHAPTER 1: Literature Review

Introduction

In market swine production, a common indicator of throughput is the total amount of pounds sold during a given period of time. Therefore, pig production throughput is composed of two components, number of pigs sold and pig growth rate (commonly measured as average daily gain (ADG)). Pigs are commonly raised indoors in production facilities where they can be easily cared for and managed. A market pig cycle includes birth in a sow farm, being transferred to a nursery facility after weaning, before being transferred to a finishing barn where pigs are reared for the longest period of time before harvest. Improving the growth and fitness of individuals in the herd leads to increased pounds which can lead to greater profit for the producer.

The traditional breeding structure of the swine industry is shaped like a pyramid and consists of three tiers. At the top of the pyramid are nucleus farms, next are multipliers and at the bottom of the pyramid are commercial units which comprise of the majority of the breeding stock. Depending on the production system, gilts are selected from the herd at different production stages based on potential reproductive ability. They are then incorporated into sow farms to become the next generation of mothers. At the nucleus level, replacement gilts are selected based on their genetic potential to produce a large litter of lean fast-growing pigs. Selection strategies at the genetic nucleus consist of evaluations of information on the sire and dam and all available relatives for traits of economic importance. Traits of importance may include reproduction, growth, and carcass traits. Progressing down the breeding pyramid, visual appearance becomes more important and is used for selection at multiplication and commercial levels. Visual selection characteristics may include age, weight, frame size, feet and leg

structure, teat number and vulva appearance and shape. These phenotypic traits can help form a balanced approach to selection for replacement gilt longevity and performance. By improving reproductive fitness, producers can capitalize on the value of breeding females within their herd at the commercial level.

Since the mid to late 1900's, genetic improvement in swine has been focused on growth, backfat and litter size (Tarrés et al., 2006). More recently, the relationships between production and reproduction have been analyzed more extensively. This paper will focus on pig growth at different stages and associated reproductive characteristics in female swine.

Section 1. Growth

1.1 Definitions

1.1.1 Throughput

Throughput is a general term used to describe the amount of material passing through a system or process. In regards to swine production, it refers to the total pounds of pig going through a production system, whether it be pork product or live weight. It is a combination of growth and the number of pigs raised in a given space. This can be related to pig flow. Flow as many salable pigs through a given set of facilities to maximize profits (income minus expense), while at the same time providing proper animal care. Expenses can be subdivided between fixed and variable costs while income primarily includes a combination of price and pig weight at market. The two factors which the producer can directly influence are variable costs and pig weight. Total pig weight being the major unit of throughput.

1.2 Economic Impacts

1.2.1 Throughput

Pig breeding programs aim to acquire future generations of pigs which more efficiently produce desirable products under future economic and social circumstances. This implies the pig will satisfy both the producer and the consumer thus making a profitable, competitive, and sustainable production system even more important. Within the United States, profitability is a logical unit in the final evaluation of the pig (MacNeil et al., 1997). Throughput can be a common predictor for determining profitability. Throughput is related to number of pigs, growth and mortality.

Increasing the number of pigs produced within a production facility can positively impact producer profits. For example, say the fixed cost of producing a weaned pig is \$33 on a sow farm with an average litter size at weaning of 11 pigs and 2.3 litters per year. If a farmer is able to increase litter size by one pig at weaning, from 11 to 12 pigs weaned per litter or 25.3 to 27.6 pigs per year, the producer can save \$2.75 per piglet on all piglets weaned per year ($\$33 \times 25.3 \text{ pigs} = \$834.9/\text{sow}/\text{year}$. $\$834.9 \div 27.6 \text{ pigs} = \$30.25/\text{pig}$. $\$33 - \$30.25 = \$2.75$ saved per pig). Increasing throughput helps alleviate fixed costs at the various stages of production by dividing costs by a larger number of pigs or total pounds produced.

Two other primary factors influencing pig production throughput and profitability are growth rate and survival. Throughput, in relation to growth rate, is comprised of growth during preweaning, nursery and finishing phases. Increasing throughput at any of these stages can impact production profits. In fixed weight systems, De Vries (1989) describes the economic value of daily gain is primarily derived from cost savings due to shorter periods during finishing

or nursery growing periods. While in fixed timed systems, added growth equals more pounds of pork to sell. Baker et al. (1943) describes rate of gain as a good indicator of general health, feed efficiency, and carcass composition. Another major contributor to throughput is survival rate. Hermes et al. (2014) estimates economic weights of selected breeding objectives in a sire-line index based on the standard deviation of the traits post weaning survival, feed conversion ratio, average daily gain, and carcass fat depth to be 44.5, 27.0, 17.4, and 11.1%, respectively. This indicates post weaning survival as one of the most important traits for economic profitability followed by feed conversion ratio and average daily gain. Producers may experience slight variations in economic weights based on feed prices and space availability within the production system. For example, feed conversion ratio may play a larger role as feed prices increase while average daily gain may play a larger role to producers focusing on cycling as many hogs through a facility due to time or space constraints.

1.3 Genetics of Growth

1.3.1 Growth rate

Studies have evaluated the genetics of growth and estimated variance components across different growth stages. Primarily studies have focused on preweaning growth or weight (Solanes et al., 2004) and postweaning growth (Bryner et al., 1992; Chen et al., 2002; Johnson et al., 2002). Variance components are typically estimated in animal models containing direct genetic effects of the animal and common litter effects. However, the inclusion of maternal genetic effects is less commonly utilized. Nonetheless, attempts have been made to further improve characterization of variance components associated with direct/maternal models and better understand maternal genetic effects of swine for various traits.

Solanes et al. (2004) investigated how direct (h^2) genetic effects, maternal (m^2) genetic effects, and litter environmental (c^2) effects influenced early growth, the finishing period and carcass traits of pigs, providing further insight into the relationship between early and late growth. Individual weights were measured on Yorkshire pigs ($n=20,000$) at birth, 3 weeks of age and 9 weeks of age. Average daily gain was calculated between birth and 90 kg (DG_{0-90}) and between 25 and 90 kg (DG_{25-90}) on approximately 4000 pigs. Results showed c^2 and m^2 had a greater impact on piglet weight before weaning than h^2 . The proportion of variation accounted for by c^2 , m^2 and h^2 were 0.19, 0.17, and 0.03, respectively, for weight at 3 weeks and 0.21, 0.09, and 0.12, respectively, for weight at 9 weeks. This demonstrates maternal genetic effects having a greater impact on growth during earlier stages than later stages. Estimates of h^2 for DG_{0-90} and DG_{25-90} were 0.43 and 0.32, respectively. However, when estimating variance components for DG_{0-90} and DG_{25-90} , no significant maternal genetic or common litter effects were found. Maternal effects were present in analysis of weight prior to 9 weeks of age but were not present in analysis of daily gain prior to 90 kg. Similarly, Crump et al (1997) and Zhang et al (2000) found no significant maternal effects when estimating genetic effects for post-weaning growth. Maternal effects for growth rate may not have been significant due to sample size. Solanes et al. (2004) estimated low genetic correlations were found (-0.00 to 0.37) between piglet weight and growth during the finishing period which indicates a different origin of genetic control for early and late growth traits. The same author suggests this may be evidence to treat direct and maternal traits separately within breeding evaluations.

Genetic and maternal influences of growth rate were further analyzed by Bryner et al. (1992). Bryner et al. (1992) estimated the variance and covariance components for backfat and growth rate across 26 central boar test stations. Traits analyzed were average daily gain from 36

to 104.5 kg and backfat adjusted to 104.5 kg on purebred Yorkshire boars (n=7,951). Variance components were estimated within a multiple-trait, sire-maternal grandsire model. Direct and maternal heritability for average daily gain during the testing period were estimated to be 0.24 and 0.23, respectively. The estimate of maternal genetic effects is relatively large when compared to other studies analyzing maternal genetic effects during a similar period of time. Perhaps this estimate is inflated as common litter was not included in the study causing a confounding between common litter and maternal effects.

A large study, analyzing genetic trends for lean growth in pigs, was conducted at Iowa State University by Chen et al. (2002). Data was collected on 362,300 Yorkshire, 154,833 Duroc, 99,311 Hampshire and 71,097 Landrace pigs between 1985 and 2000 from herds within the National Swine Registry Swine Testing and Genetic Evaluation System. Animal models contained random effects of common litter, direct genetic and maternal genetic for lean growth rate and several carcass traits. Two models were conducted for each of the four breeds, one with maternal genetic effects and other without maternal genetic effects. Lean growth rate was calculated for the period from birth to 113.5 kg. Estimates for common litter effects ranged from 0.07 to 0.16. Direct genetic heritability ranged from 0.37 to 0.48 across both models and all breeds. Maternal genetic effects ranged from 0.01 to 0.05 for all traits across all breeds. Although maternal genetic effects were present, they had little effect on direct genetic effects of lean growth rate. Chen et al. (2002) used Spearman rank correlations between two sets of estimated breeding values for direct genetic effects of lean growth rate, under models containing and excluding maternal genetic effects. Over the 15-year period correlations ranged from 0.92 to 0.96. This indicates direct genetic effects are similar with or without maternal effects being

included in the model. Ferraz and Johnson (1993) and Crump et al. (1997) also reported maternal genetic effects could be excluded from the analysis of most performance traits in pigs.

Johnson et al. (2002) investigated the importance of maternal genetic effects on postweaning performance traits of swine. Average daily gain was calculated for populations of Landrace (15,594), Yorkshire (n=55,497), Duroc (n=12,267) and Hampshire (n=9,782) from approximately 100 to 177 days of age. For statistical analysis, four models were used containing different combinations of the three random traits, additive genetic, common litter environmental and maternal genetic effects. The first model contained only additive genetic effects; the second model added common litter environmental effects; the third model added maternal genetic effects, assuming no correlation between additive and maternal genetic effects. While fourth model contained all three random effects and assumed a correlation between additive and maternal genetic effects. In the fourth model, additive genetic heritability estimates were 0.28, 0.26, 0.14 and 0.17 for Landrace, Yorkshire, Duroc and Hampshire breeds, respectively. Maternal genetic heritability estimates were 0.02, 0.02, 0.03 and 0.0 for each breed, respectively. Results suggest maternal effects may need to be considered in genetic evaluations of performance traits such as average daily gain in some breeds of swine.

Generally previous studies agree there are significant maternal genetic effects during the preweaning period (Baker et al., 1943; Nordskog et al., 1944; Robison, 1981; Solanes et al., 2004). However, studies tend to differ when analyzing maternal effects for post weaning growth. Maternal influences were found to be significant with Bryner et al. (1992), Johnson et al. (2002) and Chen et al. (2002) but not with Crump et al. (1997) and Zhang et al. (2000). Bryner et al. (1992) estimated a maternal genetic heritability of 0.23 for average daily gain in Yorkshire boars while both Johnson et al (2002) and Chen et al. (2002) reported lower estimates of 0.01 to 0.04

for Yorkshire, Landrace, Duroc and Hampshire pigs. These results suggest a greater amount of research is necessary to better understand the relationship between direct/maternal animal models where it relates to swine growth at different stages of production. The majority of studies have focused on either lifetime growth or post weaning growth as an all-inclusive period of time (Bryner et al., 1992; Crump et al., 1997; Zhang et al., 2000; Johnson et al. 2002; Chen et al. 2002). This indicates further research may be required to analyze maternal effects during specific periods of time, such as immediately following weaning.

1.3.2 Impact of maternal and direct effects over time

Few published studies have analyzed how direct and maternal effects change throughout the first six months of a pig's life (essentially birth to market). However, having a better idea of how heredity and environmental interact over time and impact growth is of considerable practical importance. Heritability of direct and maternal effects has been known to vary across different stages of production (Baker et al., 1943; Nordskog et al., 1944). With improved estimates of heritability, it can provide an important practical effect on the accuracy of selection response to growth rate.

Studies generally agree common litter environmental effects and maternal genetic effects are relatively more important, in relation to growth, in younger pigs while direct genetic effects explain more variation in older pigs. The increasing impact of direct genetic effects and the decreasing impact of maternal genetic and common litter effects on growth rate coincide with age (Kaufmann et al., 2000; Zhang et al., 2000; Hermesch et al., 2001). Yet the extent to which direct genetic, maternal genetic, and common litter effects change over time is disputed.

The growth and composition of gain changes gradually throughout the growing period. For example, prenatal growth largely consists of the growth of structures and organs essential to life. However, during postnatal growth body tissues develop in the following order skeleton, muscle and fat. Pigs become increasingly independent of maternal influences as development progresses beginning with prenatal growth and followed by pre-weaning and post-weaning. This being the case, it is reasonable to conclude that the extent of gains is under genetic control and vary according to circumstances at a given age. Nordskog et al. (1944) reported estimated effects of average daily gain over the following time periods: 21 to 56 days, 56 to 84 days, 84 to 112 days and 112 to 140 days of age were N/A, 17.7, 25.8 and 27.8%, respectively, for direct heritability and 30.7, 24.2, 21.4 and 14.2%, respectively, for common litter. After 140 days of age, direct heritability slightly declined while litter environment increased however this may be due to the methods of determining variance components available at the time of the study in combination with a relatively lower population size. Baker et al (1943) estimated a similar trend of additive genetic heritability increasing while common litter environmental effects decrease over time.

1.3.3 Genetic associations between direct and maternal effects

Genetic correlations between direct effects and maternal effects for the same trait have been estimated across a variety of pig traits. In the majority of studies, the genetic correlation between direct and maternal effects are negative, regardless of the trait. A similar genetic relationship between direct and maternal genetic effects for growth traits has been shown (Robison, 1981; Bryner et al., 1992; Zhang et al., 2000). This suggests an antagonistic

relationship is present between a sow's genes, dedicated to providing a favorable environment for her offspring, and the offspring's genes dedicated towards growth.

Two studies have analyzed the relationship between direct and maternal genetic effects for a number of different production traits in swine. Bryner et al. (1992) estimated a negative genetic covariance between direct and maternal effects for backfat and growth rate. The genetic correlation between direct and maternal effects for backfat and average daily gain were -0.51 and -0.23, respectively. These results are in agreement with Chen et al. (2002) who analyzed maternal effects for lean growth rate, days to 113.5 kg, loin eye area adjusted to 113.5 kg and backfat adjusted to 113.5 kg. The study estimated negative correlations between maternal and direct genetic effects across all traits and breeds evaluated. Estimated genetic correlations ranged from -0.31 to -0.61 for lean growth rate and -0.28 to -0.58 for all other traits. These results further support the existence of negative genetic associations between maternal and direct effects in swine.

1.4 Environmental Factors Influencing Growth Rate

1.4.1 Health status

Disease and other unfavorable health factors can cause an increase variation of production phenotypes such as growth rate. Fix et al. (2010) describes variations in production phenotypes that ultimately cause some pigs to be less than full value market hogs at slaughter. There is no synonymous definition for a full value market hog within the commercial industry or scientific research. The point at which a market hog leaves a production facility varies between production systems primarily due to available finishing space with biosecurity being a key factor pertaining to the tail end portion of hogs leaving a barn. For example, fixed timed production

systems require all animals to leave at a certain date regardless of weight. These biosecurity measures may lead to an increased number of hogs not considered full value. Yet other producers may take hogs to market based on target weight, allowing greater time for slower growing animals to reach the target. Either way, this would lead to additional costs for the production system as light weight hogs are worth less and may be penalized for not meeting certain weight requirements (Boys et al., 2007).

Other factors influencing the percentage of full value market hogs and health status of a farm include animal stressors such as immunological, metabolic, social and environmental interactions (Martínez-Miró et al., 2016). There are many stressors that can impact swine performance and profitability. For example, the porcine reproductive and respiratory syndrome (PRRS) virus costs the swine industry an estimated \$560 million annually in the United States (Cho and Dee, 2006). Another common reason for pigs to have lower feed intake and consequently lower performance is heat stress (Guy et al., 2017) which costs the swine industry in the United States \$299 million a year (St-Pierre et al., 2003). Mycotoxins have been known to impact feed intake in immature swine (Smith et al., 1997). Social interactions and stocking density are yet another common stressor in swine (Hyun et al., 1998). These are just a few of the factors that influence the health status of swine and consequently impact the growth performance at various stages of production. Diseases and other health challenges cost the swine industry millions of dollars each year through lower production efficiencies and/or increased mortalities.

Managing stress is a vital step towards enhancing pig growth and performance. The impact of temperature stress on growth performance and carcass quality were examined on grow-finish pigs (White et al., 2008). The study tracked pig body weights, average daily gain, and feed efficiency during the final 35 days of the finishing period. Pigs were housed within (at

23.9° C) or above (at 32.2° C) their thermoneutral zone and were provided either 0.66 or 0.93 m²/pig. Pigs were weighed at the beginning and the end of the trial period. Pigs housed at 32.2° C had lower (113 vs 103 kg) body weights at the end of the trial due to significantly ($P < 0.05$) reduced average daily gain (0.89 vs 0.54 kg/day) and gain to feed ratio (0.28 vs 0.24). The increased stocking density of 0.66 m²/pig resulted in a significantly ($P < 0.05$) reduced average daily gain (0.78 vs 0.65 kg/day) and gain to feed (0.28 vs 0.24) when compared to housing at 0.93 m²/pig. However, results suggest that increasing space allocation per animal may be an appropriate method to alleviate the negative effects of temperature stress on growth performance.

1.4.2 Air quality

A major concern in swine production facilities is air quality which can influence swine and worker health and perhaps growth rate. From the beginning of raising hogs in confinement, dust particles in hog barns have been an issue for producers. The majority of airborne particles in confinement swine facilities are made up of feces, feed, dander and other particles. Iverson et al. (2000) reports these irritants have been known to cause health complications in both swine and humans. The author suggests concentrations of dust below 100 ng/m³ to within a safe threshold for animal well-being and worker safety. Above 100 ng/m³, pigs and humans are at greater risk of lung dysfunction and a vigorous cardiopulmonary response. As discussed previously, the health of swine and production traits such as growth rate are linked.

DeJong et al. (2014) developed a system which creates polarized air particles. The author presented data of the impact of electrostatic particle ionization (EPI) on air quality, emissions and growth performance of pigs housed in a thermo-regulated facility. Once polarized the particles collide with other particles in the air, causing the other particles to also become

polarized. Due their charge, polarized particles attach to grounded surfaces within the barn such as slats or fencing, thus removing them from breathing air. Two identical 200-head nurseries in Kansas were used in the study over five 6-week periods in a single year. The study alternated which nursery was ionized over the five time periods. Results show that the EPI system significantly reduced airborne particles by up to 50% leading to reduced particulate matter released outside the barn. Although no significant differences in ammonia or hydrogen sulfide concentrations between the barns there was a tendency for improved average daily gain during the nursery period. More research is required to analyze the effects of air quality on animal well-being and growth performance however this study suggests there may be methods with which air quality can be improved.

Section 2. Reproduction

2.1 Definitions

2.1.1 Age at puberty

Gilt sexual development involves three phases, sexual maturation, attainment of puberty and pregnancy. Sexual maturation is comprised of hormonal and anatomical changes which lead to puberty. This phase is completed at 140 days on average and is followed by a resting period until the attainment of puberty. Puberty occurs an average of 60 days following the completion of sexual maturation (Dyck, 1988). Thus, average age at puberty is about 200 days. Age at puberty is also commonly referred to as the age at first observed estrus or the age at first ovulation. Observed estrus is often determined by the gilt's reaction to the back-pressure test in the presence of a boar (Hemsworth and Barnett, 1989). While first ovulation is determined by

analysis of progesterone levels to determine the presence of corpora lutea on the ovary, which indicates ovulation has occurred (Esbenshade et al., 1983).

Age at puberty is not considered a trait which is commonly recorded on nucleus, multiplier, or commercial farms. However, age at first service and age at first farrowing have been used as comparable traits to age at puberty and have been used to measure early gilt reproductive performance (Tummaruk et al., 2001, Holm et al., 2004, Knauer et al., 2011). Age at first service is the age at which a gilt is first bred. Age at first farrowing is the age at which a gilt delivers her first litter. Holm et al. (2005) reported the genetic correlation between age at first service and age at first farrowing was 0.98, indicating they are similar traits. However, using either age at first service or age at first farrowing in place of age at puberty may cause inaccuracies in estimating a females' reproductive ability. Both management (Le Cozler et al., 1998) and genetics (Bidanel et al., 1996) can greatly influence age at puberty and related traits. For example, not accounting for age at boar exposure can dramatically impact estimation of variance components for age at puberty and related traits. Including farm within contemporary groups may accumulate some of the increased variance if groups of gilts begin boar exposure at different ages. This strong interaction between environmental effects and genetic effects among the aforementioned traits may have led to limited usage in genetic evaluations.

2.2 Economic Impacts

2.2.1 Non-productive days

Reducing nonproductive days can be accomplished by decreasing the days between birth and first service, the interval between weaning and mating, and the interval between weaning and culling (Le Cozler et al., 1998). The onset of puberty can directly impact days in-between birth

and first service. This allows for manipulation of pubertal development for the purpose of decreasing nonproductive days. As previously mentioned, age at first service and age at first farrowing have a genetic correlation of 0.98 (Holm et al. 2005). This indicates gilts serviced sooner are more likely to farrow a litter sooner.

Amer et al. (2014) developed a model to determine economic values of single maternal breeding traits. A delay in pubertal development increases the period before first service, increasing maintenance and operating costs for replacement gilts. The model determined economic value by summing all operating costs per gilt per day and the additional cost of one day increase in feed cost for maintenance. A scenario was developed to estimate the increase in energy requirements of a replacement gilt. Base energy requirements were calculated to be 3,985 MJ Me and the cost of an additional day longer to reach puberty was 25 MJ ME higher than the base amount. Assuming the cost of energy utilized is \$0.024/MJ ME, the economic value of gilts reaching puberty one day longer is \$0.60 per animal per day. This study demonstrates that animals reaching puberty sooner decreases the cost of raising replacement gilts by lowering non-productive days.

2.2.2 Gilt retention

High rates of gilt culling increase the need for replacement gilts and has negative effect on a production system's profitability (Christenson, 1986; Stalder et al., 2003; Serenius and Stalder, 2004). Replacement rates with the swine industry are reported to range between 42% and 59% (Lucia et al., 2000; Tarrés et al., 2006) with 3.1 to 3.7 parities being the average age at culling (Lucia et al., 2000; Stalder et al., 2003). The primary reason why females are removed is due to reproductive issues (Lucia et al., 2000; Patterson et al., 2010). This being said, improving

female retention can increase economic efficiency in gilt/sow production systems and increase profits by reducing expenses associated with replacement gilts.

The introduction of replacement females into the sow herd presents a large, critical financial investment (Lucia et al., 2000; Tarrés et al., 2006). The percent of gilts that farrow a first litter ranges from 61% to 92% (Moeller et al., 2004; Knauer et al., 2011). The investment towards gilts which did not farrow a first litter is then placed on those that did farrow a litter as the total cost of replacement females is distributed over a smaller group. For example, Stalder and Goodwin (2000) estimated the cost of replacement gilts between groups with different farrowing percentages. The percentage of gilts successfully farrowing a litter and entering the breeding herd was 84, 82, 79, and 72% in four separate groups of gilts. Cost of replacement females included initial costs, feed, labor, and other associated costs. The cost of gilts which did not farrow a litter was assessed against gilts that did produce a litter, minus cull value. The cost of each gilt farrowing a litter was estimated to be \$227, \$232, \$240 and \$261, respectively, for each farrowing percentage above. This demonstrates how gilt groups with a lower rate of farrowing a first litter present a production system with a higher investment per animal.

2.2.3 Sow longevity

The economics of sow longevity are important when discussing age at puberty. Multiple studies have shown that a young age at puberty or first farrowing is correlated with improved sow longevity (Serenius and Stalder, 2004; Serenius et al., 2008; Knauer et al., 2010a). That being said age at puberty has an impact beyond replacement gilts and impacts sow lifetime productivity or longevity.

Improved sow longevity can reduce economic inputs and increase profit margins in several ways on commercial swine operations. A major contributor to reducing economic inputs would be lowering the required number of gilt replacements, decreasing genetic input and gilt rearing costs. Stalder et al. (2003) estimates sows don't typically reach a positive net present value until the third parity. Sows culled before their third parity would consequently have negative net present values and if culled would lead to decreased profits for the producer. Older parity sows typically weigh more than young sows and thus would likely bring a greater value at the time of culling.

Amer et al. (2014) developed an economic model to determine the value to sow breeding objective traits, including sow longevity, considering the Australian pig production system. Economic value was defined as the marginal economic benefit of a sow attaining an extra parity. Net returns were calculated based on weaned pig sales. Net returns per sow per parity were calculated assuming that first-, second- and third- or higher- parity sows would wean 9.15, 9.86, and 9.86 live pigs, respectively. Gilt development, piglet disposal, and energy requirement costs were adjusted for each parity and subtracted from net returns. The model assumed 90% of sows were sold as culls and the remaining 10% of sows were considered on farm death loss. For a 1.0% increase in retention between parties following parity one there was a 0.8% decrease in replacement costs. This retention increase contributed to \$2.35 lower in replacement costs per parity. This demonstrates that sows whom remain in the herd longer are more profitable as long as they remain productive. Age at puberty effects sow retention in the long term due to previously mentioned correlations between age at puberty with sow longevity and consequently increases net returns for production.

2.3 Genetics of Reproduction

2.3.1 Puberty

Age at puberty, or similar traits such as age at first service or age at first farrowing, have been shown to be heritable (Hutchens et al., 1981; Bidanel et al., 1996; Rydhmer, 2000, Knauer et al., 2012, Morrison, 2016). In a study of 737 crossbred and purebred gilts, Hutchens et al. (1981) reported heritability estimates of 0.19 and 0.40, based upon paternal and maternal half-sib estimates, respectively. Bidanel et al. (1996), Rydhmer (2000) and Knauer et al. (2012) reported heritability estimates of 0.29 to 0.30 for age at puberty or first observed estrus. Morrison (2016) reported heritability estimates of 0.24 and 0.20 for age at first service and age at first farrowing, respectively. The same author found a genetic correlation between age at first service and age at first farrowing of 0.995. Age at first service may have a somewhat lower heritability than age at puberty due to reduced variation as age at first service may not capture gilts that cycle before boar exposure begins.

2.3.2 Gilt retention

Differences in gilt retention rates have been reported between genetic lines (Moeller et al., 2004; Knauer et al., 2012). Moeller et al. (2004) studied six different maternal lines in the National Pork Producers Council Maternal Line National Genetic Evaluation Program. The six lines evaluated were American Diamond Swine Genetics (ADSG), Danbred North America (DB), Dekalb-Monsanto DK44 (DK44), Dekalb-Monsanto GPK347 (GPK347), Newsham Hybrids (NH) and National Swine Registry (NSR). The ADSG, DB, DK44 and NH lines were commercially available Landrace x Large White F₁ crossbreds. The GPK347 line consisted of F₁ Dekalb-Monsanto Genepacker Line 34 sows mated to Nebraska Index boars. The NSR female

was a Landrace x Yorkshire F₁ cross. Each genetic line entered with at least 590 weaned gilts to be included with the test. Gilt retention rates for the ADSG, DB, DK44, GPK347, NH and NSR lines were 77, 77, 75, 92, 76 and 78, respectively. Perhaps some of the differences in retention rates between genetic lines can be explained by differences in age at puberty. The GPK347 line gilts were 13 days younger at puberty than all other genetic lines in the study combined. The differences in gilt retention rates between genetic lines reported by Moeller et al. (2004) support the strong relationship between age at puberty, gilt retention and sow longevity.

Few studies have estimated variance components for gilt retention (Knauer et al., 2011; Lewis and Bunter, 2011; Morrison, 2016). The study by Knauer et al. (2011) used THRGIBBS1F90 to estimate variance components for whether a gilt farrowed a first litter (STAY) with gilt estrous, growth, body composition and structural conformation traits. The authors reported a heritability estimate of 0.14 for STAY. Similarly, Morrison (2016) reported a heritability for STAY of 0.11. In contrast, Lewis and Bunter (2011) reported a lower heritability estimate for STAY (0.04) using ASReml. One apparent difference between the studies by Knauer et al. (2011), Morrison (2016) and Lewis and Bunter (2011) was the percentage of gilts farrowed, 72, 84.3 and 61%, respectively. The lower percentage of gilts farrowing a first litter may be due to the design of the study by Lewis and Bunter (2011) as a larger number of gilts was initially selected to account for culling due to structural soundness. The authors reported culling 32% of the gilts before they had the opportunity to be mated. Taken together, the heritability estimates for gilt retention by Knauer et al. (2011) and Morrison (2016) indicates sufficient genetic variation for selection, while Lewis and Bunter (2011) perhaps describes gilt retention as a non-heritable trait. Morrison (2016) proposes that improvements in gilt retention may be possible through genetic selection for younger age at first service.

Knauer et al. (2011) estimated genetic and phenotypic correlations between gilt retention (STAY) with gilt estrous, growth, body composition and structural conformation traits. The authors reported genetic correlations between STAY with length of estrus, standing reflex traits, age at puberty, days to 114 kg and backfat of 0.34, 0.34 to 0.74, -0.27, 0.52 and -0.29, respectively. These genetic correlations suggest increased gilt retention is perhaps associated with a longer length of estrus, stronger standing reflex, younger age at puberty, slower growth and increased backfat. Hence, selection for slower growing, early estrous animals may be a useful strategy to improve gilt retention rates.

2.4 Environmental Factors Influencing Reproduction

2.4.1 Boar exposure

There are numerous studies examining the biological responses of gilts and their relationship to boar exposure. Exposing a boar to gilts has been shown to decrease the age of puberty in gilts (Mavrogenis and Robison, 1976). Moreover, studies have reported differing pubertal responses depending on the on the gilt's age at the initiation of boar exposure (Kirkwood and Hughes 1979; Eastham et al. 1986). Kirkwood and Hughes (1979) suggests the optimal gilt age to introduce boar exposure is 160 to 170 days. However, more reports have suggested there are several other factors besides age at puberty to consider when preparing gilts for boar exposure.

Kirkwood and Hughes (1979) studied the impacts of gilt age at boar exposure on attainment of puberty. Data included 36 Large White x (Large White x Landrace) allocated to one of nine treatment groups. Groups included 30 min daily boar contact beginning at 125, 132, 139, 146, 153, 160, 167, 174, or 181 days of age. Gilt feed level was adjusted so all groups were

gaining 0.46 kg per day. Gilts were mated at the estrous period following the first observed estrus. Results concluded the interval from first boar contact to puberty was significantly longer among gilts at ages below 139 days. Gilts in groups above 139 days of age demonstrated a similar interval to each other. However, those in the 174 or 181 day groups were significantly older at puberty when compared to earlier age groups. Eastham et al. (1986) showed similar results with 34 Landrace x (Landrace x Large White) gilts allocated between groups with a mean age of first boar exposure to be 160, 180 and 200 days. Interval from first boar contact to puberty was significantly shorter for gilts within the 200 day of age group when compared to the 160 or 180 day of age group. Results from both studies suggest that as the age at which gilts are first exposed to boars increases the interval between exposure and attainment of puberty decreases. These results show how younger gilts at first boar exposure tend require a greater number of days of boar exposure, thus increasing labor costs when compared to older gilts.

Amaral Filha et al. (2009) proposed that rate of gain or weight may be an important biological factor when determining to begin boar exposure in gilts. Gilts (n=1486) were evaluated according to two groups of age at boar exposure (A = 130 to 149 days and B = 150 to 170 days) and three categories of growth rate (Low = 550 to 830 g/day; Intermediate = 650 to 725 g/day and High = 726 to 830 g/day). Across the study 85% of gilts expressed estrus within 40 days of boar exposure. Within group A, a greater percentage of High gilts expressed puberty within 20 days post boar exposure when compared to Intermediate and Low, 59.7, 48.7 and 48.2%, respectively. While group B showed no significant difference in percentage of estrus across growth rates, 63.8, 67.3 and 63.7%, respectively. These results suggest with proper management of boar exposure, faster growing gilts within a group may be able to successfully reach puberty at an earlier age. If a production system were able to identify those with a high

lifetime growth rate puberty may be achieved at an earlier age compared to those with intermediate to low growth rates. This could allow producers to promote higher longevity and lifetime performance in high growth rate gilts by stimulating puberty at a younger age, limiting the occurrence of overweight gilts at the time of mating.

2.4.2 Season

Several studies have reported variation in the induction of puberty due seasonal effects in swine. Early findings suggest puberty is delayed in females born in early springs months compared to those born during other seasons of the year (Wiggins et al., 1950). Others have tried to identify what specific environmental factors occurring during the spring could cause delay of puberty. Flowers et al. (1989) indicates that chronic exposure to elevated temperatures delay puberty in gilts.

Tummaruk et al. (2000) gathered data (n=14,761) from Swedish Landrace and Yorkshire gilts from 22 nucleus herds born during the five-year period of September 1993 to October 1998. Traits analyzed included age at first mating, growth rate and backfat thickness. Gilts had to meet the following requirements in order to be mated: 7 to 9 months of age, second observed estrus and at least 120 kg. Models included effects of herd-year to account for management differences. The study found 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 coincides with results published by Paterson et al. (1991) which found gilts born in early spring to show delayed puberty. These results suggest there is a significant effect of season on age of puberty in gilts, however it is likely caused by the characteristics of that season (Paterson et al., 1991).

Temperature during the growing phases is also a factor in determining the cause of seasonal effect on puberty in gilts. Tummaruk et al. (2007) observed seasonal variations between groups of gilts when analyzing the impact of age, body weight, and lifetime growth rate on subsequent reproductive performance. Fecal samples were collected on 214 of 696 gilts observed in the study to determine fecal progesterone profiles around the time of first estrus. During the three seasons classified by the study, rainy, summer, and winter the proportion of gilts that did not ovulate during estrus the first observed estrus (Group C) was 45.2, 78.5, and 23.8%, respectively. Each season was significantly different from one another. Results suggest the percentage of gilts who do not ovulate during first observed estrus increases as temperatures increase. Within gilts sampled at first observed estrus during the summer the percentage of gilts in Group A, B, and C were 15.4, 6.2, and 78.5%, respectively. Results suggest higher temperatures during the summer lead to an increased percentage of gilts not ovulating during first observed estrus. This data is supported by Flowers et al (1989) which suggests that temperature drives seasonal differences in age at puberty, implying that increased ambient temperature delays the onset of puberty through heat stress.

2.4.3 Growth rate

The relationship between growth rate with subsequent reproductive performance and longevity has been a major focus of swine genetic studies (Rozeboom et al., 1995; Bidanel et al., 1996; Stalder et al., 2005; Tarrés et al., 2006; Knauer et al., 2011; Vallet et al., 2016). Increased growth rate has been demonstrated to accelerate the induction of puberty by effecting important developmental points during the growth cycle of developing gilts. Yet slow growing gilts are less likely to be culled (Hoge and Bates, 2011) and have a greater number of total pigs produced over

their lifetime (Stalder et al., 2005). Knauer et al. (2010b) reported an unfavorable genetic relationship between average daily gain and sow longevity in three of six genetic lines analyzed, where reduced growth was favorable for longevity. Tholen et al. (1996) also reported an unfavorable genetic correlation between average daily gain and sow longevity, particularly in early parities ($r_g = -0.16$). Hutchens et al. (1981) reported favorable genetic and phenotypic correlations between age at puberty and post weaning average daily gain ($r_g = -0.38$; $r_p = -0.34$).

Tarrés et al. (2006) found gilts with rapid growth 167 days of age until the point of breeding were at the greatest risk for being culled, indicating the timing of growth to be a major factor in the impact on gilt reproduction. These studies indicate the impact of growth rate on age at puberty and subsequent reproduction varies depending on developmental stage in which the increased growth occurs. Growth rate and puberty has been analyzed as the correlation between prenatal, preweaning, and lifetime growth rates with age at puberty and other reproduction traits. Research indicates that regardless of the growth stage, gilt growth rate impacts subsequent reproduction and continues to impact females throughout their lifetime.

A common measure of prenatal growth rate is birth weight which has been shown to impact puberty in gilts (Flowers, 2012). Reproductive tissues and organs begin development as early as day 40 of gestation and continues through the end of gestation which in turn augments animal weight prior to birth. This leads to the assumption that birthweight can be used as a predictor of reproductive potential. There are well-established favorable relationships between birth weight and the size of most internal organs, including some of the main reproductive organs (Foxcroft et al., 2009). Larger pigs at birth grow faster and tend to weigh more as adults when compared to smaller counterparts. A negative trend between birth weight and age at puberty was shown in data presented by Flowers (2012). Animals weighing 3.5 pounds or heavier and 2.0 to

2.8 pounds reached puberty at an average of 170 and 188 days, respectively. Flowers suggests that birth weight may have a positive relationship with sow longevity. This suggests that prenatal environment impacts pubertal development and sow longevity in that higher birth weight animals are more likely to reach puberty sooner and have greater long-term potential in the herd.

Following prenatal and neonatal stages, growth continues to impact reproductive development as the gilt progresses through the pre-weaning stage. Vallet et al. (2016) examined litter-of-origin traits, primarily preweaning litter environment, and their subsequent effect on gilt reproductive development. Growth data was collected on 1,200 gilts from 300 sows with daily observation for estrus from 160 days of age to slaughter. At slaughter, reproductive tracts were collected and classified as cyclic or prepubertal. Analysis showed higher preweaning growth rate in replacement gilts was associated with a younger age at puberty. Due to a quadratic relationship between preweaning growth rate and age at puberty, Vallet et al. (2016) found the pre-weaning growth rate to be optimized at 0.26 kg/day in relation to age at puberty. The difference in age at puberty between the optimum growth rate and the minimum growth rate (0.04 kg/day) was 22.5 days. These findings are in agreement with Flowers (2012) who reported increased growth rate in light birth weight pigs compensated for prenatal restriction with the end result of increased longevity. This data supports faster growing pigs during the preweaning stage reach puberty at an earlier age.

When analyzing preweaning growth, other factors contributing to growth and the possible results of increased growth should be considered. Nelson and Robison (1976) were the first to analyze the impact of postnatal environment or litter size on subsequent reproduction. Cross fostering within the first 24 hours of parturition was used to establish small (6 pigs) and large (14 pigs) litters. The authors reported gilts reared in small litters had advantages in corpora lutea ($P <$

0.05) and embryo number ($P < 0.10$) when compared to gilts raised in large litters. Similarly, Flowers (2009) demonstrated that gilts raised in smaller litters reached puberty earlier and had subsequent improvement to retention rates in the breeding herd when compared to larger litters. It can be expected that gilts raised in smaller litters receive greater nutrition due to reduced competition and thus had higher growth prior to weaning. An increase in gain from birth to weaning is expected to lead to a higher weaning weight and extra feed for the lactating sow. If the lactating sow is not provided a higher feeding level, she will sacrifice body condition to provide for the litter. Mavromichalis (2001) estimates that a sow requires 4 grams extra feed per day during lactation for each additional 1g increase in piglet pre-weaning daily gain. As growth increases during the preweaning stage, additional feed may need to be provided to account for the increased requirements of the litter.

Lifetime growth rate and its relationship with reproductive traits has been an area of focus of many studies. A study conducted by Tummaruk et al. (2007) in Thailand involved the use of Landrace x Yorkshire replacement gilts ($n=696$) to determine the effect of age, body weight, and lifetime growth rate on subsequent reproductive performance. Gilts were housed in groups and were not sorted by growth rate. Groups were determined by time at which ovulation was observed; those that ovulated during first observed estrus (Group A), those that ovulated before first observed estrus (Group B), and gilts that did not ovulate during the first observed estrus (Group C). Group A, B, and C account for 34, 21, and 45% of the total number of gilts in the study, respectively. Body weight was measured at birth, entry into the gilt pool (24 weeks of age), and first and second estrus. Gilts were exposed to the boar after entry into the gilt pool. 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, which suggests that weight and age have a similar

relationship with age at puberty. Weaker relationships between growth and age at puberty were observed when analyzing growth rate between entry and first observed estrus. The interval from entry to the gilt pool to the first observed (EOI) estrus was 24.4 ± 18.0 days (range 0 to 88 days). Average daily gain from entry to the gilt pool until puberty was favorable with EOI, -0.19. Stronger relationships were present with measures of lifetime growth rate prior to entry (age and body weight) when compared to ADG post entry. This suggests that growth prior to gilt pool entry (24 weeks of age) influences age at puberty to a greater degree than growth later in life.

Associations between lifetime growth rate with age at puberty was further examined by Tummaruk et al (2009). Tummaruk et al. (2009) evaluated lifetime growth rate by splitting growth between two time periods. Measures of growth included growth rate from birth to 90 kg (GRe), from 91 kg to 134 kg (GRi), which added together compose birth to 134 kg (GRs). Growth traits were calculated from a population of Landrace x Yorkshire gilts (n=6,946). Entry into gilt pools occurred at 90 kg while exit from gilt pools occurred at 134 kg, signifying the end time points for each growth stage. Growth rate measures were significantly associated with one another. GRs was positively correlated with GRi and GRe, 0.46 and 0.25 respectively. However, GRi was negatively correlated with GRe, -0.65. Age at first estrus was significantly influenced by GRs and GRe with negative correlations of -0.40 and -0.20, respectively. Yet GRi was not significantly correlated with age at first estrus. This data demonstrates increased lifetime growth is associated with a decreased age at first estrus. However, within lifetime growth, early growth or GRe has a greater impact than later growth or GRi. This suggests that factors involved in growth early in life impact age at puberty to a greater degree than that of later growth.

Summarizing studies analyzing the relationship between growth and reproduction traits, it appears that optimally, gilts are to achieve faster growth rates during early developmental

periods, such as preweaning, in order to achieve a younger age at puberty (Tummaruk et al. 2009; Flowers, 2009; Vallet et al., 2016). However, following the conclusion of developmental phases gilts are to slow the rate of growth in order to lessen risk of culling (Stalder et al., 2005; Tarrés et al., 2006) as well as increase longevity and offspring per lifetime (Hoge and Bates, 2011; Knauer et al., 2010b). Further examining growth rate and its relationship to reproductive traits at specific time periods common to the swine industry could prove beneficial.

2.4.4 Nutrition

Due to the relationship between growth rate and age at puberty, a reasonable conclusion would be that nutrition also plays a major role in the induction of puberty in the gilt. As the gilt develops and progresses to the next production stage, her nutritional requirements also change. The majority of studies focus on two main areas of production pre weaning nutrition (Vallet et al. 2015; Flowers, 2009) and post weaning nutrition (Miller et al., 2011; Calderón Díaz et al., 2015).

Piglet birthweight and colostrum consumption have been shown to be influential factors of preweaning growth (Vallet et al., 2015). Colostrum impacts the development of essential piglet tissues such as the linings of the gastrointestinal (Hammon et al., 2012) and reproductive tracts (Bartol et al., 2013). These effects are partially provided by hormones in colostrum during the first 24 hours following farrowing and described as “lactocrine” effects (Bartol et al., 2008). Piglets are born with low levels of immunoglobulin however are provided with it through colostrum which indicates that serum immunoglobulin concentration can be a good indicator from colostrum intake. Immunoglobulin immunocrit measures and its relationship with pubertal development was analyzed by Vallet et al. (2015). Approximately 1100 gilts were observed for

immunoglobulin immunocrit levels and other early life traits, growth levels, and age at puberty, for the purpose of identifying 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. Low immunoglobulin immunocrit levels were associated with reduced growth, increased age at puberty, and reduced litter average preweaning growth rate. These results suggest that within a group, age at puberty can be reduced through improved preweaning growth rate which is largely influenced by colostrum consumption and lactation performance. Results suggest immunoglobulin immunocrit levels may be a useful tool for monitoring colostrum intake to predict subsequent performance.

Litter size and preweaning stocking density have also been key early factors in gilt development and consequently been shown to impact age at puberty and future reproductive performance (Flowers, 2009). Within an 80,000-sow commercial production system, replacement gilts (n=3,180) were randomly allocated within a factorial study involving season of birth, neonatal litter size, and method of estrous stimulation. Two levels of neonatal litter sizes were evaluated, small litters (≤ 7 pigs) or large litters (≥ 10 pigs) and gilts were subjected to first boar exposure at 140 or 170 days of age. Regardless of season of birth or age at boar exposure, neonatal litter size was shown to significantly impact pubertal development and subsequent reproductive performance. The proportion of gilts to reach estrus within the first 28 days of boar exposure was 82 and 60% for gilts raised in small litter and large litters, respectively, across all methods of puberty stimulation. The combination of small nursing litter sizes and early age at puberty showed significant effects on sow longevity. After 6 parities, 45% of sows raised in small litters and given boar exposure at 140 days of age were scheduled to be rebred compared to only 10% of sows raised in large litters and given boar exposure at 170 days of age. A possible

reason behind this higher reproductive efficiency may be due to increased preweaning growth which has been shown to have a relationship with age at puberty (Vallet et al., 2016). Although this would be difficult to implement in modern production systems, the effects of increased piglet nutritional regime due to neonatal litter size could prove effective in improving age at puberty, reproductive performance, and longevity in gilts.

The effects of feed restriction and reduced energy content on pubertal development were analyzed by Klindt et al. (1999) and Miller et al. (2011). Klindt et al. (1999) reported gilts fed Ad lib, ad libitum from 13 to 25 weeks of age (n=64); Control, ad libitum from 13 weeks of age to 100 kg body weight and 90% ad libitum until 25 weeks of age (n=65); or Restricted, 74% ad libitum from 13 to 25 weeks of age showed no differences ($P > 0.05$) in age at puberty or pregnancy rate. Boar exposure and heat detection was initiated at 175 day of age. The percentage of pubertal gilts by 28 days post boar exposure was 75, 65, and 67 % for Ad lib, Control, and Restricted, respectively. These results differ from Miller et al. (2011) who reported differences in age at puberty between restricted gilts (n=330) and gilts fed ad libitum (n=331). Restricted gilts were provided ad libitum access to feed until 123 days of age after which time they were restricted to 75% ad libitum until 235 days of age. Ad lib gilts were allowed ad libitum access to feed from weaning to the point of breeding at 235 days of age. Estrus detection began on 140 days of age to determine age at puberty. Gilts from Ad lib demonstrated estrus at an earlier age when compared to Restricted, 174.1 and 177.5 days, respectively. Gilts fed Ad lib diet had increased rate of backfat deposition compared to gilts fed the Restricted diet. This presents possible confounding effects on nutrient intake and growth rate due to the effects of backfat and body composition on age at puberty. Results suggest that nutritional regiment and growth rate's impact on age at puberty may depend on the period of time at which growth is observed.

2.4.5 Housing

A limited number of studies have been conducted to analyze the effects of housing conditions and gilt socialization on the induction of puberty in gilts. Previous reports appear to indicate housing gilts in groups of 10 to 30 pigs per pen does not hamper the attainment of puberty while gilts in groups greater than 50 to 60 have shown delayed puberty (Levis, 2000). This appears to be due to overcrowding and limited contact with a boar during the exposure period. Observational reports from producers have noted increased pubertal development in groups of gilts housed on partial slatted flooring compared to total slatted floors. Young et al. (2008) suggest that gilts with at least 1.13 m² of pen space per gilt tend to reach puberty at an earlier age than those housed in conditions with only 0.77 m² per gilt. Boar exposure took place from 140 to 200 days of age. Exposure methods were the same for both space allotments allowing for the same boar exposure per gilt. These results are consistent with Clark et al. (1985). However, the effect seemed limited which suggests this method may not be economically effective in a facility constrained by the pen space and number of replacement gilts.

Bryan and Hagen (1992) observed a socialization effect with an increase in attainment of puberty of peripubertal gilts with addition of prepubertal gilts. Prepubertal Duroc gilts (n=54, 88 kg, 164 days of age) were exposed to boars to induce puberty. Gilts were observed for estrus twice daily through 245 days of age. Fifty percent of gilts attained puberty within 42 days of the start of the study. After 42 days of boar exposure, the portion of gilts attaining puberty tended to plateau. A second group of prepubertal Yorkshire and Duroc gilts (n=36, 80 kg, 159 days of age) were introduced into the breeding facility at day 73 following initial boar exposure for the original group of gilts. This second group of gilts were not mixed with the original group.

However, twenty nine percent of the original gilts demonstrated signs of estrus within 10 days of introducing the second group. Results suggest the addition of new prepubertal gilts into a breeding facility may increase the frequency of estrus in gilts around the age of puberty. However, this socialization effect may be due to increased libido in the mature boars thus enhancing male pheromone levels and induction of estrus.

Housing methods and their relationship to induction of puberty in gilts has been the focus of few authors. Few studies have investigated the potential impacts of the number of females per pen, social interactions or other housing methods and their relationships with puberty. A primary reason behind lower interest levels may be due to vertical integration within the swine industry. Majority of large-scale producers have standardized methods of replacement gilt management and thus there is a relatively small amount of variation within a system and even between different systems. Studies on the impact of housing also present many challenges due to increased labor demands and population size required for statistical power.

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CHAPTER 2. Estimates of Variance Components for Genetic Correlations among Growth and Gilt Service Traits

Abstract

The objective of this study was to associate swine growth traits, at different phases, with subsequent gilt service traits. Landrace (n=62,208) and Large White (n=61,743) pigs were reared in three Smithfield Premium Genetics nucleus farms located in eastern North Carolina. Weights were collected at birth, weaning (25 days of age), nursery exit (67 days of age) and finishing exit (162 days of age) in both Landrace and Large White. Growth traits evaluated were pre-weaning average daily gain (PWADG; 0 to 25 days of age), nursery average daily gain (NADG; 25 to 67 days of age), finishing average daily gain (FADG; 67 to 162 days of age) and weight per day of age (WDA; 0 to 162 days of age). Weights at birth, weaning and finishing exit were collected January 2013 to January 2020 while weights at the end of nursery began collection January 2018. After editing, growth traits for PWADG, NADG, FADG and WDA were 61,895, 13,807, 10,267 and 51,234 records, respectively, for Landrace and 61,435, 12,458, 7,671 and 40,331 records, respectively, for Large White. Gilts were reared with the rest of the herd during preweaning, nursery and finishing. Gilts were selected within a week following the capture of finishing exit data. After finishing, males and non-selected females were sold to slaughter. Selected gilts entered the herd at 171.7 ± 7.2 and 172.5 ± 9.3 days for Landrace and Large White, respectively. After three weeks of management protocols, gilts were observed daily for signs of estrus. The following service traits were extracted: age at first service (AFS); entry to the gilt pool to first service interval (ENTRY_FSI); whether a gilt was serviced (SERV); and whether a gilt was serviced within 60 days of entry to the gilt pool (SERV60). Age at first service was 231 ± 18 and 240 ± 27 days for Landrace and Large White, respectively. Gilts with service records and

PWADG, NADG, FADG and WDA growth traits were 5,056, 682, 687 and 5,079, respectively, for Landrace and 4,575, 557, 557 and 4,581, respectively, for Large White. Pre-weaning average daily gain, NADG, FADG, WDA, ASF and ENTRY_FSI were treated as continuous traits while SERV and SERV60 were treated as categorical traits. Variance components were estimated with GIBBS3F90 and THRGIBBS1F90 using an animal model for continuous and categorical traits, respectively. Estimated heritability for direct effects of PWADG, NADG, FADG, WDA, AFS, ENTRY_FSI, SERV and SERV60 were 0.03, 0.12, 0.31, 0.21, 0.15, 0.14, 0.15 and 0.14, respectively, for Landrace and 0.011, 0.06, 0.031, 0.23, 0.08, 0.08, 0.17 and 0.17, respectively, for Large White. Estimated maternal heritability for PWADG, NADG, FADG and WDA were 0.141, 0.068, 0.026 and 0.029, respectively for Landrace and 0.115, 0.044, 0.001 and 0.019, respectively, for Large White. In general, genetic correlations between growth and service traits were favorable for Landrace and unfavorable for Large White. The strongest genetic correlations, whether favorable or unfavorable, typically occurred during PWADG and FADG. Results suggest genetic progress for market throughput can be increased by selection for FADG vs. WDA. Early and late growth appear to have the greatest impact on gilt service traits.

Introduction

Genetic evaluation of pigs is based on multi-trait best linear unbiased prediction (BLUP) procedures. In pig breeding, BLUP models can be used to make genetic predictions based on an animal population's breeding value for a specific trait of interest. Estimates may differ between animal populations due to a combination of management and genetic differences. Multi-trait analysis allows producers to obtain genetic correlations between analyzed traits. Genetic correlations provide insights into the associated impacts of selection for a specific trait.

Pig breeding programs aim to acquire future generations of pigs which produce desirable products more efficiently under future economic and societal circumstances. This implies the pig will satisfy both the producer and the consumer therefore making a profitable and sustainable production system even more important. Within the United States, profitability is a logical unit in the final evaluation of the pig (MacNeil et al., 1997). Throughput can be a common predictor for determining profitability. In regards to swine production, throughput refers to the total pounds of pig going through a production system and is related to number of pigs, growth and mortality. Throughput can be applied to both market and reproductive pig populations.

As heritability is a measure of a population, it can vary over time and between populations. Studies generally agree common litter environmental effects and maternal genetic effects are relatively more important, in relation to growth, in younger pigs while direct genetic effects explain more variation in older pigs. The increasing impact of direct genetic effects and the decreasing impact of maternal genetic and common litter effects on growth rate coincide with age (Baker et al., 1943; Nordskog et al., 1944; Kaufmann et al., 2000; Zhang et al., 2000; Hermesch et al. (2001). Yet the extent to which direct genetic, maternal genetic, and common litter effects change over time is disputed. Gaining a better understanding of how heritability of

growth rate changes over time is beneficial as it provides potential insight into different methods of genetic selection to further improve production throughput.

Ideally, replacement gilts grow rapidly, efficiently and have superior subsequent fertility. However fast gilt growth rate has generally been shown to unfavorably impact subsequent reproductive performance and longevity (Tholen et al., 1996; Stalder et al., 2005; Tarrés et al., 2006; Knauer et al., 2010b; Knauer et al., 2011; Hoge and Bates, 2011). Slower growing gilts are less likely to be culled (Knauer et al., 2010b; Hoge and Bates, 2011) and more likely to have a greater number of pigs produced over their lifetime (Stalder et al., 2005). However, research indicates increased pre (Tummaruk et al., 2009; Flowers, 2012; Vallet et al., 2016) and post (Hutchens et al., 1981; Tummaruk et al., 2007) weaning growth rate has been demonstrated to accelerate the induction of puberty by impacting important developmental points during the growth cycle of developing gilts. In general, it appears early growth has a greater impact on subsequent reproduction than later growth. Tarrés et al. (2006) found gilts with rapid growth 167 days of age until the point of breeding were at the greatest risk for being culled, indicating the timing of growth to be a major factor in the impact on gilt reproduction. Further examining growth rate and its relationship to reproductive traits at specific time periods common to the swine industry could prove beneficial. Therefore, the objective of this study is to further analyze the direct and maternal genetic components of growth rate at different stages and evaluate their respective impact on gilt estrus and retention traits.

Materials and Methods

Animals

Data was collected from January 2013 to January 2020 on 62,208 Landrace and 61,743 Large White pigs (Smithfield Premium Genetics, Rose Hill, NC). Pigs were born and raised on 3 nucleus farms located in eastern North Carolina. Male and female pigs used for analysis were raised together within the same facility throughout pre-weaning, nursery and finishing periods. Cross foster rate in Landrace and Large White was 5.7 and 4.9%, respectively. In the nursery and finishing phases, Landrace and Large White were penned on slatted flooring in groups of 15 to 20 within their respective breed. Following finishing, analysis of off-test and genetic data was used to select gilts to be maintained within the nucleus herd. Males and non-selected females were then sent to market. Selected females were then used for reproductive trait analysis.

Birth to Finishing Exit

Weights were collected at birth, weaning, nursery exit and finishing exit. Weaning, nursery exit and finishing exit weights were collected at approximately 25, 67 and 162 days of age, respectively, for both Landrace and Large White pigs. These time points were then used to calculate pre-weaning average daily gain (PWADG; 0 to 25 days of age), nursery average daily gain (NADG; 25 to 67 days of age), finishing average daily gain (FADG; 67 to 162 days of age) and weight per day of age (WDA; 0 to 162 days of age) which accounts for average daily gain during the entire trial period. Birth, weaning and finishing exit weights were collected January 2013 to January 2020 while nursery exit weights began being collected January 2018. Descriptive statistics for exit ages and weights for each growth trait are reported in Table 2.1. The collection of nursery exit weight allowed for the calculation of nursery and finishing average

daily gain. Therefore, fewer records were available for NADG and FADG relative to the other growth traits. Number of records analyzed for each growth trait are presented in Table 2.2. Records per growth trait ranged from 10,267 to 61,895 and 7,671 to 61,435 for Landrace and Large White, respectively.

Data included pedigree information for each pig, sex of the pig, birth and wean litter identification, contemporary group, nursery and finishing penning information and dates of birth, weaning, nursery exit and finishing exit. Contemporary groups for growth data of Landrace and Large White were farm identification plus the time which best portrayed a common herd under similar environmental conditions. The time for each growth trait is as follows: PWADG contained weaning week and year; NADG contained nursery exit month and year; FADG contained finishing exit month and year; WDA contained birth week and year.

Gilt Selection to First Service

Gilts were selected within a week following the collection finishing exit data. Females selected were then introduced into the gilt pool located within the same facility. Data from 5,086 Landrace and 4,610 Large White gilts were available for analysis. Gilt entry date, service date and removal date were recorded for each animal. Fence-line boar exposure occurred after entry to the gilt pool at approximately 172 days of age in both breeds. Estrous was recorded after the first standing reflex for the back-pressure test occurred during boar exposure. After estrous was observed, gilts were first serviced 12 to 24 hours after standing heat.

The following traits were extracted: age at first service (AFS); entry to the gilt pool to first service interval (ENTRY_FSI); whether a gilt was serviced (SERV); and whether a gilt was serviced within 60 days of entry to the gilt pool (SERV60). Age at first service and ENTRY_FSI

were linear traits while SERV and SERV60 were binomial traits. Descriptive statistics for selected gilt weight at finishing exit, entry age, age at first service and entry to the gilt pool to first service interval are reported in Table 2.3. Contemporary groups for reproductive data of Landrace and Large White were farm identification plus gilt entry month and year.

Gilts with Growth Data

Growth data and reproduction data were combined for final analysis to obtain variance components among growth and reproductive traits. Records of selected gilts with both service data and growth data ranged from 682 to 5,079 and 557 to 4,610 for Landrace and Large White, respectively (Table 2.4).

Data editing

Data was edited using RStudio v. 1.2.1335. Pigs with trait values greater than 3.5 standard deviations away from the mean were excluded from analysis for that respective trait. Pigs with a finishing exit weight below 205 pounds (Smithfield Premium Genetics threshold) and those weighing 3.5 standard deviations above the mean were excluded from FADG and WDA analysis. However, pigs excluded from analysis for a particular trait remained in the dataset if values for other traits were within the bounds described above. Final analysis included animals which contained at least one of the growth traits; PWADG, NADG, FADG, WDA. After editing, total animals available for analysis were 62,208 Landrace and 61,743 Large White.

Statistical analysis

Final variance components were estimated with an animal model using GIBBS3F90 and THRGIBBS1F90 for continuous and categorical traits, respectively. Sequencing results from both GIBBS3F90 and THRGIBBS1F90 were used for POSTGIBBSF90 to estimate variance components. Variance components for continuous traits (PWADG, NADG, FADG, WDA, AFS and ENTRY_FSI) were analyzed using GIBBS3F90 (Misztal et al. 2016). Starting values for bivariate GIBBS3F90 and THRGIBBS1F90 models were obtained using univariate models ran through AIREMLF90 (Misztal et al., 2002). After the first 10,000 iterations were deleted as burn-in, 40,000 iterations (saving every iteration) were used to calculate posterior means. Variance components for categorical traits (SERV and SERV60) were estimated using THRGIBBS1F90 (Misztal et al., 2002) as linear models are not ideal for estimating variance components for categorical traits (Gianola and Foulley, 1983). The categorical traits followed the same burn-in and thinning rate as continuous traits. Posterior means were used to compile parameter estimates, with associated standard errors. Heritability estimates were calculated by using the following equation:

$$h^2 = \frac{(\sigma a^2 \text{ or } \sigma m^2)}{(\sigma a^2 + \sigma m^2 + \sigma c^2 + \sigma rp^2 + \sigma e^2)}$$

where h^2 is the heritability, σa^2 is the direct additive genetic variance, σm^2 is the maternal additive genetic variance, σc^2 is the common litter genetic variance, σrp^2 is the room and pen common permanent environment variance and σe^2 is the residual variance. Final analysis of variance components from growth traits and reproduction traits were estimated using complete dataset with growth records for males and females in addition to reproduction records for

selected females. Final direct and maternal genetic heritability were estimated through an average of binary analysis in which each trait was used four times in Landrace and Large White. Direct and maternal genetic variance components greater than two times higher than its standard error were considered to be significant at the 5% level (Boldman et al., 1993). Genetic correlations were estimated between traits through binary analysis and displayed in POSTGIBBSF90 output. Phenotypic correlations were estimated between traits using RStudio v. 1.2.1335.

Best linear unbiased prediction (BLUP) methodology was used to estimate variance components. Variance components were estimated using univariate and bivariate models for all traits: pre-weaning average daily gain, nursery average daily gain, finishing average daily gain, weight per day of age, age at first service, entry to the gilt pool to first service interval, serviced and serviced within 60 days. Univariate models for each trait were first analyzed in AIREMLF90 (Misztal et al., 2002). Output from univariate AIREMLF90 models were then used as starting value for bivariate analysis.

Animal pedigrees were obtained from the Smithfield Premium Genetics. Pedigrees from 6 generations were included. Models for growth traits contained random effects of common litter, the room and pen in which pigs were housed during nursery and finishing phases and direct and maternal additive genetic effects. Fixed effect for all growth traits included contemporary group, gender and wean sow parity. Pre-weaning average daily gain had an additional fixed effect of sow's wean number to account for differences in wean litter size. Covariates for growth traits were: wean age (PWADG), nursery exit age (NADG) and finishing exit age (WDA). Both nursery and finishing exit age were used as covariates for FADG. Models

for reproduction traits contained fixed effects of contemporary group and additive direct random effects. Covariates, fixed effects and random effects for all traits are reported in Table 2.5.

Results and Discussion

Birth to Finishing Exit

Landrace grew faster than Large White. Landrace and Large White were weaned, exited nursery and exited finishing at relatively the same age. However, Landrace had higher growth rate during each growth phase. Average weight at the end of finishing for Landrace and Large White was 126.5 and 120.8 kg, respectively. In both breeds, selected females gained 3 to 4 kg more than males and non-selected females. Further descriptive statistics for growth traits are shown in Table 2.1.

Gilts within the current study had a greater rate of gain than those from previous studies. Landrace and Large White selected gilts having a slightly higher rate of gain than males and non-selected females, reached 114 kg at approximately 144.7 and 153.0 days of age, respectively. In contrast, gilts observed in Chen et al. (2002) and Knauer et al. (2011) reached 114 kg at 174 to 185 days of age. Perhaps gilts within the current study were genetically superior for growth or reared in a superior environment when compared to previous studies.

Variance components and heritability

Variance component values for Landrace and Large White can be found in Table 2.6 and 2.7, respectively. Permanent environmental effects were captured through both common litter and room/pen. Estimated common litter variances for PWADG, NADG, FADG and WDA were 21.6, 11.8, 6.0 and 8.1%, respectively, for Landrace and 23.3, 11.7, 6.0 and 7.4%, respectively,

for Large White. Similarly, Chen et al. (2002) estimated common litter to account for 12 to 16% of variance across genetic lines from 4 breeds. Common litter or nurse litter was used as a random effect to account for litter to litter differences in cross-fostered pigs. Including cross-foster status as a fixed effect with birth litter as a random effect assumes that all cross-fostered pigs regardless of the litter have a +/- impact on growth. This demonstrates permanent environmental effects from the sow impacting all growth stages from birth to market. Estimated room/pen variances for NADG, FADG and WDA were 17.8, 16.7 and 15.7%, respectively, for Landrace and 21.1, 11.7 and 15.5%, respectively for Large White. Chen et al. (2009) and Hsu et al. (2010) reported pen effects (competition and social interaction) impacting group performance and estimation of breeding values for average daily gain in pigs. The authors suggested either pen permanent environmental effects be included in genetic evaluation for growth performance under certain management conditions and genetic backgrounds. Thus, we suggest it may prove beneficial when modeling growth rate to include both common litter and room pen to account for permanent environmental effects at different stages of production.

Direct and maternal heritability are reported in Table 2.8 and 2.9, respectively, for Landrace and Table 2.10 and 2.11, respectively, for Large White. A graphical representation of Landrace and Large White direct and maternal additive heritability estimates are shown in Figure 2.1. Estimated direct heritability for PWADG, NADG, FADG and WDA were 0.03, 0.12, 0.31 and 0.21, respectively, for Landrace and 0.011, 0.06, 0.31 and 0.23, respectively, for Large White. Direct heritability of pig growth rate appears to increase in a quadratic fashion from birth to the end of finishing however was unable to be confirmed due to lack of a sufficient number of weigh points. Estimated maternal heritability for PWADG, NADG, FADG and WDA were 0.141, 0.068, 0.026 and 0.029, respectively, for Landrace and 0.115, 0.044, 0.001 and 0.019,

respectively, for Large White. Maternal heritability estimates are in agreement with Johnson et al. (2002) and Chen et al. (2002) who estimated maternal genetic effects for lean growth from birth to 113.5 kg ranged from 0.01 to 0.05 across Yorkshire, Duroc, Hampshire and Landrace genetic lines. Bryner et al. (1992) estimated a higher maternal genetic heritability of 0.23 for average daily gain from 36 to 104.5 kg in Yorkshire boars. However, these estimates may be inflated as common litter was not included within the model possibly causing confounding between common litter and maternal effects. Heritability estimates for growth traits indicate direct heritability increased and maternal heritability decreased from birth to market. Similarly, Baker et al. (1943) and Nordskog et al. (1944) reported direct and maternal heritability varying over time; as a pig ages maternal effects are less prominent while direct effects impact increases. With improved estimates of heritability, it can provide an important practical effect on the accuracy of selections made at various ages.

Direct effects were significant ($p < 0.05$) in PWADG, NADG, FADG and WDA in both Landrace and Large White while maternal additive effects appeared to only be significant during PWADG, NADG and WDA. These estimates are in agreement with Johnson et al. (2002) and Chen et al (2002) who suggested maternal genetic effects may need to be included in performance traits such as average daily gain in some breeds of swine. In contrast, Ferraz and Johnson (1993) and Crump et al. (1997) suggest maternal effects could be ignored for most pig performance traits. Ferraz and Johnson (1993) reported maternal heritability for average daily gain from 30 to 104 kg between 0.5 to 1.5% in Landrace and Large White. In the current study, 30 to 104 kg would represent a portion of finishing growth. Ferraz and Johnson (1993) and Crump et al. (1997) only analyzed later growth during the finishing and thus did not evaluate maternal effects for earlier growth. The authors' estimates for maternal effects for growth are

similar to the current study's estimates for finishing growth. The current study is in agreement with Ferraz and Johnson (1993) and Crump et al. (1997) that maternal effects could be ignored when analyzing growth solely during finishing. Collectively results suggest the growth phase being analyzed should be considered when evaluating maternal genetic effects. The current study suggests maternal genetic effects should be included when analyzing growth rate from birth to the end of finishing.

Genetic correlations

Landrace and Large White genetic and phenotypic correlation between growth traits can be found in Table 2.8 and 2.10, respectively. Estimates of genetic correlations between FADG and WDA for Landrace and Large White were 0.96 to 0.98, respectively, indicating they are similar traits. Genetic gain can be limited when genetic selection for growth is based on either lifetime growth or post weaning growth as an all-inclusive period of time. As reported in the current study, direct heritability of WDA was lower than FADG. Perhaps differing selection methods can prove to be a beneficial technique to genetically improve throughput. For example, in this situation there are two methods to improve growth rate during the market phases of swine; direct selection of WDA using the formula below from Falconer and McKay (1996):

$$R_{WDA} = i(h)_{WDA} * \sigma_{G,WDA}$$

or indirect selection of WDA by directly selecting for FADG using the formula below:

$$CR_{WDA} = i(h)_{Finishing} * r_G * \sigma_{G,WDA}$$

The current study suggests indirect selection for WDA through FADG, when compared to direct selection for WDA, would result in 14.0 to 15.4% increased genetic gain for the two breeds evaluated.

Estimates for genetic correlations between direct and maternal effects by respective trait were negative for all growth traits, ranging from -0.01 to -0.67, in Landrace and Large White and (Table 2.12). In agreement, Chen et al. (2002) estimated genetic correlations between maternal and direct genetic effects of lean growth rate of -0.31 to -0.61. In both Landrace and Large White, NADG had the lowest negative correlations between direct and maternal effects while FADG had the highest negative correlations. Perhaps this is because during nursery growth in both breeds direct and maternal genetic effects are present in similar quantity while during finishing growth direct effects are at their peak and maternal genetic effects are at their lowest. These findings are in agreement with Bryner et al. (1992), Robison (1981), Zhang et al. (2000) and Chen et al. (2002). This indicates an antagonistic relationship between the individual sow's genes dedicated to providing a favorable genetic environment for her offspring and the offspring's genes for growth.

Gilt Selection to First Service

Of the 5,086 selected Landrace gilts, 4,327 (85.1%) were serviced and 2,338 (46.0%) were serviced within 60 days post entry. Of the 4,610 selected Large White gilts, 3,657 (79.3%) were serviced and 1,540 (33.4%) were serviced within 60 days post entry. These findings are in agreement with Cronin et al. (1983), Lucia et al. (2000) and Arango et al. (2005) who reported that 71, 81 and 73% of gilts, respectively farrowed a litter. Holm et al. (2005) reported a genetic correlation of 0.98 between age at first service and age at first farrowing, indicating service data and farrowing data are similar genetic traits. Due to their dependency upon one another, the author reported that age at first service and age at first farrowing were not able to be included together within the same multi trait analysis. Age at first service can provide greater benefit in

selection as it is available earlier in the sow's life compared to age at first farrowing. Thus, age at first service was included in the multi trait analysis in the current study.

Average age at first service was 231 and 240 days for Landrace and Large White, respectively. Further summary statistics for service data can be found in Table 2.3. This is in agreement with Hanenberg et al. (2001) who reported an age at first service of 234 days in Landrace gilts. In contrast, Holm et al. (2005) reported a younger age at first service, 220 days, for Norwegian Landrace pigs born in nucleus herds and raised within nucleus or multiplier herds. Similarly, Knauer et al. (2011) reported an average age at puberty of 211.6 days of age. Perhaps, the higher age at first service observed in the present study can be attributed to differences in management as gilts underwent management protocols following selection procedures specific to Smithfield Premium Genetics. For example, gilts in the present study may have been bred during a later estrus than gilts evaluated in Holm et al. (2005) and Knauer et al. (2011). This along with other management procedures such as age at first boar exposure may help explain differences in age at first service.

Heritability estimates for gilt service traits

Estimated heritability of AFS was 0.15 ± 0.02 and 0.08 ± 0.02 in Landrace and Large White, respectively. Similarly, heritability estimates of ENTRY_FSI were 0.14 ± 0.02 and 0.08 ± 0.02 in Landrace and Large White, respectively. Hanenberg et al. (2001), Holm et al. (2005), Knauer et al. (2011) and Morrison (20016) reported heritability estimates of 0.29, 0.31, 0.22 and 0.24, respectively, for age at first service. Perhaps the estimate for AFS in the current study was less due to management procedures that reduced genetic variation in the nucleus herd.

In the current study, heritability estimates for SERV and SERV60 were 0.15 ± 0.05 and 0.14 ± 0.04 , respectively, for Landrace and 0.17 ± 0.05 and 0.17 ± 0.04 , respectively for Large

White. In univariate analysis of each trait, heritability estimates were 0.04 to 0.07 for both traits in both breeds with a standard deviation no greater than 0.02. We suspect values from the simpler, univariate analysis are closer to actual estimate. Perhaps these values were inflated in bivariate analysis due to low significance and interaction with the growth traits within THRGIBBS1F90 models.

Models estimating variance components for additional random effects were analyzed for each service trait. Common litter and maternal genetic effects were analyzed and accounted for 2 to 7% of variation in Landrace. In general, DIC values, a measure of model fit, were slightly lower with the addition of common litter and maternal genetic effects however direct heritability did not differ between models. Common litter also may have lacked sufficient genetic variation. For example, 25.2% of the 5,086 Landrace gilts were the only gilt selected from their litter and 72.3% of the 2,016 Landrace sows had gilts selected from their litter during only one parity. Similar proportions were observed in Large White. Thus, common litter and maternal genetic effects were not included in final analysis to maintain a simpler model for correlation to growth traits. In contrast, Knauer et al. (2011) included common litter as a random effect for gilt age at puberty which accounted for 9.0% of variation. The author evaluated genetic correlations between average daily gain and age at puberty for 1,172 Landrace x Large White gilts. Perhaps the current study lacked sufficient observations for NADG and FADG to justify utilizing the more complex model.

Genetic correlations among gilt service traits

Age at first service was used as an indicator trait for age at puberty or the time at which a gilt reaches reproductive maturity. Capturing accurate data for age at puberty can be labor intensive, therefore the trait is often times not recorded within current swine breeding programs.

Age at first service is an appropriate representation of age at puberty when analyzing field data (Tummaruk et al. 2001; Holm, 2004). Knauer et al. (2011) estimated genetic correlation between age at puberty and age at first farrowing to be 0.76. Morrison (2016) estimated genetic correlation between age at first service and age at first farrowing to be 0.995. This indicates that age at puberty, first service and first farrowing are all similar traits. Studies have shown that a young age at puberty and related traits are linked to improved sow longevity (Serenius and Stalder, 2004; Serenius et al., 2008; Knauer et al., 2010a). Both genetics (Bidanel et al., 1996) and management (Le Cozler et al., 1998) and can greatly influence age at puberty and related traits. Thus, in order for implementation of AFS to be fully incorporated within genetic selection it is vital that management procedures such as boar exposure are consistent and closely monitored. The lower heritability of AFS in the current study likely indicates management protocols may need to be addressed to improve estimates and genetic gain.

In the current study, AFS and ENTRY_FSI appeared to be similar traits as did SERV and SERV60. Genetic and phenotypic correlations between AFS and ENTRY_FSI were 0.89 to 0.94 across both breeds, signifying they are similar traits. Correlations between SERV and SERV60 were unable to converge as SERV60 is simply a stricter threshold than SERV. However, heritability for SERV and SERV60 were similar across all models analyzed in the same fashion. Perhaps, ENTRY_FSI and SERV60 could be used as suitable replacements of AFS and SERV, respectively, as they are easier to capture. We summarize when analyzing field data genetic selection for age at first service can perhaps serve as a functional replacement for age at puberty while the categorical trait of being serviced requires further research. Perhaps there is not sufficient genetic variability in SERV or SERV60 as there are a number of different environmental factors playing a role in whether a gilt is serviced.

Associations Between Growth with Gilt Service Traits

Genetic correlations

Direct genetic and phenotypic correlations of Landrace and Large White can be found in Tables 2.8 and 2.10, respectively. Genetic correlations between growth and service traits were both favorable and unfavorable for Landrace and Large White. In general, Landrace appeared to have low to moderate favorable correlated genetic associations between growth rates at the different stages of production and the service traits analyzed. This means faster growing Landrace gilts were more likely to be serviced and serviced at a younger age. In contrast, Large White appeared to have low to moderate unfavorable genetic associations. This indicates faster growing Large White gilts were less likely to be serviced and serviced at an older age. Phenotypic associations were low, ranging from -0.14 to 0.13 across all growth and service correlations for Landrace and Large White. In both Landrace and Large White, the strongest genetic correlations were observed in FADG and second in PWADG. In general, lower genetic correlations were observed in NADG and WDA, indicating early and late growth have a greater impact on reproduction. Knauer et al. (2011) reported an unfavorable genetic correlation (0.52) between growth rate (days to 114 kg) and if a gilt farrowed a litter. This indicates faster growing gilts were less likely to farrow and remain in the herd. Tummaruk et al. (2009), Flowers (2009) and Vallet et al. (2016) have shown that gilts who achieve faster growth during early developmental periods, such as preweaning, attain a younger age at puberty as demonstrated within Landrace. However, Knauer et al. (2011) also reported a favorable genetic correlation (-0.25) between age at puberty and whether a gilt farrowed a litter indicating gilts reaching puberty at an earlier age are more likely to stay in the herd. Similarly, Serenius and Stalder (2004) reported a favorable genetic correlation between age at first farrowing and sow lifetime

reproductivity ($r = -0.29$). In contrast, Moeller et al. (2004) reported that growth rates did not differ upon whether a gilt farrowed across 5 genetic lines. Perhaps differences can be attributed to differing methods of selection or developmental differences.

Correlations between maternal genetic effects of growth traits and direct genetic effects of service traits of Landrace and Large White are reported in Tables 2.13 and 2.14, respectively. In general, correlations had a similar but inverse correlation of what was observed between direct effects growth and service traits discussed in the paragraph above. Maternal effects of NADG exhibited stronger genetic correlations with AFS and ENTRY_FSI than compared to direct correlations in Table 2.9. Excluding this, FADG exhibited the strongest genetic correlations in both Landrace and Large White. WDA exhibited the lowest genetic correlations. Perhaps variations between direct and maternal effects of growth with direct effects of service traits is due to the difficulty involved in estimating additive maternal genetic variance. Nonetheless, results were consistent with expectations as additive direct and maternal genetic effects have a negative correlation. This explains why additive genetic direct correlations and maternal correlations have inverse associations with additive direct effects of reproductive traits. This antagonist relationship is in agreement with previous literature (Robison, 1981; Bryner et al., 1992; Zhang et al., 2000; Chen et al., 2002). Further research into correlations between maternal genetic effects of growth traits and service traits could prove beneficial, especially during early growth where maternal heritability is highest.

Implications

The understanding of how additive direct and maternal effects change over time is an important factor to consider when selecting for growth, in terms of pigs meant for market and

reproduction. Favorable genetic correlations were observed in both Landrace and Large White between growth traits, suggesting pigs who gain well during pre-weaning continue to do so until slaughter. Additive maternal effects, permanent and genetic, are most prominent during earlier stages of growth and continue to play a role until the pig reaches maturity. While additive direct effects are lowest during early growth periods and rise over time until maturity. High genetic and phenotypic correlations were observed between finishing average daily gain and weight per day of age. Perhaps producers can attain higher throughput from their herd through genetic selection for finishing growth. Pre-weaning growth has also shown to be an important factor especially in developing gilts. Results show a similar trend in additive direct and maternal genetic heritability by growth phase between Landrace and Large White. The current study suggests indirect selection for WDA through FADG, when compared to direct selection for WDA, would result in a higher response to selection and thus increased genetic gain for the two breeds evaluated.

Previous literature has shown both favorable and unfavorable genetic associations between growth traits and age at puberty or service data which this holds true in this study. Low to moderate genetic correlations were observed between direct additive effects of growth traits and service traits in Landrace and Large White. Landrace being primarily favorably while Large White being primarily unfavorable. This begs the question should there be different genetic selection methods placed upon maternal genetic lines based on breed as growth was shown to have differing effects on each line. Although mixed results were observed between breeds concerning the direction of the impact, it appears that growth during preweaning and finishing phases have the greatest impact on reproduction in the traits analyzed.

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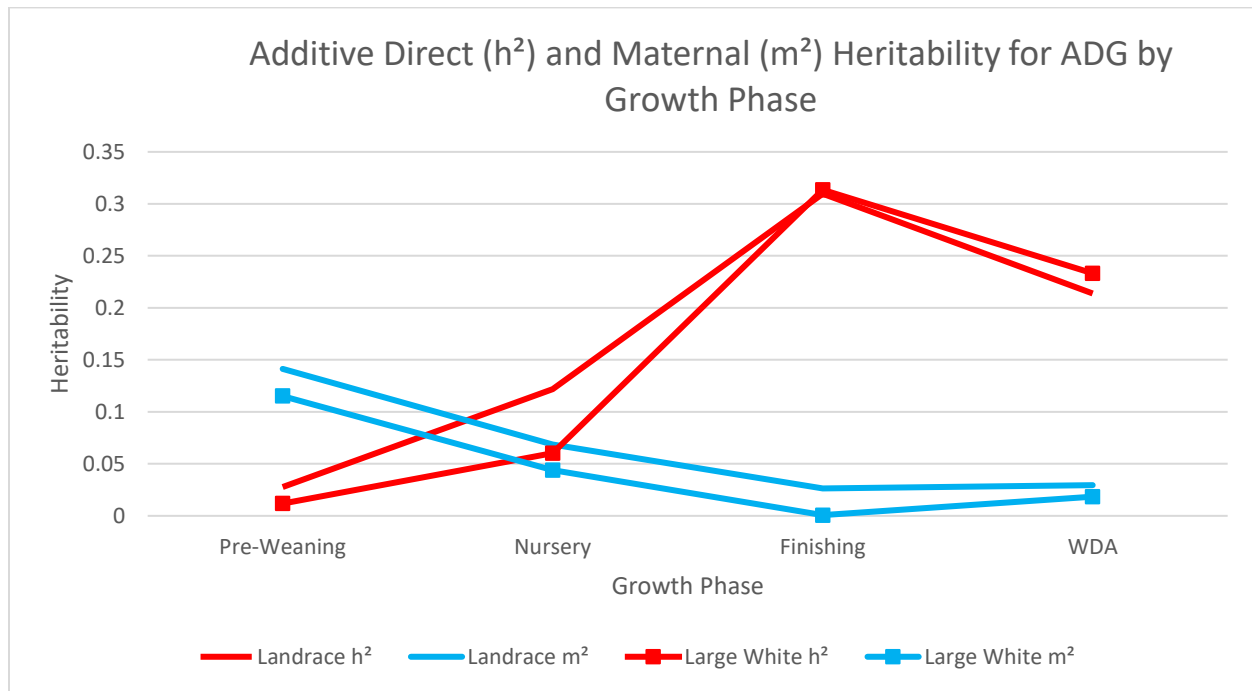
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Figure 2.1. Additive direct (h^2) and maternal (m^2) heritability for ADG by growth phase for Landrace and Large White.



¹ Trait Abbreviation: WDA = weight per day of age; average of pre-weaning, nursery, and finishing production phases

Table 2.1. Descriptive statistics for growth traits for Landrace and Large White.

Trait	Landrace	Large White
	\bar{x} (SD)	
ADG Pre-Weaning (g/d)	225 (62)	213 (67)
Age at Weaning (days)	25.3 (3.0)	25.6 (3.3)
ADG Nursery (g/d)	467 (104)	419 (113)
Age at Nursery Exit (days)	67.1 (4.1)	67.9 (4.5)
ADG Finishing (g/d)	1081 (111)	1044 (119)
Weight per Day of Age (g/d)	768 (75)	734 (78)
Age at Finishing Exit (days)	162.4 (6.7)	162.1 (6.5)

Table 2.2. Number of pigs with growth records (by trait) for Landrace and Large White.

Trait	Landrace Records	Large White Records
Pre-Weaning ADG	61,895	61,435
Nursery ADG	13,807	12,458
Finishing ADG	10,267	7,671
Weight per Day of Age	51,234	40,331
Total Records	62,208	61,743

Table 2.3. Descriptive statistics for service traits for Landrace and Large White.

Item	Landrace	Large White
	\bar{x} (SD)	
Finishing Exit Weight (kg)	130.4 (11)	123.4 (12)
Age at Entry (days)	171.7 (7.2)	172.5 (9.3)
Age at First Service (days)	231 (18)	240 (27)
Entry to First Service Interval (days)	59.6 (18.2)	67.4 (25.4)
Serviced (%)	85.1	79.3
Serviced within 60 days of entry (%)	46	33.4

Table 2.4. Number of selected gilts with growth records (by respective trait) for Landrace and Large White.

Trait	Landrace Records	Large White Records
Pre-Weaning ADG	5,056	4,575
Nursery ADG	682	557
Finishing ADG	687	557
Weight per Day of Age	5,079	4,581
Total Records	5,086	4,610

Table 2.5. Covariates, fixed effects and random effects by trait for Landrace and Large White.

Models	Covariates			Fixed Effects				Random Effects				
	Wean Age	Nursery Exit Age	Finishing Exit Age	Wean Number	CG	Gender	Nurse Sow Parity	Nurse Litter	Room Pen Nursery	Room Pen Finishing	Additive Direct	Additive Maternal
PWADG	X			X	X	X	X	X			X	X
NADG		X			X	X	X	X	X		X	X
FADG		X	X		X	X	X	X		X	X	X
WDA			X		X	X	X	X		X	X	X
AFS					X						X	
ENTRY_FSI					X						X	
SERV					X						X	
SERV60					X						X	

¹ Trait Abbreviation: PWADG = pre-weaning average daily gain; NADG = nursery average daily gain; FADG = finishing average daily gain; WDA = weight per day of age; AFS = age at first service; ENTRY_FSI = gilt pool entry to first service interval; SERV = whether a gilt was serviced; SERV60 = whether a gilt was serviced within 60 days of entry; CG = contemporary group.

Table 2.6. Landrace Variance Components.

Trait	σ_a^2	σ_m^2	σ_c^2	σ_{rp}^2	σ_e^2
	Estimate (SE)				
PWADG	0.05 (0.01)	0.24 (0.02)	0.36 (0.01)	-	1.02 (0.01)
NADG	0.51 (0.11)	0.29 (0.08)	0.49 (0.04)	0.74 (0.05)	2.13 (0.06)
FADG	1.69 (0.36)	0.14 (0.01)	0.32 (0.05)	0.89 (0.06)	2.30 (0.19)
WDA	0.50 (0.04)	0.07 (0.01)	0.19 (0.01)	0.37 (0.01)	1.22 (0.02)
AFS	31.49 (5.49)	-	-	-	183.24 (5.70)
ENTRY_FSI	29.26 (5.91)	-	-	-	186.23 (6.09)
SERV	0.19 (0.07)	-	-	-	1.00 (0.01)
SERV60	0.16 (0.05)	-	-	-	1.01 (0.07)

¹ a = animal genetic, m = maternal genetic, c = common litter, rp = room and pen, e = residual

² Trait Abbreviation: PWADG = pre-weaning average daily gain; NADG = nursery average daily gain; FADG = finishing average daily gain; WDA = weight per day of age; AFS = age at first service; ENTRY_FSI = gilt pool entry to first service interval; SERV = whether a gilt was serviced; SERV60 = whether a gilt was serviced within 60 days of entry.

Table 2.7. Large White Variance Components.

Trait	σ_a^2	σ_m^2	σ_c^2	σ_{rp}^2	σ_e^2
	Estimate (SE)				
PWADG	0.02 (0.01)	0.23 (0.2)	0.45 (0.01)	-	1.23 (0.01)
NADG	0.32 (0.14)	0.24 (0.08)	0.62 (0.05)	1.14 (0.07)	2.99 (0.08)
FADG	1.99 (0.4)	0.17 (0.07)	0.38 (0.07)	0.74 (0.07)	3.04 (0.21)
WDA	0.63 (0.05)	0.05 (0.02)	0.20 (0.01)	0.42 (0.01)	1.41 (0.03)
AFS	32.88 (10.89)	-	-	-	363.95 (12.42)
ENTRY_FSI	32.90 (7.40)	-	-	-	368.59 (10.82)
SERV	0.21 (0.07)	-	-	-	1.00 (0.01)
SERV60	0.21 (0.06)	-	-	-	1.01 (0.01)

¹ a = animal genetic, m = maternal genetic, c = common litter, rp = room and pen, e = residual

² Trait Abbreviation: PWADG = pre-weaning average daily gain; NADG = nursery average daily gain; FADG = finishing average daily gain; WDA = weight per day of age; AFS = age at first service; ENTRY_FSI = gilt pool entry to first service interval; SERV = whether a gilt was serviced; SERV60 = whether a gilt was serviced within 60 days of entry.

Table 2.8. Landrace estimates of direct heritability (h^2) (diagonal), genetic correlations (r_g) (above diagonal) and phenotypic correlations (below diagonal).

Trait	PWADG	NADG	FADG	WDA	AFS	ENTRY_FSI	SERV	SERV60
PWADG	0.03 (0.01)	0.70 (0.28)	0.78 (0.31)	0.26 (0.13)	0.11 (0.25)	-0.39 (0.14)	0.07 (0.20)	0.10 (0.14)
NADG	0.30	0.12 (0.02)	0.37 (0.15)	0.51 (0.10)	0.01 (0.15)	0.14 (0.17)	-0.02 (0.23)	0.03 (0.21)
FADG	0.20	0.27	0.31 (0.05)	0.96 (0.01)	-0.20 (0.11)	-0.15 (0.11)	-0.43 (0.25)	0.16 (0.24)
WDA	0.32	0.54	0.91	0.21 (0.02)	-0.07 (0.09)	-0.05 (0.12)	-0.07 (0.15)	0.04 (0.15)
AFS	0.04	0.07	-0.13	0.04	0.15 (0.02)	0.91 (0.02)	-	-
ENTRY_FSI	0.02	0.01	-0.14	0.03	0.92	0.14 (0.02)	-	-
SERV	0.01	-0.12	0.00	0.03	-	-	0.15 (0.05)	-
SERV60	0.00	-0.05	0.07	-0.02	-	-	-	0.14 (0.04)

¹ Trait Abbreviation: PWADG = pre-weaning average daily gain; NADG = nursery average daily gain; FADG = finishing average daily gain; WDA = weight per day of age; AFS = age at first service; ENTRY_FSI = gilt pool entry to first service interval; SERV = whether a gilt was serviced; SERV60 = whether a gilt was serviced within 60 days of entry.

Table 2.9. Landrace estimates of maternal heritability (m^2) (diagonal), genetic correlations (r_g) (above diagonal).

	PWADG	NADG	FADG	WDA
	Estimate (SE)			
PWADG	0.141 (0.01)	0.61 (0.15)	0.59 (0.35)	0.62 (0.07)
NADG		0.068 (0.017)	0.98 (0.18)	0.97 (0.66)
FADG			0.026 (0.014)	0.97 (0.01)
WDA				0.029 (0.006)

¹ Trait Abbreviation: PWADG = pre-weaning average daily gain; NADG = nursery average daily gain; FADG = finishing average daily gain; WDA = weight per day of age.

Table 2.10. Large White estimates of direct heritability (h^2) (diagonal), genetic correlations (r_g) (above diagonal) and phenotypic correlations (below diagonal).

Trait	PWADG	NADG	FADG	WDA	AFS	ENTRY_FSI	SERV	SERV60
PWADG	0.011 (0.004)	0.32 (0.57)	0.30 (0.15)	0.31 (0.34)	0.52 (0.18)	0.31 (0.45)	0.18 (0.17)	-0.39 (0.23)
NADG	0.23	0.06 (0.02)	0.46 (0.15)	0.64 (0.08)	0.08 (0.28)	0.27 (0.25)	0.23 (0.24)	-0.14 (0.20)
FADG	0.15	0.18	0.31 (0.05)	0.98 (0.004)	0.41 (0.15)	0.21 (0.23)	0.06 (0.28)	-0.04 (0.25)
WDA	0.29	0.46	0.91	0.23 (0.02)	0.02 (0.14)	0.16 (0.10)	0.002 (0.17)	0.04 (0.13)
AFS	0.04	0.09	-0.11	-0.06	0.08 (0.02)	0.89 (0.08)	-	-
ENTRY_FSI	0.04	0.00	-0.13	-0.06	0.94	0.08 (0.02)	-	-
SERV	0.02	0.04	0.11	0.08	-	-	0.17 (0.05)	-
SERV60	-0.02	-0.01	0.13	0.04	-	-	-	0.17 (0.04)

¹ Trait Abbreviation: PWADG = pre-weaning average daily gain; NADG = nursery average daily gain; FADG = finishing average daily gain; WDA = weight per day of age; AFS = age at first service; ENTRY_FSI = gilt pool entry to first service interval; SERV = whether a gilt was serviced; SERV60 = whether a gilt was serviced within 60 days of entry.

Table 2.11. Large White estimates of maternal heritability (m^2) (diagonal), genetic correlations (r_g) (above diagonal).

	PWADG	NADG	FADG	WDA
	Estimate (SE)			
PWADG	0.115 (0.01)	0.53 (0.36)	-0.19 (0.15)	0.65 (0.16)
NADG		0.044 (0.01)	0.92 (0.05)	0.93 (0.05)
FADG			0.001 (0.0002)	0.73 (0.07)
WDA				0.019 (0.007)

¹ Trait Abbreviation: PWADG = pre-weaning average daily gain; NADG = nursery average daily gain; FADG = finishing average daily gain; WDA = weight per day of age.

Table 2.12. Correlations between direct and maternal additive effects (by respective trait) for Landrace and Large White.

Trait	Landrace	Large White
	Estimate (SE)	
PWADG	-0.22 (0.13)	-0.56 (0.14)
NADG	-0.13 (0.20)	-0.01 (0.30)
FADG	-0.42 (0.17)	-0.67 (0.12)
WDA	-0.22 (0.08)	-0.14 (0.11)

¹ Trait Abbreviation: PWADG = pre-weaning average daily gain; NADG = nursery average daily gain; FADG = finishing average daily gain; WDA = weight per day of age.

Table 2.13. Correlations between maternal effects of growth traits (rows) and direct effects of gilt traits (columns) in Landrace.

Trait	AFS	ENTRY_FSI	SERV	SERV60
	Estimate (SE)			
PWADG	0.14 (0.09)	0.26 (0.10)	0.13 (0.14)	-0.25 (0.09)
NADG	0.17 (0.22)	-0.13 (0.14)	0.10 (0.21)	0.13 (0.18)
FADG	0.40 (0.15)	0.18 (0.12)	0.01 (0.42)	-0.31 (0.24)
WDA	-0.10 (0.11)	-0.07 (0.15)	0.03 (0.20)	0.03 (0.19)

¹ Trait Abbreviation: PWADG = pre-weaning average daily gain; NADG = nursery average daily gain; FADG = finishing average daily gain; WDA = weight per day of age; AFS = age at first service; ENTRY_FSI = gilt pool entry to first service interval; SERV = whether a gilt was serviced; SERV60 = whether a gilt was serviced within 60 days of entry.

Table 2.14. Correlations between maternal effects of growth traits (rows) and direct effects of gilt traits (columns) in Large White.

Trait	AFS	ENTRY_FSI	SERV	SERV60
	Estimate (SE)			
PWADG	-0.16 (0.12)	-0.10 (0.12)	0.21 (0.15)	0.23 (0.12)
NADG	-0.39 (0.24)	-0.55 (0.17)	-0.01 (0.18)	0.24 (0.17)
FADG	-0.57 (0.21)	0.06 (0.23)	0.001 (0.409)	-0.22 (0.37)
WDA	-0.13 (0.18)	-0.43 (0.16)	-0.15 (0.27)	-0.09 (0.19)

¹ Trait Abbreviation: PWADG = pre-weaning average daily gain; NADG = nursery average daily gain; FADG = finishing average daily gain; WDA = weight per day of age; AFS = age at first service; ENTRY_FSI = gilt pool entry to first service interval; SERV = whether a gilt was serviced; SERV60 = whether a gilt was serviced within 60 days of entry.