Genetic associations between voluntary feed intake of females, finisher performance, and sow longevity

Project 2E-101

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By

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Executive Summary

An adequate level of sow feed intake during lactation is important for piglet survival and growth and to prevent excessive loss of sow body weight or condition during lactation, thereby contributing overall to improved production performance and sow longevity. It has been hypothesised that selection for efficient lean growth of finishing pigs reduces sow lactation intake as a correlated response, potentially hindering sow and piglet performance. Therefore, it was proposed that lactation feed intake should be included as a selection criterion in modern breeding programs (Eissen, 2000, Eissen et al., 2000). This study was designed to obtain data for estimating the genetic and phenotypic parameters which describe the associations between the suite of traits relating finisher feed intake and performance with the attributes of breeding sows, such as lactation intake, changes to sow body composition during gestation and lactation, their reproductive performance, and sow longevity to later parities. This information was largely unavailable prior to this study, but is essential to establish whether lactation feed intake, or for that matter other traits, are potential selection criteria for future breeding programs designed to improve overall outcomes for pig producers.

Results from this study demonstrated that lactation feed intake was a moderately heritable (h^2: ~0.15-0.25) and variable trait under *ad-libitum* feed delivery, and therefore could be considered as a selection criterion. However, the genetic correlation (ra) between feed intake of the growing pig (finisher) and lactating sow was relatively low (ra: ~0.30), implying that any correlated response in sow lactation feed intake resulting from selection for finisher intake attributes would likely be relatively small. Further, other traits typically in the breeding goal (eg growth traits) are positively correlated with sow lactation feed intake, providing a mechanism to counteract correlated reductions in feed intake typically associated with strong selection emphasis on efficiency or leanness. The genetic correlation between lactation intake and sow size is moderately positive, indicating that genetically larger sows also have greater intake capacity during lactation. Overall, the impact of selection for finisher characteristics on sow lactation feed intake will depend on the relative emphasis placed on individual traits. Further, it is important to note that low lactation intake also results from many non-genetic factors such as season, low parity, poor sow health pre- or post-farrowing, and feed delivery regimes, amongst other things, which can potentially be ameliorated through management changes, thereby contributing to improved longevity through to the following parities. Therefore, recording lactation feed intake data may be relatively more useful from a management compared to a breeding program perspective.

As a result of correlated responses in sow body composition, it is clear that breeding programs focussing on selection for efficient lean growth in finishers generally places sows at more risk during lactation because on average they have higher requirements, for sow maintenance and during gestation and lactation, along with lower fat reserves. This makes adequate provision of nutrition for individual sows increasingly difficult when selection occurs under breeding goals which contain both maternal and slaughter pig attributes, as occurs in Australia due to strong market pressures and the lack of more extreme genotypes for developing sire lines. This is particularly evident in the first parity when there is strong competition between maternal growth and litter requirements, where primiparous sows carrying large litters show evidence of reduced maternal weight and fat gains during gestation, which are risk factors for failed lactation and reduced retention to the second parity. In the face of several antagonistic genetic associations between sow and piglet outcomes, and evidence also for environmental constraints on sow performance, there is a clear need for more detailed models to evaluate outcomes from selection at both the genetic and phenotypic levels; thereby facilitating appropriate breeding program design and selection emphasis. Maternal breeding goals may benefit from using additional

selection criteria on breeding sow attributes, although parameters obtained in this study need validation from other populations to identify the most robust and reliable selection criteria. In addition, development of strategies to better meet requirements of individual sows and their litters during both gestation and lactation is required.

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1. Introduction

Phenotypic associations show the importance of lactation intake for sow and piglet outcomes

Several studies have demonstrated that sows need an adequate feed intake during lactation to minimise the probability of excessive weight loss during lactation and improve litter weight gains. In concert with direct effects on weight loss, insufficient feed intake in lactation has also been shown to have a negative impact on subsequent reproductive performance through increased weaning to oestrus interval, increased incidence of anoestrus, decreased conception rate and higher embryonic mortality rate (see review by Eissen et al., 2000). Clowes et al. (2003) estimated that losses of >9-12% of the parturition protein mass have an increasingly detrimental effect on ovarian function and lactation performance. Thus, poorer lifetime reproductive performance could be expected for sows with lower than required lactation feed intakes.

Based on commercial data (PigChamp), Koketsu and Dial (1997) showed that a high feed intakeduring lactation was associated with improved subsequent reproductive performance through reduced weaning to service interval and increased farrowing rate, litter size and litter weight at weaning (Table 1). They further suggested that a high feed intake during lactation alleviates at least some of the detrimental effects of short lactation (through early weaning) on subsequent reproductive performance. However, of note, in the comparison of Koketsu and Dial (1997), the daily feed intake of 2kg in the “Low” group would be very low by today’s standards, being lower than the average daily feed intake of a finisher. A more typical average lactation intake is 3-4 times that of a finishing pig, depending on lactation length.

Table 1 - Change in reproductive performance resulting from an increase of daily feed intake during lactation from 2 kg to 6 kg, by parity group (Koketsu and Dial, 1997).

Parity	Weaning to service interval	Farrowing rate (%)	Litter size (piglets)	Litter weight at weaning (kg)
First parity	8.4 to 7.3	82.5 to 89.1	10.5 to 10.8	42.5 to 46.7
later parities	5.5 to 5.0	82.0 to 89.2	10.9 to 11.5	45.5 to 50.5

Under conventional weaning systems, it is likely that the underlying mechanism of lactation feed intake on sow reproductive performance is mediated at least partly through the influence of sow body composition. Hughes et al. (1993) demonstrated that weight and back fat levels at weaning were significantly related to weaning-to-oestrus interval. Sows with a P2 back fat at weaning of less than 10 mm had a weaning to oestrus interval of 8.1 days. In comparison, sows with a P2 back fat of more than 13 mm had an average weaning to oestrus interval of 5.8 days.

High lactation feed intake also improves growth performance of offspring. At around 8 to 10 days of lactation, milk production of the sow limits growth rate of the piglet (Harrell et al. 1993, cited in Williams, 1995). The two main factors influencing milk production of the sow at this stage are the protein and energy supply in the diet and the body reserves of the sow (for a discussion see Williams, 1995). The effect of an increased feed intake on piglet weight gain was analysed by Eissen et al. (2003) using three genotypes. For each of these lines, total litter weight gain increased by 0.058, 0.19 and 0.12 kg/d with each additional 1kg/day of lactation feed intake. This is equivalent to an increase in piglet growth rate of 5.5, 18.1 and 11.4 g/d for a litter size of 10.5 piglets per litter. Higher pre-weaning performance also has a "carry-over" effect on the post-weaning performance, making early growth benefits cumulative. Mahan et al. (1998) showed that piglets with higher weaning weight also had higher post-weaning growth until slaughter and consumed less feed from weaning to 105 kg body weight than piglets with lower weaning weight. Supporting this observation, Hermesch (2002) reported phenotypic correlations of 0.32 and 0.26 between weight at or gain to 14 days of age and lifetime average daily gain.

Feed intake during lactation was previously recorded at Rivalea Australia (formerly QAF Meat Industries) on a small sample of sows during 1999/2000. In this study, mean feed intake during lactation was lower in first parity (5.78 kg/d) compared to the second and third parity (6.34 kg/d and 6.58 kg/d) sows, and considerable variability between sows was evident (Table 2). QAF sow feed intakes were consistent with the earlier NRC (1987) summary of intake from several sources. For comparison, Cooper et al. (2001) reported mean intake values for the corresponding parities of 6.90, 7.40 and 7.20 kg/day. A later internal study at Rivalea Australia (2002) with 4× per day feeding exhibited higher feeding rates of 6.5 kg/day for primiparous sows, or 7.6 to 7.8 kg/day for higher parity sows, demonstrating the importance of knowledge on factors such as feed delivery schedule when comparing lactation intakes across populations. In a comparison of six sow genotypes at a single site, the range of sow line differences in average lactation feed intake was 8.7 kg, or 0.58 kg/day over an average 15-day lactation (Moeller et al. 2004).

Table 2 - Number of records (N), mean, standard deviation (SD) along with minimum and maximum for feed intake (kg/d) of the sow during lactation (Rivalea Australia, 1999/2000).

Parity	N	Mean	SD	Minimum	Maximum
First parity	237	5.78	0.82	3.67	7.80
Second parity	166	6.34	0.75	4.43	7.91
Third parity	98	6.58	0.76	4.20	8.20

In the previous Rivalea studies, there were no concurrent data to illustrate the direct association of feed intake with the post-weaning growth performance of their piglets. However, some of this effect may be represented by the sow parity effect on growth performance of the piglet through to the finishing pig. In a separate data set (UNE23P/1335: Hermesch 2002), parity of the sow influenced both piglet growth and lifetime average daily gain. Piglet growth from birth to 14 days increased from 188 to 216 and 225 g/d across the first three parities. Further, lifetime growth rate was lower (20 g/d) for pigs born in a first parity litter in comparison to pigs born in later parity litters. However, in addition to the effects of lactation intake, observed parity effects on piglet growth are a combination of multiple factors, such as the parity effect on piglet birth weight and immune status, as well as mothering ability and the influence of intake on milk production attributes.

Feed intake of the lactating sow is also influenced by season (Figure 1). Data on feed intake during lactation at Rivalea were available from October 1999 to July 2000. A clear seasonal trend was apparent, with intake being lowest in the summer months and highest during winter, reflecting adaptation of feed delivery to feed clearance during lactation. Moreover, these trends might also partly reflect seasonal changes to gestational delivery of feed, which can subsequently affect intake levels during lactation. The difference in daily intake between winter and summer exceeded 1 kg/d, although considerable variation between sows in their feed intake was evident over all seasons. Low feed intake during lactation in summer probably contributes to the phenomenon of seasonal infertility, through the mechanisms outlined above. However, it is important to note that some research suggests that altered lactation performance at high ambient temperatures is only partially explained by accompanying reductions in sow feed intake (de Braganca et al., 1998; Farmer and Prunier, 2002).

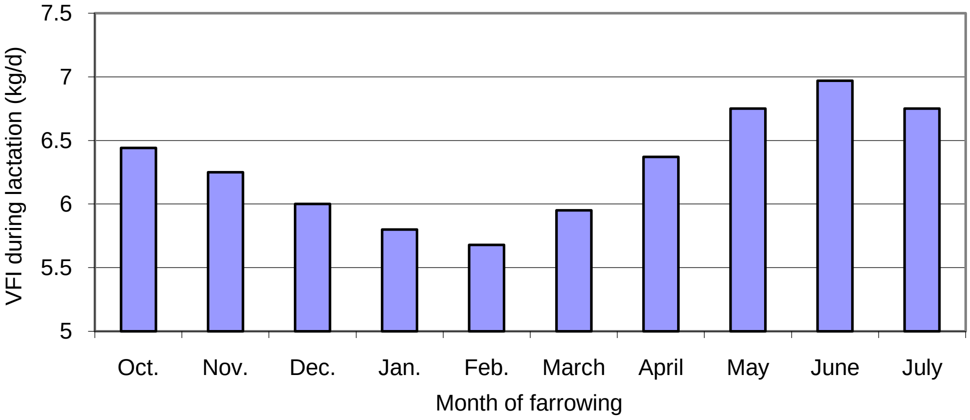

Figure 1- Mean feed intake during lactation for different months of farrowing

Genetic associations between lactation intake and other traits are unknown

While the phenotypic associations between lactation feed intake characteristics of sows and outcomes for sows and their piglets have been the subject of much research, previous research has generally been inadequate to elucidate the genetic contributions to trait associations. Moreover, it is unclear what implications historical selection might have for current sow and piglet attributes.

It was hypothesized that feed intake of sows during lactation may be correlated with feed intake and performance during the grower/finisher phase. Therefore, selection for improved efficiency of finishers under *ad-libitum* intake, which can be associated with reduced feed intake, may result in a correlated reduction in feed intake of sows during lactation, which downstream may be contributing to increasing problems with poor sow longevity (Smits et al., 2005). Even if appetite and feed intake capacity of the modern sow were not reduced through the selection process, Eissen (2000) argued that higher maintenance requirements and increased milk production of the modern sow place heavier demands on maintaining high enough levels of intake for modern sows. Therefore, increasing the capacity for lactation intake might be more desirable than simply maintaining intake capacity. Further, sows must be able to rapidly adapt their feed intake to these higher levels after farrowing, following the typically restricted delivery of food during gestation and prior to farrowing.

This project was designed to obtain the necessary data on feed intake, during both finishing and lactation phases, growth performance and reproductive performance to establish the effects of selection on sow attributes and lactation feed intake. The very small data set of van Erp et al. (1998) previously demonstrated that sow lactation feed intake was heritable and likely correlated with finisher intake (rg: 0.92±0.50), but their parameter estimates were very imprecise. Generating more detailed data in this area will facilitate development of breeding programs that consider reproductive performance of a sow over her lifetime along with traits targeted to improved efficiency of production in growing pigs.

Are there alternatives to directly recording feed intake during lactation?

In the absence of automated feeding systems for farrowing crates, accurate measurement of lactation feed intake under *ad-libitum* feeding is relatively labour intensive and therefore costly. Previous studies have shown that feed intake of the finisher is genetically (rg) and phenotypically (rp) correlated (averages of rg: 0.41; rp: 0.09) with IGF-I measured in weaner pigs (Bunter et al., 2005). Thus, measuring IGF-I of the sow at weaning could potentially be an alternative to measuring lactation feed intake directly. More importantly, weaning IGF-I may be a better indicator of sow physiological status at weaning and therefore rebreeding success than measures such as actual feed intake or sow body composition.

Moyes (2004) indicated that in mature dairy cows IGF-I is a good measure of energy status and can be used to predict reproductive performance of dairy cows. IGF-I recorded during lactation is low in cows with high milk production, subsequently having a negative association with ovulation and fertility (eg Taylor et al., 2004). Van den Brand et al. (2001) also showed that plasma IGF-I concentrations recorded during lactation were associated with body condition and the intensity of the pre-ovulatory LH surge in primiparous sows. However, a very small study (N=25 sows) by Clowes et al. (2003) showed no association between plasma IGF-I concentrations measured during lactation and sow body composition or ovarian function, which is unsurprising given the small N. Apart from potential consequences of results for breeding program development, it is also plausible that through identifying sows in poor energy balance at the end of lactation, it will be possible to implement management interventions for individual sows more accurately, that will improve the chance of their rebreeding success.

Purpose of this project

Retrospective phenotypic studies, such as that of Koketsu and Dial (1997), do not necessarily elucidate underlying causes observed associations between sow feed intake during lactation and lactation or rebreeding outcomes. For example, “Low” intake may simply reflect other underlying conditions leading to anorexia, lactation and rebreeding failures, making intake an indicator trait of other problems, rather than a root cause of outcomes *per se*. In this project, recording concurrent information on genetic merit, health status and the thermal environment may better identify the development of associations between feed intake and other traits.

Secondly, estimation of genetic associations between lactation feed intake and other traits requires data collection in pedigreed populations. There are very few studies with the necessary data volume and structure to accurately estimate genetic parameters between sow lactation intake and other traits. In particular, feed intake is rarely recorded in maternal line finishers. This project will seek to evaluate how selection traits are correlated with sow attributes and reproductive performance in commercially relevant maternal lines.

Hypotheses considered in this project

1. Feed intake of the sow during lactation is a heritable trait, and genetically correlated with feed intake of finishers

2. Higher feed intake of the sow during lactation improves lifetime reproductive performance of the sow, pre- and post-weaning piglet growth, and subsequently lifetime performance of the growing pig
3. Sow IGF-I concentrations measured at weaning are heritable, are related to feed intake and are associated with reproductive success

2. Methodology

Data collection

Feed intake of growing gilts. Post selection at 20 weeks, feed intake of project gilts from two maternal lines (Large White and Landrace) was recorded using electronic feeders, while under *ad-libitum* feeding in group pens. Prior performance test data (ie finishing weight, fat depth and loin muscle measures) was available for these gilts, their unselected cohorts and as historical data. This strategy maximised the number of feed intake tested female finishers that entered the boar shed, without introducing significant bias to genetic parameters through un-recorded selection.

The fate of gilts performance tested for feed intake was subsequently recorded until they were culled (reasons for culling were known). During the project period, sow turn over to maximize genetic progress in the breeding program was relaxed. Longevity was established within the four-year project until parity 4 for all sows. Longevity to parity 6 on all sows would be completed in late 2010, after the project completion date.

Feed intake of sows during lactation. Feed intake of sows that farrowed was subsequently recorded during their first lactation. A proportion of project sows also had feed intake recorded during their 2nd lactation. Concurrent data collection included fostering events and piglet deaths, along with medication events for sows and suckling piglets.

The feed intake level of lactating sows is limited by the ability of staff to deliver feed regularly, including overnight, feed hopper size characteristic of farrowing crates (outlined in results from the previous Rivalea lactation trial: 01R108) and feed delivery or diet during the gestation period. Prior to farrowing sows were fed a restricted diet (maximum ~3kg per day, seasonally dependent). Following farrowing, lactating sows were then fed ‘to appetite’ a minimum of three times daily and recorded for their daily feed intake. The proportion of hoppers empty first thing in the morning was monitored to establish how closely feed delivery and intake reflected *ad-libitum* feeding, and sow-feeding levels were adjusted to accommodate this if necessary. Since spoiled food can reduce feed intakes, uneaten spoiled food was removed and weighed (if dry) to adjust daily feed intake records. Daily records were subsequently used to assess the information content of partial lactation data.

Sow body condition. Changes to sow body condition during lactation along with sow protein reserves, ultimately related to mature weights, influence sow reproductive performance. Data on finisher sow weights were augmented with additional weights recorded immediately prior to entry to the boar shed, and sow weights at each weaning where the prior lactation feed intake was recorded. Sows which were weaned early were generally not weighed or scanned at weaning but, if they were remated, they were weighed and scanned at mating. Sow condition was monitored through P2 and P4 fat depth, measured pre-farrowing and post-weaning when sows were weighed. In addition, first parity sows were bled to assay

IGF-I levels at weaning, while a sub-sample of second parity sows were also bled. All sows bled for IGF-I testing were fasted overnight.

Ambient temperature. Since ambient temperatures influence feed intake of lactating sows (Renaudeau et al., 2005) it was intended to record ambient temperature using data loggers fixed at sow height in the farrowing sheds. However, validated hourly data from the Rutherglen station, approximately 16km from the piggery) were instead purchased from the Australian Bureau of Meterology.

Litter records. Uni-directional cross-fostering of piglets was generally conducted within 24 hours of farrowing for project sow litters. Therefore, in addition to litter birth weight and number, the number of piglets and litter weight on day 1 after fostering was recorded. Piglet transfer dates, but not weights, were recorded for later fostering events. Litter weights were recorded again at 10-days post farrowing, along with the number of pigs contributing to these weights. Details on the health status of the sow and piglets at 10 days were recorded via medication events.

Analyses

Analyses were targeted at:

1. establishing whether sows can be recorded for feed intake over part of their lactation, assuming feed intake during lactation warrants inclusion as a selection criterion in breeding programs. It will also highlight if partial lactation records (ie stages of lactation) have differential associations with piglet or sow reproductive performance.
2. estimation of the genetic relationships between feed intake of gilt finishers and their *ad-libitum* feed intake as a lactating sow, along with correlations with performance, reproduction and longevity traits.
3. estimating the associations (genetic and phenotypic) between sow IGF-I at weaning with lactation intake and rebreeding.

Models for analyses were developed and genetic parameters estimated using standard statistical procedures and methodology. Estimates of heritability and genetic correlations between performance traits and subsequent sow body composition or reproductive attributes were estimated using ASREML (Gilmour et al., 2006). Parameters for binary traits were estimated on the underlying scale using a logit link under a sire model for all trait combinations involving a binary trait.

Project Deliverables

The project specifically establishes genetic and phenotypic relationships between several sow traits (lactational feed intake, sow IGF-I, sow weight and fat depths) and other economically important performance and reproductive traits. This information is required to develop appropriate breeding programs that can concurrently target efficient production and improved sow lifetime reproductive performance.

3. Outcomes

The range of analyses performed on data arising from this project, in combination with data collected in project 2D-104-0506, extends beyond the estimation of genetic parameters alone. In this section the primary outcomes only are detailed.

The accompanying peer reviewed publications arising from these analyses provided further technical detail.

Data Characteristics

Raw data characteristics for pre-selection performance, feed intake (as post-finisher gilts), weight and fatness pre-mating and the farrowing incidence for specific parities are summarised in Table 3. Due to prior selection, project gilts were younger, faster growing and leaner than historical gilts at selection, with a lifetime average growth rate of 611 g/day to 19.5 weeks of age. Growth rate from 20 to 25 weeks averaged 844 g/day, with an average daily intake of 2.50 kg/day and an FCR of 3.03. By 29 weeks of age, which was just prior to entry to the breeding facility, sows averaged 142 kg and 15.2 mm fat depth (averaged across P2 and P4 sites). The weight and fatness of sows at their first mating in parity one averaged 157 kg and 17.1 mm, and in their second parity averaged 198 kg and 17.6 mm. Litter size and birth weight traits for project females were similar to or slightly better than historical data.

The percentage of selected gilts which farrowed in parity 1 was 64%. However, this relatively low percentage was primarily due to over-selection of gilts prior to feed intake testing, followed by elevated culling rates to maintain constant mating numbers. Selection above requirements was required to maximize the amount of feed intake data recorded and to allow for increased culling losses following early selection, which limits the accuracy of evaluating locomotion, and the impact on soundness of subsequent high growth under *ad-libitum* feeding in the electronic feeders. The percentages of first parity sows that subsequently farrowed (or were transferred in late pregnancy) in later parities were 76, 63, 51 and 42%, up to parity five. The relatively low percentage of sows farrowing in the second parity reflected a deliberate policy, for at least part of the data recording period, of culling primiparous sows which had a failed in their first lactation.

Sow characteristics pre- and post-farrowing, along with their reproductive performance, are shown for each parity in Table 4. Predicted sow weight post-farrowing (SWPF) was based on equations developed from purebred and F1 commercial sows, which had data for pre- and post-farrowing sow weight and litter weight traits. SWPF was calculated separately by parity as:

$$\text{SWPF} = \text{WT110} - (6.28 + \text{TB} \times 1.164) + (\text{days until farrowing} \times 0.69) \quad \text{(Parity 1)}$$

$$\text{SWPF} = \text{WT110} - (5.19 + \text{TB} \times 1.164) + (\text{days until farrowing} \times 1.20) \quad \text{(Parity 2)}$$

Table 3 - Performance trait characteristics of project sows and their historical counterparts, along with the incidence of herd entry and survival to later parities

Trait	N	Mean (SD)	Min-Max	CV
		Traits recorded prior to selection (historical records)		
TAGE	56529	147 (7.26)	112-173	5
FWT	56305	88.1 (12.0)	56-147	14
LADG	56305	594 (72.5)	366-936	12
AVEMD	56124	10.7 (2.38)	6-22	22
EMD	56271	42.7 (5.84)	22-70	14
		Traits recorded prior to selection (project records)		
TAGE	3369	137 (2.76)	120-158	2
FWT	3370	84.0 (8.79)	50-115	11
LADG	3369	611 (61.9)	362-822	10

Trait	N	Mean (SD)	Min-Max	CV
AVEMD	3369	9.96 (1.97)	5-20	20
EMD	3370	41.9 (2.76)	25-65	7
Feed intake test data				
TADG	3270	844 (162)	298-1405	19
ADI	3269	2.50 (0.41)	1.1-4.4	16
FCR	3269	3.03 (0.54)	1.4-5.2	18
Pre-mating data				
29WT	2958	142 (12.6)	99-194	9
29FT	2951	15.2 (3.41)	6-29	22
Binary traits				
PAR1	3372	0.64	0 or 1	-
PAR2	2259	0.76	0 or 1	-
PAR3	2259	0.63	0 or 1	-
PAR4	2259	0.51	0 or 1	-
PAR5	2259	0.42	0 or 1	-

Trait Abbreviations

TAGE: age when performance test was completed (days)
FWT: weight at end of performance test (kg)
LADG: lifetime average daily gain (g/day)
AVEMD: fat depth averaged across P2 and P4 sites (mm)
EMD: loin muscle depth (mm)
TADG: average daily gain on feed intake test (g/day)
ADI: average daily feed intake (kg/day)
FCR: feed conversion ratio (ADI/TADG: kg/kg)
29WT: weight at 29 weeks of age (kg)
29FT: average fat depth at 29 weeks (mm)
PAR1: selected gilt farrowed in parity 1 (0/1)
PAR2-5: farrowed sow (P1) has later farrowed in P2, P3, P4 or P5 (0/1)

Compared to historical data, the average weight of sows at first mating and later parities has increased (Table 4), thereby increasing sow maintenance requirements. Maternal weight and fat gains during gestation were moderately (CV: 28 & 40) to extremely (CV: 176 and 602) variable amongst sows, and this variability amongst sows increased with parity. Maternal weight and fat gains were lower in the second compared to the first parity, such that sows were heavier but leaner pre-farrowing in the second parity. On average, sows failed to fully regain subcutaneous fat depths observed in the first parity by their second farrowing. Of note, some sows lost significant percentages of maternal weight and fatness during the gestation period.

Table 4 - Sow characteristics pre- and post-farrowing, along with reproductive performance, lactation feed intake, and changes to sow body composition during gestation and lactation

Trait	Parity	N	Mean (SD)	Min-Max	CV
Traits recorded prior to farrowing (~ day 110 of gestation)					
WT110	1	2279	224(19.8)	150-289	9
	2	1558	259(22.7)	179-362	9
FT110	1	2260	19.3(3.98)	7.5-35.5	20
	2	1552	18.4(3.70)	8.5-35.0	20
Post farrowing data (including historical sows)					
TB	1	19680	12.0(3.30)	1-29	28
	2	13991	12.1(3.04)	1-22	25
NBA	1	19681	10.3(2.80)	0-19	27

Trait	Parity	N	Mean (SD)	Min-Max	CV
	2	13991	11.2(2.95)	0-21	26
APBW	1	6140	1.40(0.25)	0.63-2.50	18
	2	4258	1.57(0.26)	0.63-2.50	17
SWPF	1	2259	209(19.2)	135-271	9
	2	1553	247(22.5)	172-349	9
MWG	1	2225	51.7(14.7)	-10 to 108	28
	2	1522	47.1(18.8)	-27 to 131	40
MFG	1	2221	2.06(3.62)	-13.5 to 14.5	176
	2	1477	0.56(3.37)	-12.0 to 13.0	602
LITG	1	1979	10.0(6.11)	-13 to 33	61
	2	1219	13.3(6.62)	-18.0 to 37.2	50
			Lactation feed intake data		
LADI	1	2027	4.99(1.10)	0.5-9.0	22
	2	1431	6.11(1.09)	1.67-8.57	18
LADINS	1	1778	5.20(0.88)	2.02-7.85	17
	2	1354	6.21(0.98)	2.89-8.57	16
SHORT	1	2052	0.13	0 or 1	-
	2	1441	0.06	0 or 1	-
			Sow traits at weaning		
WTW	1	1952	197(17.9)	129-265	9
	2	1476	230(20.7)	141-292	9
FTW	1	1912	17.4(3.49)	6.5-32.0	20
	2	1458	16.9(3.45)	6.5-30.5	20
WΔL	1	1931	-11.3(15.1)	-74 to 39	133
	2	1468	-16.7(16.6)	-112 to 53	100
FΔL	1	1882	-1.99(3.17)	-16 to 8.5	159
	2	1448	-1.46(3.02)	-15.0 to 13.5	207
SIGF	1	1510	381 (121)	55-933	32
	2	540	361 (136)	46-864	38

Trait Abbreviations

WT110: pregnant sow weight at entry to the farrowing shed
FT110: fat depth averaged across P2 and P4 sites (mm)
TB: total born (NBA+stillbirths only, pigs/litter)
NBA: number born alive (pigs/litter)
APBW: average birth weight of live born piglets (kg)
SWPF: estimated sow weight post-farrowing (kg)
MWG: maternal (not total) weight gain during gestation (kg)
MFG: maternal fat gain during gestation (mm)
LITG: total litter gain from day 1 to day 10 (kg)
LADI: average daily lactation feed intake (kg/day)
LADINS: LADI with short or failed lactations removed (kg/day)
SHORT: lactation was completed or failed (0/1)
WTW: sow weight at weaning (kg)
FTW: sow fat depth at weaning, averaged across P2/P4 (mm)
WΔL: weight change during lactation (WT110-WTW: kg)
FΔL: fat change during lactation (FT110-FTW: mm)
SIGF: Sow IGF-I concentration recorded at weaning (ng/ml)

Overall, sow weight was lowly variable (CV~10%). However, sow fatness was more variable (CV~20%), and fat gain during gestation was extremely variable (CV 176-602%) compared to weight gain in gestation (CV 28-40%) or weight and fat loss during lactation (CV 107-207%). Mean values essentially do not convey the high variability amongst individual sows in the change to their body condition during gestation and lactation, which will have an impact on their physiological status prior to farrowing and therefore lactation outcomes. Maternal weight and fat losses during lactation averaged 11.3 (16.8) kg and 1.99 (1.46) mm in the first (and second) parity. Piglet birth weight in each parity averaged 1.42 and 1.57 kg/pig (CV<20%) for TB of 11.6 and 12.5 pigs/litter (CV<10%). Litter gain in this study, which is a trait combining weight gain and piglet mortality components, was relatively low to day 10, but substantially higher in litters with good survival rates because piglet mortality has a large impact on this measure of total litter weight.

Raw data for insulin-like growth factor-I concentration, assayed for sows bled at weaning, was more variable with respect to the mean than weight or fatness at weaning. However, about 28% (40% in parity 2) of the observed variation in SIGF was explained by the systematic effects of farrowing month, assay batch and to a lesser extent, line effects.

Attributes of lactation intake as a trait and the implications of partial recording of lactation feed intake

Average lactation intake, defined as the average intake across the entire lactation period, is confirmed as a moderately heritable trait in primiparous (h^2=0.14) and second parity sows (h^2=0.24)(Table 5). Increasing estimates of heritability with parity suggest that genetic potential for intake is better expressed in later parities. However, the lower heritability for primiparous sows in this study was predominantly because residual variation was proportionally larger. Primiparous sows are more prone to post-farrowing complications which affect both daily feed intake records and the lactation length (Bunter et al., 2009a), as was illustrated by the higher incidence of shortened lactations due to lactation failure (Table 4). Higher heritability estimates for lactation feed intake reported by other researchers are generally estimated from multi-parity data (Hermesch, 2007; Bergsma et al., 2008).

Table 5 - Heritability estimates (h^2×100) and the phenotypic variance (σ^2p) by parity (1 & 2), along with environmental (re), additive genetic (ra) and phenotypic (rp) correlations between parities

	Systematic effects fitted in models	Parameter Estimates				
		h^2×100	σ^2p	re	ra	rp
SWPF	YM,L,AGE(L)	26	278	51±3	88±7	59±2
	YM,L	21	464			
WTW	YM,L,AGE(L)	36	286	64±3	88±5	72±1
	YM,L,AGE(L)	31	413			
WTΔG	YM,L,AGE(L)	13	190	11±4	88±17	22±1
	YM,L,AGE(L)	16	295			
WTΔL	YM,L,AGE(L),ND1	20	196	13±5	88±14	28±2
	YM,L,AGE(L)	19	251			
FT110	YM,L,AGE(L&Q)	37	11.9	34±4	88±7	50±2
	YM,L	26	12.0			
FTW	YM,L,AGE(L)	36	11.3	64±3	88±5	72±1
	YM,L,AGE(L)	23	10.4			
FTΔG	YM,L,AGE(L)	21	9.93	7±4	46±52	10±3
	YM,L,AGE(L)	2	10.3			
FTΔG*	YM,L,AGE(L),FTM(L)	21	7.87	16±4	57±25	21±3
	YM,L,AGE(L),FTM(L)	4	8.19			
FTΔL	YM,L,AGE(L),ND1(L)	11	8.56	-2±4	B	3±3
	YM,L,AGE(L)	1	8.72			

	Systematic effects fitted in models	Parameter Estimates				
		h^2×100	σ^2p	re	ra	rp
FTΔL*	YM,L,AGE(L),ND1(L),FT110(L)	18	6.72	8±4	120±23	22±3
	YM,L,AGE(L),FT110(L)	9	6.60			
TB	YM,L,MOD,AGE(L)	12	10.7	11±1	77±5	18±1
	YM,L,MOD,AGE(L)	9	9.01			
NBA	YM,L,MOD,AGE(L)	9	7.60	14±1	73±7	19±1
	YM,L,MOD,AGE(L)	7	8.42			
APBW	YM,L,AGE(L),NBA(L)	36	0.047	18±3	86±4	42±1
	YM,L,AGE(L),NBA(L)	33	0.047			
LITG10	YM,L,ND1(L)	9	36.1	16±4	68±36	20±3
	YM,ND1(L)	7	41.7			
LADI	YM,L,LL(L)	14	0.62	14±5	91±14	28±3
	YM,TMT,AGE(L&Q)	24	0.71			

See Table 4 for trait definitions. YM: recording year-month; L: sow line; AGE: age at first farrowing (days); FTM: average fat depth at mating (mm); ND1: number of piglets at day 1; MOD: farrowing module; LL: lactation length (days); TMT: feeding treatment. (L) and (Q) indicate variable was fitted as a linear and quadratic covariate, respectively.

Variation in lactation length was a significant factor describing average lactation feed intake in both parities because average intakes are higher for sows that do not suffer a lactation failure (Table 4). However, lactation length itself was a heritable trait (h^2: 0.06±0.03) in this population for the first lactation. This phenomenon might arise directly through genetic differences in lactation potential of first parity sows. Alternatively, or concurrently, it might also arise through the effects of heritable variation in sow body composition attributes prior to their first farrowing on lactation outcomes. This contrasted with second parity results. The absence of any genetic component to variation in lactation length in the second parity was accompanied by a lower frequency of lactation failure (Table 4), but could also indicate that lactation failure in multiparous sows does not generally have a genetic basis. Other researchers have indicated that lactation length was not heritable in their multi-parity data (eg. Bergsma and Hermesch, pers. comm.), suggesting that overall the heritability of this component will likely be low.

Fitting lactation length in models for average daily feed intake is also an indirect way of accounting for variation in sow health during lactation. In addition to previously demonstrated effects of parity and season on average lactation intake in this and other (Jones and Hermesch, 2007) populations, it has also been shown in this project that average lactation intake is lower in sows which have required medication prior to farrowing or within the lactation period (Bunter et al., 2008; Bunter et al., 2009a; Lewis and Bunter, 2009). This is consistent with expectation, since the type of health issues for which sows are generally medicated typically are associated with an anorexic response. Moreover, the favourable phenotypic associations observed between lactation intake, sow longevity and piglet performance are stronger in the subset of data for medicated sows, suggesting maintaining high intake during health challenges is very important for favourable phenotypic outcomes (Bunter et al., 2009a). The higher incidence of lactation failures (and medication events) in primiparous compared to second parity sows suggests greater attention to developing strategies to improve gilt health and screening during gestation, pre- and post-farrowing may be required to improve first parity lactation intakes and reduce sow attrition rates prior to the second parity (see Lewis and Bunter, 2009). An increased rate of complications during the first pregnancy and lactation, compared to later parities, is common in most species of mammals, particularly when parturition occurs at a physiologically young age. In France, the recommended age at first mating for sows has increased to 250 days after data has shown that this strategy results in improved sow longevity and piglet survival (Isabelle Merour, IFIP, 2010, pers comm).

In contrast to results for average lactation intake, and also to comparable results for finishing pigs recorded for daily lactation intake (Schnyder et al., 2001), lactation intake recorded on a single day has very low heritability (Lewis et al., 2010). This means that also in contrast to results for finishers, the day to day expression of feed intake during the lactation phase is highly variable and provides little information on the genetic potential of sows for lactation intake. It is therefore very necessary to record lactation intake over a sufficient interval to generate a consistently heritable trait. The number of days over which recording is required depends on the measurement error associated with daily records (see Lewis et al., 2010), which will depend on the method of feed delivery and recording. In addition, the most appropriate interval to record will depend on which phase of lactation feed intake is considered to be most limiting or informative, whether feed delivery systems limit data recording, and what attrition in sow numbers occurs before the recording period (since it is generally desirable not to have censored data). For example, the time period immediately following farrowing is directly influenced by farrowing outcomes, often “step up” feeding systems and is also not a period of high piglet demand for milk production, making it a less desirable and/or informative period for recording from the perspective of genetic evaluation for appetite. In a separate study, Hermesch (2007) reported a heritability of only 0.02±0.02 for average lactation intake recorded in the first week post farrowing under a step up feeding program, which increased to 0.12-0.17 for records in later time periods as sows were fed more to individual demand. Recording lactation intake after week one may be beneficial in this scenario.

The effect of thermal environment on the heritability for lactation intake was also investigated in further detail. Since maintaining high lactation intakes during Summer is of considerable interest in the Australian Industry, genetic variation for intake during high temperatures is of greater relevance than genetic potential for intake at lower temperatures. Random regression analyses were used to demonstrate that the heritability of lactation intake gradually declined with increasing temperature at recording (Lewis et al., 2010). That is, at high temperatures less of the variability in intake amongst sows is due to genetic variation. In contrast, expression of genetic variation for lactation intake is increased in the colder months, where the heat increment of feed is less problematical for sows to dissipate and they are more able to express intake.

Finally, the repeatability of average lactation intake across the first and second lactations was evaluated via the estimated phenotypic correlation (Table 5). The very low phenotypic correlation between the first and second parity for lactation intake (r=0.28) indicates that individual sows generally did not consistently display the same relative ranking for lactation intake across their consecutive farrowings. For comparison, phenotypic correlations between parities for average lactation intake ranged between 0.31 and 0.46 in the study of Hermesch (2007). Since sows adapt their lactation intake to their own body condition at farrowing, to farrowing outcomes and health status, along with the suckling litter size (Bunter et al., 2007; Bunter et al., 2008), which are also lowly repeatable, this result is perhaps not surprising. However, a low repeatability for lactation intake suggests that the phenotypic association between lactation intake and survival to the subsequent farrowing is driven by temporary environmental influences rather than permanent characteristics of the individual sows. Therefore, culling associated with low lactation intake is due largely to unfavourable current parity outcomes, which could potentially be addressed through developing better management strategies, rather than permanent attributes of the sow.

With respect to systematic effects, solutions for these were discussed in detail in Bunter et al. (2008) and are only outlined briefly here.

The impact of selection for finisher attributes on sow characteristics

Mature size, reproductive performance and longevity of a genetically similar sample of gilts can be altered by varying the environment and management under which the gilts are reared both prior to herd entry and throughout subsequent reproductive cycles. What is not well quantified is how gilt attributes at selection (individual phenotype) and genetic potential (EBV) are associated with subsequent body development of the sow, particularly since maternal development in early parities occurs concurrently (in competition) with the demands of reproduction. Genetic and phenotypic correlations between attributes at selection and pre-mating characteristics, along with subsequent characteristics as a breeding sow are shown in Table 6. All traits are as defined previously.

Heritability estimates (Table 6) demonstrate that weight and fatness remain moderately heritable traits throughout a sow's life: heritability estimates (×100) for LADG, 29WT, SWPF (parity 2: p2) and WTW (p2) were 21, 29, 24 (18) and 33 (27); additive genetic variation for weight increased with parity. Corresponding heritability estimates for BF, 29FT, FT110 and FTW were 38, 53, 33 (22) and 35 (26), but additive genetic variation for fatness declined with parity.

Table 6 - Estimates (×100) of additive genetic (ra) and phenotypic (rp) correlations between performance traits and later sow attributes along with sow survival to later parities

Trait	**h^2×100**	**σ^2p**	**LADG 21 4789**		**BF 38 3.47**		**EMD 19 20.9**		**TADG 16 21848**		**ADI 25 0.14**		**FCR 25 0.24**	
			ra	rp	ra	rp	ra	rp	ra	rp	ra	rp	ra	rp
29WT	29	150	**87**	**66**	**18**	**5**	**-16**	**-7**	**61**	**46**	**50**	**43**	-6	**-11**
29FT	53	8.32	6	**-8**	**90**	**64**	4	0	6	3	**45**	**28**	29	**18**
SWPF	24	273	**74**	**42**	-5	-2	-4	**-5**	**54**	**27**	**29**	**15**	-21	**-15**
	18	452	**62**	**32**	-12	-1	12	-5	**47**	**16**	**27**	**7**	-15	**-10**
WTW	33	285	**61**	**39**	4	-3	-2	**-8**	**60**	**26**	**47**	**19**	-15	**-11**
	27	395	**55**	**37**	-3	0	14	-5	**64**	**24**	**42**	**16**	-19	**-12**
WTΔG	15	179	7	**-5**	-13	-2	3	0	-2	**-8**	**-42**	**-18**	**-37**	**-8**
	16	295	6	-2	-14	0	11	3	-12	-5	-24	**-10**	-11	-2
WTΔL	23	194	-16	0	13	1	6	-1	22	3	24	5	-2	1
	20	249	-5	4	13	0	6	1	**37**	**8**	**35**	**12**	-1	0
FT110	33	11.9	**28**	**12**	**75**	**38**	5	-2	11	5	**46**	**17**	**31**	**9**
	22	12.0	**28**	5	**83**	**32**	11	-2	22	**6**	**54**	**11**	**36**	4
FTW	35	11.3	**17**	**11**	**73**	**41**	3	**-5**	19	**9**	**53**	**21**	**27**	**9**
	26	10.5	7	**7**	**70**	**33**	16	-2	23	**6**	**55**	**14**	**28**	**6**
FTΔG	22	9.76	**-36**	**-15**	**-37**	**-14**	16	**4**	-8	**-16**	**-33**	**-23**	-22	**-5**
	2	10.3	5	-9	-66	**-13**	39	**5**	19	-3	-83	**-11**	-63	**-6**
*	8	8.13	42	-3	**61**	**11**	26	2	33	1	29	-1	15	-2
FTΔL	10	8.53	-18	0	-5	-4	9	-1	2	2	6	2	-3	0
	1	8.72	B	2	-17	-2	44	1	-57	0	-3	3	4	3
*	7	6.40	-22	5	**68**	**19**	26	-1	1	3	**55**	**10**	37	**6**
TB	12	10.7	-1	**7**	-4	**-3**	-4	-1	-3	**6**	1	3	7	-2
	9	8.98	**-15**	**4**	-7	-2	2	1	-6	2	-7	1	-3	-2
NBA	9	8.98	-9	**3**	**9**	0	5	0	1	**4**	1	1	5	-3
	6	7.58	**-21**	1	-1	0	11	2	-9	0	-15	-1	-7	-1

Trait			**LADG**		**BF**		**EMD**		**TADG**		**ADI**		**FCR**	
	h^2×100		**21**		**38**		**19**		**16**		**25**		**25**	
		σ^2p	**4789**		**3.47**		**20.9**		**21848**		**0.14**		**0.24**	
APBW	36	0.048	**47**	**7**	**-36**	**-10**	**-14**	-1	-11	5	-6	4	5	-2
	31	0.047	**55**	**5**	-30	**-6**	**-11**	-2	4	2	-1	-2	-2	-3
LITG10	8	36.1	**40**	1	-7	-2	-5	-3	-29	2	-34	0	-2	-3
	5	41.4	**39**	-3	10	**6**	21	-2	17	1	-35	-1	-55	-2
LADI	15	0.62	**42**	**9**	-11	**-6**	3	-3	14	**6**	26	**7**	10	1
	24	0.70	**50**	**14**	-18	-4	-8	-2	**34**	**10**	**39**	**10**	7	-2
SHORT	15	3.42	2	**-4**	10	3	-18	-1	38	2	26	2	-5	0
	32	3.57	35	0	12	3	-7	**-4**	**73**	2	**63**	**6**	-1	2
PAR2	6	3.34	24	0	45	**8**	-29	**3**	2	0	-42	**3**	-42	3
PAR3	8	3.36	-11	-2	37	**7**	-14	**4**	-3	-2	-39	0	-31	2
PAR4	6	3.34	-29	**-4**	**60**	**10**	-27	**4**	-14	-2	-38	0	-15	1
PAR5	14	3.41	-28	**-5**	**37**	**10**	1	**5**	-19	-3	-21	0	-2	3

See text for trait abbreviations; correlations sig. different to zero in bold; first line: parity 1 data; second line: parity 2 data; * Covariate for starting point included in the model for parity 2 data; underlined rp have opposing residual and genetic correlations.

The heritabilities of maternal weight changes during gestation and lactation (15 and 5 week periods respectively) were of similar magnitude to estimates for weights but variances were lower. Heritability estimates for WTΔG and WTΔL were 15 (16) and 23 (20). In stark contrast, the heritability estimates were moderate (22) for FTΔG in parity 1, but low or negligible for FTΔG in parity 2 and for FTΔL in both parities. Grandinson et al. (2005), with data from considerably lighter, fatter sows than in this study, reported similar heritability estimates for weight and fat loss during lactation. However, Gilbert at al. (2010), with considerably older, fatter sows, reported a heritability of 0.13 for FTΔL to weaning. Since the amount of fat that can be lost during lactation is affected by initial fat levels at farrowing, it seems likely that the heritability for FTΔL will be affected also by initial fat levels.

In this study, for parity 2 data, genetic variation for FTΔG and FTΔL was negligible unless covariates for fatness at mating or at the start of lactation were concurrently fitted in the model. This implies that the underlying genetic potential of the sow for fat gain during gestation was largely unable to be expressed during the second parity unless initial fat levels were accounted for. Under the expanded models containing initial fat levels as covariates, genetic variation in FTΔG and FTΔL represents variable expression relative to a common phenotypic starting point. Regression coefficients for FTΔG or FTΔL on fatness at the start of each period were negative indicating that fat gain in gestation was less and fat loss in lactation was more substantial for fatter sows. These coefficients were almost identical in parity 2 (-0.435±0.022 and -0.432±0.020) supporting the theory that lactating mammals have a tendency to return to their pre-parturition body composition for fatness (Butte and Hopkinson, 1998). Other studies with relatively fat sows at farrowing (eg. Gilbert et al. 2010) were observed to have lower lactation intake and larger fat losses during lactation than was observed in this study. It appears that sows attempt to meet their energy demands during lactation by co-ordinating lactation intake with their body condition attributes.

Genetic correlations between early growth (LADG) and other traits generally supported the concept that selection for growth will result in heavier sows with heavier piglets and higher lactation intake capacity. However, negative residual (not presented) and phenotypic correlations indicate that high growth sows (LADG and TADG) have reduced maternal weight and fat gain in gestation, especially in parity 1. Both low maternal gain and low fat depth prior to the first farrowing were identified as adverse risk factors for sow survival to the second parity (Bunter et al., 2008). Compared to LADG, correlations between TADG and APBW were negligible while the associations with WTΔG or FTΔG were stronger. While the overall phenotypic association of growth with birth weight was positive, the residual correlations also indicate that piglet weight was negatively affected.

This pattern of correlations for growth traits suggests environmental limitations to performance of sows with high genetic potential for growth. Neutral correlations between LADG or TADG with PAR2 were followed by increasingly unfavourable associations between early growth and later parity longevity, as larger sow size with increasing parity is accompanied by higher maintenance requirements, which become more limiting under a fixed resource provision (eg feed). The changing correlations between growth and sow longevity by parity demonstrate that the overall association between these traits is not linear. Therefore, many studies which attempt to establish the relationship between finisher traits (such as ADG) and sow longevity could be expected to arrive at a non-significant result.

Gilts that were genetically fatter at selection remained phenotypically fatter throughout repeated parities despite gaining less fat during each gestation. After fitting the initial phenotype as a covariate, there is evidence that genetically fatter sows retained a small but positive potential for fat deposition at higher initial phenotypic levels of fatness. The genetic correlation of BF with PBWT was negative as expected (Hermesch et al., 2001), but residual correlations between BF and APBW were favourable; environmental causes of sow fatness favour a positive outcome for APBW, and also for litter gain in the second parity. The net association between BF and APBW remained negative at the phenotypic level. However, genetic and phenotypic correlations indicate that fatter sows had consistently better survival to later parities. Correlations between EMD and sow body development or reproductive characteristics were generally small. Genetically muscular gilts on a weight constant basis were phenotypically lighter and leaner, but gained more fat during gestation. The net effect on longevity to later parities was positive.

Gilts with high genetic potential for feed intake between 21 and 26 weeks were heavier and fatter as sows, but with diminished weight and fat gains during gestation. Genetic correlations of ADI with litter size and birth weight traits were negligible. High finisher ADI was associated with increased LADI and diminished weight or fat loss during lactation. Of note, the genetic correlations between ADI and LADI were significantly and substantially lower than one, suggesting that appetite expression in the different physiological states (growing vs lactation) is controlled by different stimuli and genetic pathways. Given the numerous pathways that are involved in appetite regulation (Matteri, 2001) this is perhaps not surprising. The negative genetic correlations between ADI and LITG10, combined with an increased chance of a shortened lactation, suggest some antagonism of ADI with mothering performance despite the genetically favourable association of ADI with lactation feed intake. The net associations of ADI with LITG10 or longevity were neutral phenotypically, although genetic correlations were consistently negative. Sows with high FCR tended to be lighter and fatter, with significantly lower weight and fat gain during gestation. FCR was uncorrelated with litter size or birth weight traits, but was negatively (favourably) correlated genetically with sow longevity, probably because sows were both smaller and more efficient.

The associations between sow body composition, reproductive performance and litter outcomes, lactation feed intake and longevity

Within parity and trait, correlations between measurements at the start and completion of lactation are high. Genetic correlations were 0.75 between WT110 and WTW and 0.90 for FT110 and FTW whereas corresponding phenotypic correlations of 0.56 and 0.63 (not presented). Further, genetic correlations of weight with fat loss were also very high; 0.76 in parity 1 and 0.97 in parity 2; whereas phenotypic correlations were again much lower at 0.41 and 0.40. Since the genetic correlation between weight and fat loss is high, this supports a co-ordinated genetic mechanism for simultaneous catabolism of fat and protein to generate energy during lactation, although as noted previously the expression of genetic variation in fat loss was more limited in parity 2. Correspondingly, the correlations of weight with fatness were weaker at the start compared to the end of lactation. This is a reasonably important observation from a biological perspective, as it highlights that it is likely BOTH fat and protein reserves are important for lactation. Further, it may be expected that a deficiency of sow fat reserves prior to farrowing is deleterious as it increases the necessity for protein degradation to supply energy during lactation. This is a less efficient process for generating energy, and excess protein loss is known to negatively affects subsequent reproductive performance.

The size of litter also had consequences for sow body composition at farrowing in parity 1 (Table 7). Negative correlations indicate that sows gestating larger litters had lower maternal weight gain and sow fatness pre-farrowing, whereas sows producing individually heavier piglets had lower pre-farrowing fatness only. Higher APBW and LITG10 was associated with lower sow weight and fatness levels at weaning, resulting from increased weight and fat loss during lactation, despite increased LADI. Sows with reduced weight loss during lactation, but more significantly higher fat at weaning, were the most likely to farrow in later parities. Of significance, phenotypic correlations between LADI and sow longevity traits were positive, in spite of strong negative genetic correlations. Sows with a high phenotypic lactation feed intake reared the litter more effectively and reduce their own weight or fat loss (Table 7), which are desirable outcomes. They are also more likely to be healthy (Bunter et al., 2009a).

Table 7 - Estimates (×100) of genetic (ra) and phenotypic (rp) correlations between sow body composition attributes, reproductive traits and sow survival to later parities.

Trait	SWPF		FT110		LADI		WTW		FTW		WTΔL		FTΔL	
	ra	rp	ra	rp	ra	rp	ra	rp	ra	rp	ra	rp	ra	rp
TB	-7	-3	-13	**-9**	1	**7**	-8	2	0	-1	-3	**9**	**35**	**11**
	-16	2	-10	1	-21	3	-5	3	-11	-3	14	2	11	-2
NBA	1	**-4**	4	**-4**	-3	**8**	-5	1	9	1	-5	**7**	21	**7**
	-21	0	-7	1	-30	4	-17	1	-17	-2	3	2	-27	-2
APBW	**45**	**22**	-8	**-8**	13	-2	-12	**-8**	-17	**-13**	**-72**	**-37**	-19	**-11**
	9	**18**	-14	-2	35	**10**	-18	-4	**-38**	**-12**	**-36**	**-29**	-64	**-9**
LITG10	-14	2	-10	-1	6	**16**	**-38**	**-17**	-27	**-20**	**-31**	**-23**	-42	**-22**
	-58	3	-23	7	2	**25**	**-**	**-16**	-43	**-10**	-60	**-26**	-43	**-21**
LADI	33	**-9**	-16	**-12**	-	**-**	**56**	**38**	20	**16**	**43**	**54**	**87**	**33**
	-26	**-16**	-19	**-13**	-	**-**	21	**21**	-12	3	**65**	**47**	57	**18**
PAR2	9	0	46	**8**	13	**9**	20	**10**	24	**14**	33	**15**	-24	**7**
	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PAR3	2	-2	41	**8**	-14	**7**	3	**4**	24	**12**	19	**9**	-32	**4**
	18	-1	56	**6**	**-74**	**13**	8	**8**	44	**13**	4	**12**	-	**7**
PAR4	-18	-3	**69**	**9**	**-**50	**6**	4	1	46	**11**	39	**5**	-44	1
	17	-5	58	**7**	**-96**	**6**	0	1	62	**9**	-14	**7**	-	1

Trait	SWPF		FT110		LADI		WTW		FTW		WTΔL		FTΔL	
	ra	rp	ra	rp	ra	rp	ra	rp	ra	rp	ra	rp	ra	rp
PAR5	-10	-4	54	**10**	-35	**5**	-5	-2	25	**10**	12	**4**	-48	-1
	10	-3	33	**9**	**-74**	**4**	-2	-1	41	**10**	-15	3	-	0

However, sows with higher genetic potential for lactation feed intake are larger and leaner with a neutral genetic capacity for rearing a litter, once birth weight is accounted for (Table 7). This might explain the apparently counter-intuitive results of Bergsma et al. (2008) and (Bunter et al., 2009b), showing antagonistic genetic, but favourable phenotypic correlations, between *ad-libitum* lactation intake and sow longevity. In this study, higher sow weights were beneficial in early parities and indeed, for successful entry into the herd in the first place (not presented). But they were increasingly less beneficial in later parities where the nutritional demands of prolific and heavier sows are less likely to be met under a conventional feeding system which does not differentiate amongst the requirements of individual sows. The transition of sow weight with increasing parity from a beneficial to a detrimental effect (Tables 6 & 7), and the inconsistency between genetic and phenotypic correlations (eg LADI with longevity) serve to mask important associations between these traits and sow longevity because of non-linear relationships.

Genetic parameters for sow IGF-I and correlations with other traits

Sow IGF-I was measured at weaning after overnight fasting in the farrowing crates. Sow IGF-I concentrations were moderately to highly heritable, with estimates taking values of 0.23 and 0.30 in parities 1 and 2 respectively (Table 8).

Table 8 - Correlations (×100) between sow IGF-I at weaning and other traits (within parity 1: first line; within parity 2: second line)

	Parameters		Correlations with IGF-I		
Trait	**h^2×100**	**σ^2p**	**re**	**ra**	**rp**
SIGF1	23	10520	**27±8**	**110±14**	**48±4**
SIGF2	30	11180			
ADG	21	4921	4±4	**20±10**	**7±3**
			1±7	**30±14**	**8±5**
BF	38	3.47	1±4	**23±9**	**8±3**
			-14±7	**32±13**	1±5
EMD	19	20.9	-1±4	**21±9**	4±3
			-1±6	13±14	2±5
TADG	16	21860	-1±5	21±16	3±3
			-1±8	30±24	6±5
ADI	25	0.14	-6±5	**36±14**	5±3
			-5±9	31±19	5±5
FCR	25	0.24	-3±5	12±15	1±3
			-4±8	6±21	-1±4
SWPF	25	328	2±5	-7±16	0±3
	19	467	-1±8	18±25	3±5
WTW	34	311	**34±5**	**18±15**	**29±3**
	27	395	**20±9**	**43±20**	**27±4**
WTΔG	14	190	0±5	**-39±18**	**-7±3**
	16	294	3±8	-37±29	-5±5
WTΔL	20	196	**38±4**	**38±15**	**38±2**
	20	249	**24±9**	**38±23**	**28±4**
FT110	35	12.2	0±5	27±14	**7±3**
	27	12.0	-4±9	30±24	5±4
FTW	35	11.2	**19±5**	15±15	**18±3**
	26	10.5	7±9	20±23	**10±4**

	Parameters		**Correlations with IGF-I**		
Trait	**h^2×100**	**σ^2p**	**re**	**ra**	**rp**
FTΔG	21	9.94	-4±5	-8±17	-5±3
	3	10.3	-3±8	-35±61	-6±5
FTΔG*	21	7.87	-3±5	17±17	1±3
	6	8.13	-5±8	26±45	-1±5
FTΔL	11	8.58	**18±5**	-19±22	**12±3**
	1	8.72	8±8	-24±85	5±4
FTΔL*	17	6.74	**22±5**	2±19	**18±3**
	9	6.57	9±8	13±35	**10±4**
TB	12	10.8	3±4	7±14	4±3
	8	8.98	4±6	-39±22	-3±4
NBA	9	7.60	0±3	23±15	3±3
	6	8.39	-1±6	-20±25	-3±4
APBW	36	0.048	3±5	**-27±12**	**-6±3**
	33	0.047	-2±8	19±18	4±5
LITG10	9	36.1	**-24±4**	47±25	**-14±3**
	6	41.4	-7±9	-26±46	-9±5
LADI	14	0.62	8±5	23±20	**11±3**
	23	0.70	0±9	34±25	**9±5**

Heritability estimates are very similar to what is typically obtained for IGF-I concentrations recorded in juvenile pigs (Bunter et al., 2005). The estimated genetic correlation between SIGFI records from different parities exceeded the parameter space and does not differ from 1, indicating that these traits are genetically identical. Residual and phenotypic correlations were also moderate and positive, showing that both genetic and non-genetic factors affecting concentrations at weaning in parity 1 carried over to parity 2 IGF-I values.

ADG or BF in finishers had positive genetic correlations with IGF-I concentrations at weaning in sows. Therefore animals with high genetic potential for growth and deposition of fat have a tendency towards genetically higher IGF-I values as a weaned sow. This was accompanied by positive genetic correlations between ADI and sow IGF-I (0.31 and 0.36) but relatively neutral correlations with FCR (0.12 and 0.06). In combination with the moderate and positive genetic and phenotypic correlations between finisher and later fatness measures (Table 6), these results suggest that these associations are generally driven more strongly by sow fatness and to a lesser extent feed intake attributes.

Moderate positive genetic and phenotypic correlations between sow weight at weaning or WTΔL and SIGFI show that sows with reduced weight loss during lactation and higher weaning weight have higher IGF-I levels at weaning. However, correlations between SWPF and IGF-I were close to zero; sow weight *per se* is not genetically or phenotypically associated with sow IGF-I at weaning. This suggests that the sow IGF-I concentration at weaning is effectively a reporter for the change in a sow’s energy balance during lactation. Owens et al. (1997) had previously concluded that IGF-I measured in young animals was also a better reporter of prior performance than a predictor of future outcomes, which is consistent with results from this study. The correlations between fat at weaning and fat loss with sow IGF-I at weaning were of similar magnitude and direction to those between weight attributes and sow IGF-I, with the exception that there was some evidence for a positive association between fatness pre-farrowing and sow IGF-I at weaning.

With respect to reproductive traits, results are more ambiguous. Phenotypic correlations suggest a neutral association between sow IGF-I and litter size traits, whereas genetic correlations vary in both magnitude and direction with parity. Genetic and phenotypic correlations between APBW and sow IGF-I concentrations were significant and negative in parity 1 only. Sows producing heavier piglets at birth in their first parity had reduced IGF-I at weaning. Based on phenotypic correlations, sows with higher litter gains were also likely to have lower IGF-I at weaning, whereas sows with higher lactation intake would have higher IGF-I, consistent with expected changes to their energy balance during lactation. However, of note, the genetic correlation between LITG10 and SIGF was moderate and positive (0.47±0.25) suggesting that genetic potential for litter gain in parity 1 was positively associated with IGF-I from a genetic perspective, but not observed at the phenotypic level. Unfortunately, large standard errors limit the usefulness of interpreting this observation further.

Predicting subsequent performance from weaning IGF-I

In the previous section it was demonstrated that sow IGF-I was associated generally with other traits in a manner consistent with a prior expectation that this measure reports on changes to sow energy balance during lactation. Therefore, it is useful to see if there is any association between weaning IGF-I on subsequent performance, as would be expected from previous reviews which illustrate the antagonistic relationships between poor energy balance at weaning and subsequent reproductive performance. Results from this study show that phenotypic correlations between sow IGF-I at weaning in parity 1 were significant and lowly positive with NBA, APBW, SWPF and FT110 recorded in parity 2 (Table 9). That is, sows with higher IGF-I at their first weaning tended to enter their second farrowing with higher body weight and condition and had larger litters with heavier piglets, supporting the previously observed associations within parity (Table 8). However, there was no apparent association between SIGF at the first weaning and litter gain in the second parity. Genetic correlations between sow IGF-I at weaning in parity one and sow attributes in the second parity were negative, suggesting that high IGF-I sows in parity 1 had lower genetic potential for growth during their second gestation. It appears that energy sparing sows were genetically smaller and potentially closer to maturity at farrowing in parity 1.

Genetic correlations were also moderate and positive (Table 9), supporting the observed phenotypic associations between IGF-I (parity 1) with litter size (parity 2). However, it should be noted that this result is completely inconsistent with the within parity estimates of correlations between these traits (Table 8). The genetic correlation between SIGF in separate parities is one (Table 8), but the genetic correlation between litter size traits recorded in the primiparous versus second parity is not (ra: ~0.75, Table 5). Therefore, it is possible that the genetic potential for litter size in parity 2 is correlated with separate genetic mechanisms preserving more favourable energy balance in the parity 1 lactation, as measured using IGF-I. This result could also arise because of bias in parameters introduced through sow culling decisions in parity 1. For example, sows that were not weaned at the normal time were less likely to have IGF-I and later litter traits recorded because of deliberate culling decisions, and sows with very low IGF-I at weaning were less likely to become pregnant and generate later parity records, or to express their genetic potential for litter size if they did become pregnant.

Table 9 - Correlations (×100) between sow IGF-I in parity 1 (SIGF1) and 2nd parity performance, along with sow IGF-I (SIGF1 or SIGF2) and survival until farrowing in subsequent parities

		h^2×100	σ^2p	re	ra	rp
Sow IGF-I at weaning in parity 1 with parity 2 outcomes						
SIGF1	TB2	9	8.99	0±4	**32±15**	4±3
SIGF1	NBA2	7	8.39	1±4	**40±16**	**6±3**
SIGF1	APBW2	33	0.047	15±5	-7±14	**9±3**
SIGF1	LITG10	3		**-9±5**	46±53	**-3±3**
SIGF1	SWPF2	18	467	**23±5**	-22±21	**13±3**
SIGF1	FT1102	27	12.0	**23±6**	-19±18	**13±3**
SIGF1	WTΔG2	16	294	1±5	**-56±20**	**-10±3**
SIGF1	FTΔG2	3	10.3	3±5	-99±56	**-6±3**
Sow IGF-I with subsequent farrowing outcomes						
SIGF1	PAR2	5	3.33	**7±2**	81±50	**9±2**
SIGF1	PAR3	7	3.35	**5±1**	54±32	**7±2**
SIGF2				7±4	34±41	**8±4**
SIGF1	PAR4	6	3.34	3±2	55±36	4±2
SIGF2				4±3	25±46	5±3
SIGF1	PAR5	13	3.40	2±2	33±25	4±2
SIGF2				3±3	8±35	3±3

Genetic and phenotypic correlations between sow IGF-I levels and subsequent survival to later parities were all positive (Table 9), indicating that positive energy balance in the sow at weaning, as indicated by a higher weaning IGF-I level, is favourable for the ability of sows to survive and farrow in later parities. Phenotypic correlations were strongest between outcomes for adjacent parities, as expected. Genetic correlations were moderate to very high between sow IGF-I at weaning and longevity to later parities. However, low heritabilities for longevity traits meant that these estimates of genetic correlations were accompanied by very large standard errors, making these estimates generally unreliable, but likely positive.

Correlations between juvenile IGF-I and sow IGF-I

IGF-I data for weaned piglets recorded during 2003 to 2009 were subsequently extracted from the Rivalea database (N=26537) to investigate whether juvenile and sow IGF-I concentrations were genetically correlated. In maternal lines, piglets recorded for juvenile IGF-I were mostly male. Of the relatively limited number of females with records for juvenile IGF-I over this time period (N=1324), only 4 sows had records for both juvenile IGF-I and sow IGF-I at weaning. Therefore, the estimate of the genetic correlation between juvenile and sow IGF-I arises from the relationship matrix and data from juvenile males related to the sows with data (6382 piglets with juvenile IGF-I were progeny of project sows). In this situation, where sows do not have records for both traits, it is not possible to estimate the phenotypic correlation between these traits.

Estimates of heritability and common litter effects for juvenile IGFI (h^2: 0.17±0.02; c^2: 0.14±0.01) from this data were comparable generally to results from previous studies (Bunter et al., 2005). Estimates of the genetic correlation between juvenile and sow IGF-I traits were 0.25±0.12 and 0.05±0.16 (parity 1 & 2 sow data). Therefore, while the genetic correlation appears as if it is positive in parity 1 data, there is not very strong evidence for a significant genetic correlation in parity 2 data. The lack of a substantial genetic correlation between these traits indicates that circulating IGF-I levels are controlled by different genetic mechanisms in juvenile piglets compared to sows.

Index calculations

There are several limitations for accurately estimating the effects of selection on outcomes for both finisher and sow performance. These include, but are not limited to:

1. Increasing complexity with trait number, particularly with respect to obtaining positive definite matrices of covariances adequately describing genetic and non-genetic associations between all traits which are biologically plausible and consistent with the observed phenotypic outcomes
2. The presence of multiple-stage selection in reality, since the phenotype of the developing sow is associated with the probability of her being culled and obtaining future records (leading to biased parameter estimates for combinations involving later in life traits)
3. Non-linearity of genetic correlations between traits with parity, and negative residual correlations between temporally separate traits, which imply an intervening time period during which the phenotype for the first trait affects the outcome for the second

With respect to the first limitation, parameter estimates from this study required "bending" to achieve a sensible parameter set for index calculations. Genetic correlations were generally reduced towards zero, moreso for trait combinations potentially involving inestimable dam-offspring environmental covariances (eg sow traits with LG10) and combinations of binary-continuous traits (eg sow traits with PAR2). The resulting covariance matrix was generally consistent with bivariate estimates of genetic correlations in direction, but several rg were of lesser magnitude. The second and third limitations were not addressed in this study; since most index software is limiting in the number of effects or traits which can be accommodated, it was difficult to model each trait separately by parity.

Nevertheless, some preliminary but simplistic index calculations have been performed to demonstrate the implications of the genetic parameters obtained for breeding programs. These calculations assume a single generation of (single stage) truncation selection, with a selection intensity of 1. Estimates of the genetic variances and correlations used for index calculations are provided in Appendix 2, with corresponding rp as reported elsewhere throughout this report.

Index calculations were performed using three basic indices:

1. Goal1($) = $0.05×ADG - $0.60×BF + $5.00×NBA + $0.015×APBW
2. Goal2($) = $0.05×ADG - $1.50×BF -$150×FCR + $5.00×NBA + $0.015×APBW
3. Goal3($) = $5.00×NBA + $0.015×APBW + $1.50×LITG + $10.00×PAR2

Goal1 placed value solely on growth, leanness and basic reproductive traits, with economic values weighted to limit the change in BF during concurrent selection for growth, and with no emphasis on litter gain or sow longevity (standard deviation of the breeding goal: SDH=$4.59).

Goal2 increased the emphasis on selection for efficient lean growth, and had no emphasis on litter gain and sow longevity. The high economic value for efficiency in growing animals dominates this index (SDH=$37.12).

Goal3 could be considered as a maternal index. It placed ~50% emphasis on improving litter size and ~25% each on litter gain and sow survival to the second parity, when only dam records were available. This index ignores changes to the value of slaughter pigs (SDH=$7.24).

The selection criteria were varied to include combinations of:

1. Performance data
    a. Own, sire, dam, 6FS and 40HS animals with records for ADG,BF, EMD
    b. Plus 1FS and 10HS with records for TADG, ADI, FCR
2. Sow reproductive (NBA and APBW) data (2 records/dam)
3. Litter gain (2 records/dam)
4. Sow survival to parity 2 (1 record/dam)
5. Average lactation intake (2 records/dam)
6. Sow weaning IGF data (1 record/dam)

Results are presented in Table 10. It is important to note in advance that the relative economic changes are, of course, highly dependent on the economic values which are applied, which are somewhat arbitrary for this illustration. Therefore, it is important to consider the pattern of individual trait changes concurrently.

Table 10 - Predicted genetic changes under different scenarios representing alternative breeding goals and selection criteria

Scenario	1	2	3	4	5	6	7	8	9
Goal	1	2	3	3	3	3	3	3	3
Criteria	1+2	1+2	1+2	1+2+4	1+2+5	1+2+6	2+3+4	2+3+4+5	2+3+4+6
ADG	12.31	-5.10	2.18	2.09	2.23	2.15	0.09	-0.00	0.29
BF	-0.00	-0.38	0.61	0.58	0.60	0.60	0.02	0.02	0.03
EMD	0.02	0.17	-0.11	-0.11	-0.11	-0.11	-0.01	-0.01	0.01
TADG	6.98	7.88	1.13	1.10	1.25	1.50	0.18	0.07	0.67
ADI	0.01	-0.02	0.02	0.01	0.02	0.02	-0.00	-0.00	0.00
FCR	0.02	-0.11	0.01	0.01	0.01	0.01	-0.00	-0.00	-0.00
SWPF	1.09	0.64	-0.46	-0.41	-0.44	-0.45	0.04	0.02	0.03
FT100	0.04	-0.48	0.67	0.66	0.67	0.67	0.04	0.04	0.06
WTW	1.49	0.60	-0.35	-0.26	-0.27	-0.23	-0.17	-0.23	-0.06
FTW	0.01	-0.52	0.65	0.63	0.66	0.64	0.01	0.00	0.01
LADI	0.04	-0.01	-0.03	-0.03	-0.03	-0.03	0.00	-0.00	0.00
NBA	0.09	-0.02	0.12	0.11	0.11	0.12	0.12	0.12	0.12
APBW	0.01	0.00	-0.01	-0.01	-0.01	-0.01	0.00	0.00	0.00
LG10	0.07	0.05	-0.00	0.00	-0.00	-0.01	0.16	0.16	0.16
PAR2	-0.01	-0.02	0.10	0.11	0.10	0.10	0.03	0.03	0.03
SIGF	3.30	-4.48	1.85	2.26	1.96	3.95	0.66	0.59	3.25
RIH	0.23	0.43	0.21	0.22	0.21	0.22	0.16	0.16	0.17
$Response	$1.06	$15.96	$1.53	$1.61	$1.54	$1.57	$1.15	$1.15	$1.20
ΔGoal1	$1.06	$0.13	$0.34	$0.31	$0.30	$0.35	$0.59	$0.59	$0.60
ΔGoal2	-$1.93	$15.96	-$1.71	-$1.72	-$1.74	-$1.69	$0.57	$0.57	$0.57
ΔGoal3	$0.46	-$0.23	$1.53	$1.61	$1.54	$1.57	$1.15	$1.15	$1.20

Index calculations demonstrated a few key principles:

- Genetic parameters from this study indicate that it will be difficult to maintain, let alone improve, sow longevity to the second parity under breeding goals with a strong emphasis on finisher efficiency, since selection reduces genetic potential for both feed intake and fat deposition, while simultaneously increasing litter demands on the sow (eg Scenario 2). However, a French line selected for low residual feed intake, which has highly genetic correlations with feed conversion ratio, currently shows no evidence of detrimental effects on sow reproduction or longevity (Helene Gilbert, INRA, 2010, *pers.comm.*). However, the low RFI sows were significantly older, heavier and fatter at mating than the sows in this study. Therefore, it is possible that the degree of physiological maturity at mating plays an important role in the nature of the genetic and phenotypic relationship between efficiency and sow longevity to parity 2.

- When production records were available, all indices which did not place value on FCR resulted in a negative economic response for Goal2 because changes to growth and feed intake were not optimally balanced, leading to slight increases in FCR which attracts heavy penalties (Scenarios 1 & 3 to 6). However, relatively small changes to genetic parameters or economic weights might alter this outcome.
- Since production traits are genetically correlated with sow body composition and litter gain traits, there were significant benefits to using production data as selection criteria even with a fully maternal breeding goal. The response in the maternal index was about 34% higher when production data were available, mostly through an increased response in sow longevity. General trends for response in individual traits under maternal goals were reduced response in growth rates and sow weight, increased fatness and a decline in LADI (Scenarios 3 to 6). Moreover, the percent of economic gain attributed to litter size decreased from around 50% (eg Scenario 7) to 40% (eg Scenario 6).
- When only records on dams were used as selection criteria (Scenarios 7 to 9), overall economic response in Goal3 was lower because of substantial reductions in the accuracy of selection (RIH=0.16). Response per annum would be further reduced due to the extended generation interval implied by use of dam records only as selection criteria. However, since these strategies also did not incur any economic penalties associated with an undesired trend in FCR, the economic response for all breeding goals was positive. This is unlikely to be sufficient reason to exclude production data as selection criteria for maternal breeding goals, particularly since indices can be formed which would simultaneously restrict undesirable changes in FCR for slaughter pigs.

With respect to choice of additional selection criteria for improving response to selection, the following outcomes were observed.

- Where production and reproductive traits were already available, indirect selection criteria such as lactation intake or sow IGF-I at weaning were less effective at maximising response for Goal3 relative to including survival to parity 2 itself as a selection criterion (Scenario 4 vs 5&6). The latter trait is considerably easier and cheaper to implement in data capture systems than daily recording of lactation feed intake or bleeding sows at weaning for assaying IGF-I.
- Where production data was not available, data on sow IGF-I at weaning improved response to selection for the maternal goal by about 4-6% (Scenario 9 vs 7&8), whereas records for LADI had no impact on response to selection (Scenario 8 vs 7). The relative merit of sow weaning IGF-I as a selection criterion remains limited, however, considering response for

Goal3 under Scenario 9 remains only 75% of that achieved under Scenario 4.

Publications arising from the project

Bunter, K. L., C. R. G. Lewis, S. Hermesch, R. Smits, and B. G. Luxford. 2010. Maternal capacity, feed intake and body development in sows. Invited paper: 9th World Congress on Genetics Applied to Livestock Production, Leipzig, Germany

Bunter, K. L., C. R. G. Lewis, and B. G. Luxford. 2009a. Variation in sow health affects the information provided by lactation feed intake data. In: Proc. AAABG, Barossa Valley, South Australia. p 504-507.

Bunter, K. L., B. G. Luxford, R. Smits, and S. Hermesch. 2009b. Associations between sow body composition, feed intake during lactation and early piglet growth. In: Proc. AAABG, Barossa Valley, South Australia. p 203-206.

Bunter, K. L., R. Smits, B. G. Luxford, and S. Hermesch. 2008. Sow body composition and its associations with reproductive and litter growth performance of the primiparous sow. In: AGBU Pig Genetics Workshop, October 2008, University of New England, Armidale, NSW, 2351. p 67-82.

Bunter, K. L., M. Tull, and B. G. Luxford. 2007. Factors affecting feed intake during lactation for primiparous sows. In: Manipulating Pig Production, Brisbane. p 121.

Lewis, C. R. G., and K. L. Bunter. 2009. Longevity to the second parity requires good attention to sow health in the first. In: Manipulating Pig Production, Cairns, Australia. p 106.

Lewis, C. R. G., S. Hermesch, and K. L. Bunter. 2010. A random regression analysis of sow lactation feed intake and the effect of temperature on intake. In: 9th World Congress on Genetics Applied to Livestock Production, Leipzig, Germany.

Publications in preparation for peer review

C.R.G. Lewis and K.L. Bunter (in preparation). Body development in sows, feed intake and maternal capacity. Part 1: Performance, pre-breeding and lactation feed intake traits of primiparous sows.

K.L. Bunter and C.R.G. Lewis (in preparation). Body development in sows, feed intake and maternal capacity. Part 2: Gilt body condition pre- and post lactation, reproductive performance and correlations with lactation feed intake

Further analyses are continuing under Project 4C-105.

4. Application of Research

Application of the research findings in the commercial world

Through estimates of genetic and phenotypic correlations and genetic parameters, this project contributes new knowledge on the impact of selection for finisher attributes to outcomes for sows and their litters. While there is no IP as such in genetic parameters alone, the process of data analysis importantly established the genetic contribution, or otherwise, to some previously observed antagonisms between traits, and resulted in estimates for associations between new trait combinations. Separating genetic from non-genetic effects facilitates strategies for both management interventions and breeding program development to improve commercial sow performance.

Therefore, there are two areas in which results from this project have application. The primary goal was to obtain estimates of the genetic associations between sow lactation feed intake and lifetime reproductive performance of the sow, along with pre- and post-weaning piglet growth. This information is necessary to establish what effects current selection strategies have for breeding sow characteristics, and whether lactation feed intake, or other novel traits such as sow IGF-I, are potential selection criteria for future breeding programs. The role of these traits as selection criteria was illustrated via index calculations.

The second area of application lies with identifying systematic effects associated with new traits such as LADI and sow IGF-I, and patterns of phenotypic associations between these and other economically important traits. Phenotypic correlations show the degree of linear associations between traits, and are comparable (with appropriate conversion) to regression coefficients. Some phenotypic associations obtained from this project have not been observed or quantified previously.

Opportunities uncovered by the research: breeding programs

1. Selection for finisher attributes has implications for ongoing maturation and development of the breeding sow and, conversely, selection for maternal attributes also has consequences for finisher characteristics. In a commercial sow population, the balance between sow characteristics and progeny attributes obviously will be a function of the genetic potential of both the sow (for reproduction and production traits) and the genetic contribution to progeny of terminal sires (for production traits only). Better models are required to optimise breeding goals within and/or across lines to ensure that genetic gains in one area (eg finisher attributes) are not substantially offset by potentially unrecognised losses in another. There are only a few publications addressing the broad cross-section of traits used in this study, and no publications which model outcomes across the complete production system. Biological and economic efficiency may not be fully aligned, so models to investigate consequences for alternative breeding goals at both levels are desirable, particularly if it can be demonstrated that specific management practices can reduce unfavourable genetic and/or phenotypic correlations. Importantly, better knowledge of the biology of pigs will help predict in what areas future unrecognised losses may occur as selection progresses. This is essential for Industries (such as the Australian Pig Industry) where market pressures, and a relative lack of extreme terminal sire breeds, tend to force selection for finisher attributes in maternal lines, which are antagonistic for sow performance.

2. Lactation feed intake (LADI) is a moderately heritable and variable trait which has low to moderate correlations with growth generally and feed intake capacity of finishers (ADI). Therefore, it is a prospective selection criteria which may have a role in breeding programs. However, since lactation intake has a moderate positive genetic correlation with sow size (due simply to physical capacity?), it is possible that deliberately placing pressure on lactation intake will also increase sow size, such that

monitoring of mature sow size will become more important. This will also occur with selection for growth attributes. The consequences of increased mature sow size on production outcomes and profitability should also be evaluated in more complete models as noted in point 1. Current breeding goals with strong emphasis on growth traits could potentially benefit from inclusion of mature sow size as an additional selection criterion if correlated increases in mature sow size are to be limited concurrently with selection for early growth traits.

3. Genetic correlations between lactation feed intake and reproductive traits were variable with parity in magnitude and direction for litter size traits, but consistently positive for birth weight and litter gain traits. Therefore, placing selection pressure on piglet birth weight and litter gains will likely be associated with a favourable correlated response in lactation intake. However, since correlations between APBW and LG10 with weight and fat loss are of much larger magnitude and unfavourable, the net effect of placing emphasis on these traits for sow body weight and condition and weaning is negative and clearly not offset by favourable changes to LADI. Recording of birth weight should be promoted for genetic evaluation to facilitate a) counteracting the unfavourable trend of decreasing APBW with increasing litter size, b) promoting the desirable trend of increasing APBW to reduce piglet mortality, and c) for its genetic associations with early and post-weaning growth traits. However, because of antagonistic associations with other traits, recording of APBW should be accompanied by recording for other traits such as litter gain and sow longevity, to better locate selection candidates with desirable attributes for both sow and offspring performance.
4. This study does not identify in which time period lactation intake would have the biggest impact on litter gain until weaning, as litter weight gain was only recorded up to 10 days in this data. Sow feed intake during the latter weeks of lactation is likely relatively more important for litter gain traits until weaning. This particular aspect could potentially be investigated using data from other populations.
5. Transition traits during pregnancy and lactation are also potential selection criteria which are not routinely measured, but the relationship between protein and fat accretion during pregnancy or catabolism during lactation is biologically complicated. Absolute weight gain during gestation and weight loss during lactation are both moderately heritable and highly variable, at least in the first 2 parities when sows are still actively growing during their gestation. In contrast, fat gain was only heritable in the first parity and fat loss had low to negligible genetic variation in the second parity, yet estimates of genetic correlations between these traits were very high (>0.70). There is likely considerable measurement error in the recording of fat gains or losses, and the expression of genetic potential for fat deposition must be limited when there is an energy deficit limiting fat accretion, as was evident from low h^2. However, it is well known from studies on humans that weight and fat loss during periods of energy deficit (such as famine or lactation) are a function of how much weight and fat there is to lose in absolute terms, along with changes proportional to the ratio of protein to fatness at the starting point (Dulloo and Jacquet, 1999). Logistic regression demonstrated that fat depth prior to the first farrowing was the best phenotypic predictor of sow survival to their second parity. Calculated coheritabilities confirm that FT110 and weight loss during

lactation are the most informative traits for PAR2 from a genetic perspective, although these calculations clearly rely on similar accuracy of the genetic parameters for trait combinations, which is not the case here. Traits recorded at weaning were censored in the first parity when sows failed to complete a lactation. For both management interventions and breeding goal applications, recording sow weight and body condition pre-farrowing and at weaning in their first parity could prove useful and should be investigated further in other populations under different management.

6. Sow IGF concentration measured at weaning was highly heritable and variable, moderately repeatable across parities, and genetically correlated with other traits in a manner which was consistent with this trait representing overall changes to a sow's energy balance during lactation. At the phenotypic level, sows with higher IGF-I at weaning in their first parity had better second parity litter size and body condition pre-farrowing but litter gain was not significantly altered at the phenotypic level. Index calculations suggest that this trait was a useful selection criteria when production data were not routinely available, but of little additional benefit for improving selection response when production data was already known. Recording sow IGF-I for genetic evaluation purposes in pedigreed commercial sows carrying large cross-bred litters could potentially provide some additional information towards genetic evaluation for sow longevity. However, the possible benefits of this strategy need to be compared relative to costs and response from using data on comparable alternative criteria (eg sow weight, fatness and survival to parity 2). All of these measures may also provide information for grading sows into separate feeding regimes for more optimal management during the subsequent post-weaning period and gestation.

7. Generally, numerous antagonistic genetic and/or phenotypic associations were estimated between the complete suite of finisher, sow and piglet traits. In particular, sows with genetically high lean growth potential were heavier with less fat reserves, and more at risk of elevated weight and fat loss during lactation because litter demands were also high, despite positive genetic potential for lactation feed intake. This compromises the capacity of sows to remain in the herd, thereby reducing lifetime performance. Ultimately it is necessary to develop a balanced breeding goal which accommodates the complete suite of traits involved in successful piglet to finisher production and sow longevity. This can only occur when genetic parameters are known accurately. As implied in earlier points, other pig breeding companies should be encouraged to collect more accurate and complete data across trait complexes for developing both selection and monitoring applications. Worldwide data are relatively limited.

8. The best selection strategy is currently not clear and may differ according to the selection history of a population and the resulting characteristics of sows. Moreover, results currently suggest that genetic outcomes do not always align with phenotypic performance, particularly for trait combinations representing competition between sow and piglet demands. This effectively represents a GxE situation and/or the provision of sub-optimal management for individual animals which is not independent of their genetic merit. The comparison of breeding program alternatives is usually made under the assumptions of small genetic changes combined with optimal management. Unfortunately, rapid genetic change in weight

and fatness characteristics combined with relatively limited management change is more characteristic of pig breeding, which might generally explain the appearance of undesirable consequences for sows from selection. Currently there are no models that are adequate to address the complete trait complex for developing optimum breeding goals. This issue needs to be properly addressed prior to any implementation of potential new selection criteria in PIGBLUP. Further, it should be noted that significant antagonistic genetic correlations between economically important traits or relevant selection criteria will restrict rates of response to selection for individual traits. Therefore, an approach based on desired gains in one trait might become increasingly unbalanced for others and is not to be recommended.

9. More generally, the existing genetic evaluation system for Australian pig breeders (PIGBLUP) currently separates analyses for sow reproductive traits from production traits. This separation means that covariances between the traits contained within the separate analyses are assumed zero, which is clearly not true for some trait combinations, as demonstrated in this study. PIGBLUP could be developed to expand flexibility in this area, and provide the opportunity of more accurate genetic evaluation across broader breeding goals.

Opportunities uncovered by the research: management options

1. Primiparous sows gestating larger litters had reduced maternal gain and fat deposition during pregnancy, both of which were subsequently identified as risk factors for a failed first parity lactation and reduced probability of farrowing in the second parity. Factors limiting progression to parity 2 clearly impact on sow lifetime productivity. Therefore, improving feeding strategies during gestation to better meet requirements of individual sows and their (variably sized) litters may be required, particularly during the first gestation. This recommendation will be investigated further in the Pork CRC project 7A-037. Moving feeding management from the population to individual sow level has generally been informally implemented in countries such as France, via recommended targets for sow age, weight and fatness combined with individual sow assessment.
2. In this population of sows, which are genetically large and lean, there was evidence that obtaining specific outcomes at the end of the first gestation improved the subsequent survival of primiparous sows to their second parity. Minimum thresholds to obtain for sow attributes pre-farrowing were ~40kg maternal gain (57kg total gain) and a fat depth of 18 mm at the P4 site. However, these thresholds are not independent of the initial mating weight and fatness attributes summarised earlier, nor the accompanying litter size. Therefore, the suitability of these thresholds for other populations under different management is unknown.
3. More generally, there is extremely high variability amongst sows in changes to weight and body composition during gestation. This variability is not managed generally as it is mostly unobserved and unrecorded in many populations, but likely has significant consequences for the subsequent farrowing and lactation outcomes. For example, it is plausible that the adequacy, or otherwise, of nutrition supplied to an individual sow throughout the gestation may affect the degree to which development of

insulin-resistance throughout gestation occurs, with implications for individual variation amongst sows in piglet birth weights (Anderson et al., 1971) and adiposity, lactation feed intake (Mosnier et al., 2010), piglet mortality (Kemp et al., 1996) and more recently, colostrum production (Foisnet et al., 2010). Human studies indicate that there are further consequences, whereby insulin resistance limits the ability of insulin to suppress maternal lipolysis and amino-acid turnover (Catalano et al., 2003), with implications for maternal body composition. Strategies to better monitor and manipulate changes to individual sows in their body composition and metabolism throughout gestation may be an avenue to improve the consistency of pregnancy and lactation outcomes, and will be more warranted in modern genotypes due to gradual changes in metabolism, such as has been observed for muscle glycolytic potential (Larzul et al., 1998).

4. Phenotypic correlations between lactation feed intake and litter size, piglet birth weight, litter gain and sow longevity traits are generally positive, supporting favourable outcomes associated with increased sow lactation intakes. Therefore, identifying factors and strategies that facilitate high lactation intakes is desirable generally. However, it is clear that sows also adapt lactation intakes to prevailing circumstances (ie their own body condition, litter demands, etc), so there is a part-whole correlation between intake and its associated outcomes. Lactation intake as a trait must not be considered in isolation to management (diet palatability and delivery), sow body size and condition pre-farrowing, and the demands on sows during lactation. Strategic management of lactation intake for high risk sows and litters (eg primiparous sows, large litters) should accompany more targeted gestational feeding management.
5. In addition to season and parity effects on lactation intake, which should initiate deliberate nutritional interventions, low sow feed intake during lactation has been demonstrated to be an indicator of adverse parturition and health outcomes. Failed lactations are also significantly more likely in this situation. Therefore, developing better strategies for preventing, identifying and treating adverse health issues during gestation or following parturition may improve current parity outcomes for sows and their litters as well as prospects for sow longevity. A separate study by Hoy (2006) supports this outcome. Parity differences observed in this study for the incidence of farrowing difficulties and lactation failure support increased investigation of suitable interventions for primiparous sows in particular. Of note, in this data, sows which were slightly older at their first farrowing were observed to have relatively fewer problems with lactation outcomes, supporting the French strategy of increasing age at first farrowing. Recording sow feed intake shortly after lactation, for the purpose of assisting in the identification of unhealthy sows (when taken in context with sow body condition and other indicators, such as farrowing outcomes and sow rectal temperatures), would appear useful.
6. The consequences of historical selection on reproduction and finisher attributes for sow development are generally predicted to be increased sow size (unless efficiency dominates the breeding goal), reduced sow fatness and increased litter demands, which are observed in this data. This increases sow maintenance requirements during both gestation and lactation. As a consequence, it seems probable that many populations of modern commercial sows are not supplied with adequate diets on average,

as was previously proposed by Ball et al. (2008). Some breeding companies are now promoting increased feeding levels during gestation (Egbert Knol, pers. comm.) to better align resources provided to the sows with their genetic potential, in an effort to improve sow lifetime performance. Commercial producers require updated advice on sow feeding management for modern genotypes. Increased sow size also has obvious implications for their housing arrangements and farrowing crate sizing.

Commercialization/Adoption Strategies

- Potential benefits to cost of production

Developing strategies to improve sow lifetime productivity has clear benefits on the sow herd side of the equation proportional to the cost of replacement sows and the opportunity costs incurred through higher litter size and herd health status associated with increasing parity under reduced sow turnover. A "hidden" additional benefit potentially includes increased ease of herd management through a reduction in lactation failures, which require fostering intervention.

- Ease of adoption by producers

Breeding companies must invest resources into data recording and genetic evaluation procedures to obtain response to selection under increasingly complex breeding goals. Their willingness to do this depends on benefits and costs to themselves along with demands from their customers and returns from the sale of breeding stock. The benefits to producers are only realised if they make appropriate choices regarding the supplier of their breeding stock.

- Impact of the research

Results from this study are unique in that they provide the most detailed information publically available on sow development and performance following selection. The results obtained will motivate breeding companies, both in Australia and Internationally, towards further development and expansion of their breeding goals and selection criteria to help overcome some of the potentially detrimental effects on sow herd performance resulting from selection using essentially unbalanced breeding goals.

5. Conclusions

Selection for finisher traits to improve production has consequences for the ongoing body development of sows, their longevity, and the pre-natal development and pre-weaning performance of their progeny. There are some strong antagonistic genetic correlations to contend with across this trait complex. Therefore, a more complete model that aligns genetic potential with management and the prevailing environmental constraints to achieve desired phenotypic outcomes is clearly required. Breeding goals need to be expanded to halt detrimental effects on sow lifetime performance that will likely result from selection pressure on finisher characteristics.

Underlying genetic potential sets the scene for optimum management. If individual sow nutritional requirements are not met, particularly in the first parity when sows are actively growing during gestation, pre-farrowing maternal weight gain and fat deposition will be constrained, which may lead to reduced piglet birth weight and survival of the sow to subsequent parties. Genetic parameters indicate generally that it should be possible generally to identify and select for sows that perform better under existing management constraints. However, some potential selection criteria, such as fat gain in gestation and fat loss in lactation, have limited genetic variation under current management, and significant antagonistic correlations between traits can also limit genetic progress. Therefore, non-genetic strategies are also important and should be developed concurrently with the expansion of breeding goals. Non-genetic avenues for improvement of sow longevity and lifetime performance might therefore be to develop management strategies for turning genetically lean sows into phenotypically fatter sows prior to their first farrowing, and towards feeding strategies that better meet requirements of individual sows and their litters during both gestation and lactation. This reduces reliance on lactation feed intake to manage sow body condition and litter gains, which is desirable since selection for increased LADI (a strategy which has been suggested) could potentially have the undesired result of larger sows.

Should pig breeders choose to record lactation intake for use as a selection criterion, it is important also to record other traits concurrently, such as sow weight and fatness pre-farrowing and at weaning.

6. Limitations/Risks

It is well recognised that estimates of genetic and phenotypic parameters are specific to the study population (and accompanying management) in which the traits are recorded. Therefore, for confidence that the genetic and phenotypic associations obtained in this study are generally robust, it is desirable that similar work be conducted in other populations and compared with this study. To date, where parameters from other populations are publically available, a relatively consistent story seems to be emerging. The most notable area in which changes to recommendations from the current study might occur lies with specification of the most important traits to record for genetic evaluation purposes, since many estimates of genetic correlations were accompanied by large standard errors.

7. Recommendations

As a result of the outcomes in this study the following recommendations have been made:

Breeding program development

- There are some significant genetic antagonisms amongst traits in current breeding goals and sow attributes which influence reproductive outcomes and longevity. More complete models are required to better develop breeding goals, aligned within prevailing environmental constraints. A project in this area would be beneficial.
- Based on current results from this study, and limited results in other populations, there are several additional potential selection criteria which could be used to provide information towards a breeding goal which places economic value on sow longevity. These include traits such as lactation intake, sow weight and body condition pre-farrowing and at weaning, and sow IGF-I. The information content of other traits, such as fat loss during lactation, appears to be modified by the gestation environment provided. The relative merits of alternative criteria are currently not clear cut and will depend on prevailing breeding goals and existing criteria available for selection. However, it is recommended that breeding companies expand their repertoire of traits recorded on breeding sows in order to assist in validating the genetic correlations observed in this study, and to enable further breeding goal development. This requires breeding company investment in suitable equipment (eg sow weigh scales) and data recording systems.
- Comparison of commercial sow populations in the same environment is warranted. There has been no study within Australia which can be used to compare the relative merits and differences of alternative sow lines under constant management in the same environment. Outcomes from this study would provide producers with a benchmark for comparison under a well defined management and production environment. While this comparison will likely be generally unpalatable to some breeding companies in Australia, studies of this type have been performed previously in Europe and the US.
- Non-zero genetic correlations between production and reproduction traits and sow attributes highlights the need for multi-trait selection and genetic evaluation procedures. PIGBLUP is currently limited in its ability to accommodate non-zero genetic correlations across trait subsets, and further development of this software is required.

Management

- The optimum feeding management of commercial sows is clearly dependent on their overall genetic merit and therefore requirements. In the absence of information from breeding companies on the nutritional requirements of their sows, an objective strategy should be developed to evaluate for individual producers whether their feeding and management regimes are at least adequate based on the average sow in their herd. This can probably be partly achieved via targeted large cohort comparisons (within herd) from existing herd recording systems. For example, substantially better survival of below average sows in a large cohort suggests that conditions are sub-optimal for above average sows. Revision of feeding management, amongst other things, may therefore yield benefits in this situation. This could be added to existing programs such as “Target 25”, and summarised across populations of sow genotypes.

- As an alternative to the above, breeding companies with sound evidence for significant genetic gain in production and reproductive traits should be encouraged and assisted to develop more complete and up to date “management manuals” for their producers to appropriately manage specific sow genotypes. For example, minimum thresholds to target were identifiable for first parity maternal gain and fatness in the study population. Other breeding companies should also be able to develop similar recommendations for producers who use their breeding stock.
- There is good evidence from results in this study for environmental limitations to individual sow performance in some traits. Strategies should be developed to better meet requirements of individual sows during gestation and lactation. This will become more important under group housing of sows during gestation, where sow condition tends to become more variable. Such strategies imply that the requirements of individual sows (and their litters) can be accurately and easily assessed in the field, and management can be varied accordingly for individual sows or groups of sows. Research to refine strategies in this general area is required.
- There is consensus amongst animal breeders that modern sows are becoming increasingly less able to function properly when nutrition, management or the environment are sub-optimal. Following an initial maternal line comparison noted above, an additional project could be to subdivide these sow lines into low and high requirement groups for direct comparison in low and high performance environments. These environments could initially be defined on the basis of facilities (particularly with respect to climate control), nutrition, and health challenges. Characterising the type of environment under which different types of sows can perform well may generate sufficient data for models which relate genotype to environment and predict phenotypic outcomes, and could be used by breeding companies to promote more suitable genotypes to specific production environments. This would align well with the proposed Pork CRC project intended to facilitate quantification of environment quality.
- Since traits such as lactation feed intake are clearly influenced by factors such as farrowing outcomes or sow health, it is important that data recording systems are flexible enough to accommodate storing information on these areas concurrently. This is potentially less important for genetic evaluation systems (if lactation length is recorded and a good reflection of health status), but also provides information which could be used to develop strategies for better management of sow health in the peripartum period.

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Appendix 1: Genetic variances (bold diagonal) along with original bivariate estimates of genetic correlations (below diagonal) and those used for Index calculations (above diagonal).

	ADG	*BF*	*EMD*	*TADG*	*ADI*	*FCR*	*SWPF*	*FT110*	*WTW*	*FTW*	*LADI*	*NBA*	*APBW*	*LG10*	*PAR2*	*SIGF*
ADG	**1029**	0.30	-0.10	0.25	0.30	0.18	0.35	0.25	0.40	0.17	0.22	-0.09	0.20	0.10	0.06	0.10
BF	0.34	**1.32**	0.08	0.06	0.32	0.24	-0.05	0.65	0.04	0.65	-0.11	0.05	-0.10	-0.03	0.30	0.13
EMD	-0.28	0.08	**3.97**	-0.10	-0.15	-0.10	-0.04	0.05	-0.02	0.03	0.03	0.05	-0.05	-0.04	-0.10	0.11
TADG	0.37	0.06	-0.16	**3505**	0.65	-0.50	0.20	0.11	0.37	0.16	0.14	0.05	-0.05	-0.05	0.02	0.16
ADI	0.51	0.33	-0.35	0.43	**0.033**	0.13	0.15	0.35	0.35	0.41	0.19	0.01	-0.02	-0.05	-0.07	0.16
FCR	0.18	0.24	-0.16	-0.54	0.53	**0.060**	-0.15	0.21	-0.15	0.27	0.14	0.01	-0.01	-0.04	-0.12	0.12
SWPF	0.74	-0.05	-0.04	0.54	0.29	-0.21	**65.3**	0.26	0.76	0.28	0.15	-0.03	0.20	0.00	0.08	0.00
FT110	0.28	0.75	0.05	0.11	0.46	0.31	0.26	**4.43**	0.27	0.85	-0.12	0.00	0.00	-0.03	0.40	0.22
WTW	0.61	0.04	-0.02	0.60	0.47	-0.15	0.77	0.27	**103**	0.44	0.40	-0.03	-0.06	-0.30	0.20	0.25
FTW	0.17	0.73	0.03	0.19	0.53	0.27	0.28	0.91	0.44	**4.06**	0.20	0.06	-0.14	-0.20	0.24	0.10
LADI	0.42	-0.11	0.03	0.14	0.26	0.10	0.33	-0.16	0.56	0.20	**0.094**	-0.02	0.10	-0.03	0.14	0.13
NBA	-0.09	0.09	0.05	0.01	0.01	0.05	0.01	0.04	-0.05	0.09	-0.03	**0.81**	-0.21	0.07	0.06	0.06
APBW	0.47	-0.36	-0.14	-0.11	-0.06	0.05	0.45	-0.08	-0.12	-0.17	0.13	-0.10	**0.017**	0.24	0.01	-0.12
LG10	0.40	-0.07	-0.05	-0.29	-0.34	-0.02	-0.14	-0.10	-0.38	-0.27	0.06	0.07	0.36	**2.88**	0.07	-0.10
PAR2	0.24	0.45	-0.29	0.02	-0.42	-0.42	0.09	0.46	0.20	0.24	0.13	0.29	-0.01	0.34	**0.20**	0.30
SIGF	0.20	0.23	0.21	0.21	0.36	0.12	-0.07	0.27	0.18	0.15	0.23	0.23	-0.27	0.47	0.81	**2300**

Genetic correlations altered by >abs(0.15) are highlighted in blue font