

10-2016

## Effect of selection for residual feed intake during the grow/finish phase of production on sow reproductive performance and lactation efficiency

J. M. Young  
*Iowa State University*

R. Bergsma  
*Institute for Pig Genetics (IPG)*

E. F. Knol  
*Institute for Pig Genetics (IPG)*

John F. Patience  
*Iowa State University, jfp@iastate.edu*

Jack C. M. Dekkers  
*Iowa State University, jdekkers@iastate.edu*

Follow this and additional works at: [https://lib.dr.iastate.edu/ans\\_pubs](https://lib.dr.iastate.edu/ans_pubs)



Part of the [Agriculture Commons](#), [Animal Experimentation and Research Commons](#), [Animal Sciences Commons](#), and the [Genetics Commons](#)

The complete bibliographic information for this item can be found at [https://lib.dr.iastate.edu/ans\\_pubs/828](https://lib.dr.iastate.edu/ans_pubs/828). For information on how to cite this item, please visit <http://lib.dr.iastate.edu/howtocite.html>.

---

This Article is brought to you for free and open access by the Animal Science at Iowa State University Digital Repository. It has been accepted for inclusion in Animal Science Publications by an authorized administrator of Iowa State University Digital Repository. For more information, please contact [digirep@iastate.edu](mailto:digirep@iastate.edu).

---

# Effect of selection for residual feed intake during the grow/finish phase of production on sow reproductive performance and lactation efficiency

## Abstract

As feed costs continue to rise and efficiency during finishing is emphasized, the impact of selecting for more efficient grow/finish pigs on reproductive performance and feed efficiency of sows must be evaluated. Therefore, the objectives of this study were to evaluate correlated responses for sow reproductive performance and lactation feed efficiency to selection for residual feed intake (RFI) during the grow/finish phase of production ( $RFI_{G/F}$ ) in 2 selection lines of pigs developed at Iowa State University (Ames, IA) and to estimate heritabilities of these traits. One line was selected over 7 generations for decreased  $RFI_{G/F}$  (low RFI [LRFI] line) and the other line was randomly selected for 5 generations and then selected for increased  $RFI_{G/F}$  (high RFI [HRFI] line). After 7 generations of selection, LRFI sows had 1.0 more piglets farrowed ( $P = 0.11$ ) compared with HRFI sows, 1.3 more pigs born alive ( $P < 0.05$ ), similar farrowing survival, 0.4 fewer mummies ( $P < 0.01$ ), and more piglets weaned, both by litter (1.6 more;  $P < 0.01$ ) and by sow (1.1 more;  $P < 0.01$ ). Low RFI sows consumed 25 kg less feed and lost 9.8 kg more BW, 7.0 kg more fat mass, and 3.1 mm more backfat than HRFI sows ( $P < 0.001$ ) during lactation. Although LRFI sows had a greater negative energy balance ( $-19.8$  vs.  $-8.0$  MJ ME/d;  $P < 0.001$ ), they had better RFI during lactation ( $-28.6$  vs.  $8.2$  kg;  $P < 0.0001$ ), and the trend was for LRFI sows to have better lactation efficiency (61.3 vs. 57.8%;  $P = 0.47$ ) than HRFI sows. Heritabilities for sow weights, sow body composition, sow maintenance requirements (estimated from BW), and piglet birth weight were high ( $h^2 > 0.4$ ,  $SE < 0.07$ ). Traits pertaining to piglet growth during lactation and mobilization of body tissue of the sow were moderately heritable ( $0.2 < h^2 < 0.4$ ,  $SE < 0.07$ ). In conclusion, selection for decreased  $RFI_{G/F}$  has favorably affected piglet performance and lactation efficiency but has unfavorably affected sow body condition loss and energy balance during lactation. These results indicate that pigs selected for increased efficiency during grow–finish are better able to direct resources where needed during other life history phases, that is, reproduction and lactation.

## Keywords

lactation efficiency, pigs, reproduction, residual feed intake

## Disciplines

Agriculture | Animal Experimentation and Research | Animal Sciences | Genetics

## Comments

This is a manuscript of an article published as Young, J. M., R. Bergsma, E. F. Knol, J. F. Patience, and J. C. M. Dekkers. "Effect of selection for residual feed intake during the grow/finish phase of production on sow reproductive performance and lactation efficiency." *Journal of animal science* 94, no. 10 (2016): 4120-4132. doi:[10.2527/jas.2015-0130](https://doi.org/10.2527/jas.2015-0130). Posted with permission.

Running head: Residual feed intake and lactation efficiency

Effect of selection for residual feed intake during the grow/finish phase of production on sow  
reproductive performance and lactation efficiency

J. M. Young<sup>†</sup>, R. Bergsma<sup>‡</sup>, E. F. Knol<sup>‡</sup>, J. F. Patience<sup>†</sup>, J. C. M. Dekkers<sup>†</sup>

<sup>†</sup> Department of Animal Science, Iowa State University, Ames, IA 50011

<sup>‡</sup> Institute for Pig Genetics (IPG), Beuningen, the Netherlands

## Abstract

As feed costs continue to rise and efficiency during finishing is emphasized, the impact of selecting for more efficient grow/finish pigs on reproductive performance and feed efficiency of sows must be evaluated. Therefore, the objectives of this study were to evaluate correlated responses for sow reproductive performance and lactation feed efficiency to selection for residual feed intake (**RFI**) during the grow/finish phase of production (**RFI<sub>G/F</sub>**) ~~on sow reproductive performance and feed efficiency in two~~ 2 selection lines of pigs developed at Iowa State University and to estimate heritabilities of these traits. One line was selected over 7 generations for decreased **RFI<sub>G/F</sub>** (**LRFI** line) and the other line was randomly selected for 5 generations and then selected for increased **RFI<sub>G/F</sub>** (**HRFI** line). After 7 generations of selection, LRFI sows had 1.0 more piglets farrowed ( $P=0.11$ ) compared to HRFI sows, 1.3 more pigs born alive ( $P<0.05$ ), similar farrowing survival, 0.4 fewer mummies ( $P<0.01$ ), and more piglets weaned, both by litter (1.6 more,  $P<0.01$ ) and by sow (1.1 more,  $P<0.01$ ). LRFI sows consumed 25 kg less feed and lost 9.8 kg more body weight, 7.0 kg more fat mass, and 3.1 mm more backfat than HRFI sows ( $P<0.001$ ) during lactation. Although LRFI sows had a greater negative energy balance (-19.8 vs. -8.0 MJ ME/d,  $P<0.001$ ), they had better residual feed intake during lactation (-28.6 vs. 8.2 kg,  $P<0.0001$ ) and ~~they tended~~ the trend was for LRFI sows to have better lactation efficiency (61.3 vs. 57.8%,  $P=0.47$ ) ~~and had better RFI residual feed intake during lactation (-28.6 vs. 8.2 kg,  $P<0.0001$ )~~ than HRFI sows. Heritabilities for sow weights, sow body composition, sow maintenance requirements (estimated from body weight) and ~~for~~ piglet birth weights were high ( $h^2>0.4$ ,  $SE<0.07$ ). Traits pertaining to piglet growth during lactation and mobilization of ~~the sow's~~ body tissue of the sow were moderately heritable ( $0.2<h^2<0.4$ ,  $SE<0.07$ ). In conclusion, selection for decreased **RFI<sub>G/F</sub>** ~~during grow/finish~~ has positively

favorably affected piglet performance and lactation efficiency but has ~~negatively~~ unfavorably affected sow body condition loss and energy balance during lactation. These results indicate that pigs selected for increased efficiency during grow-finish are better able to direct resources where needed during other life history phases, i.e. reproduction and lactation.

**Key words:** lactation efficiency, pigs, reproduction, residual feed intake

## **Introduction**

Residual feed intake (**RFI**) is a measure of feed efficiency that is defined as the difference between observed ADFI and predicted ADFI based on average requirements for maintenance and production. Therefore, depending on genetic correlations (Kennedy et al., 1993), selection for decreased RFI in grow/finish pigs (**RFI<sub>G/F</sub>**) should result in decreased ADFI without affecting growth. When developing strategies for genetic improvement of feed efficiency in pigs, it is important to evaluate correlated responses to selection in other economically important traits.

Lactation is an energetically expensive process that results in the mobilization of body fat and body protein when nutrient intake fails to meet daily energy and nutrient requirements. This mobilization of body tissue coincides with a negative energy balance which has been shown to have negative consequences on health and reproduction in intensively managed dairy cattle (Veerkamp et al., 2001; Formigoni and Trevisi, 2003; Llewellyn et al., 2007). In pigs, a negative energy balance has been shown to result in a delayed return to estrus (Whittemore and Morgan, 1990; Clowes et al., 2003).

There is limited information on the impact of selecting for decreased **RFI<sub>G/F</sub>** on sow productivity (Gilbert et al., 2012). Results in cattle (Shaffer et al., 2011) and in chickens

(Morisson et al., 1997) differ for fertilization and embryonic survival rates. However, direct selection for leanness has impacted sow productivity, resulting in smaller litters and reduced litter weight (Kersey DeNise et al., 1983; Kerr and Cameron, 1996); and single-trait selection for decreased  $RFI_{G/F}$  has resulted in market pigs that are leaner than pigs selected for increased  $RFI_{G/F}$  (Cai et al., 2008; Smith et al., 2011; Young and Dekkers, 2012). Therefore, the objective of this experiment was to evaluate correlated responses in and heritability of sow reproductive performance and lactation efficiency traits in lines of pigs divergently selected for  $RFI_{G/F}$ .

## **Materials and Methods**

Experimental protocols for this study were approved by the Iowa State University Institutional Animal Care and Use Committee (project # 11-1-4996-S).

### *Animals*

Starting in 2001, a population of purebred Yorkshires was used to select a line of pigs for decreased  $RFI_{G/F}$  (**LRFI** line) compared to a line (**HRFI** line) that was initially randomly selected but selected for increased  $RFI_{G/F}$  starting in generation 5. Beginning with the random allocation of littermates from generation 0 to the LRFI and HRFI lines, the following traits were recorded each generation on ~90 boars from first parity sows and ~90 gilts from second parity sows of the LRFI line: electronically measured individual daily feed intake, BW recorded every 2 wk, and 10<sup>th</sup>-rib backfat and LM area measured at market weight. Backfat and LM area at market weight were evaluated by ultrasound using an Aloka 500V SSD ultrasound machine fitted with a 3.5-MHz, 12.5-cm, linear array transducer (Corometrics Medical Systems Inc., Wallingford, CT). ADFI was derived as described by Cai et al. (2008) using data collected from Feed Intake Recording Equipment (**FIRE**©) stations (Osborne Industries Inc., Osborne, KS).

ADG was obtained as the slope from simple linear regression of BW on number of days on test. After evaluation of boars from first parity sows, ~12 boars and 70 gilts were selected to produce ~50 litters of ~10 piglets for the next generation. Selection decisions were based on EBV for  $RFI_{G/F}$ , as described by Cai et al. (2008). After selection, gilts from parity 2 sows, which were full- or half-sisters of selected boars, were evaluated for  $RFI_{G/F}$  to provide additional data for the next generation. Through generation 5, the HRFI line was maintained by creating ~30 litters from ~10 randomly selected boars and 40 randomly selected gilts. Full- and half-sib matings were avoided in both lines. In addition, selected boars and gilts were assigned to mating groups to minimize inbreeding. In early generations, only LRFI pigs were evaluated for feed intake because of limited capacity to measure feed intake. Starting in generation 5 with boars from parity 1 sows, HRFI pigs were also evaluated for feed intake during the grow/finish period to make direct line comparisons and to allow for selection within the HRFI line for increased  $RFI_{G/F}$ . Further details are in Cai et al. (2008) and Bunter et al. (2010).

#### *Gilt development and sow management*

Gilts were fed ad-libitum in a conventional finishing room until reaching market weight. Lines were mixed in finishing pens. Once market weight was reached, selected animals were tagged and moved to gestation, where they were fed 2.8 kg each morning. Gilts were housed either in crates or pens. Pens in gestation were mixed between lines. Due to other projects at the research farm, breeding was dictated by finishing scheduling and not by minimizing non-productive days as would be typical in commercial production. Approximately 21 d before breeding, gilts were checked for standing estrus, mainly to allow farm personnel a better understanding of the breeding schedule so that they could plan semen collection on boars. Once bred, gilts were checked for return to estrus to determine pregnancy status.

### *Sow management and lactation traits*

Sows were housed in gestation crates from breeding and fed 2.8 kg daily. Approximately 3 to 5 d before their due date, sows gilts were weighed and moved into 1 of 4 farrowing rooms, with each room having 12 farrowing crates. Once in a farrowing crate, sows gilts were scanned using the same ultrasound equipment as described above for market pigs. Prior to farrowing, sows gilts were fed 1.4 kg twice a day. After farrowing, sows gilts were fed twice a day to appetite and the amount offered to them was recorded. If wet feed covered the bottom of the feed trough, it was removed and weighed. Cross-fostering was performed within 24 h of birth unless agalactia or sow death occurred later. Approximately 8.5% of piglets born were cross-fostered, with ~60% of cross-fostering occurring within line. Between 21 and 28 d post-farrowing, piglets were weaned and moved into the nursery and sows gilts were scanned, weighed, and moved back to the gestation barn.

Because the breeding schedule was set to match a farrowing schedule, sows were not checked for return to estrus after weaning. Typically, sows would be checked for standing estrus 1 to 2 mo after weaning, approximately 21 d before the start of breeding. Sow management post-breeding was identical to gilt management post-breeding.

### *Piglet traits*

All piglets born to a sow were recorded at processing and coded for live, dead at birth, or mummy. Farrowing survival was calculated as the percent born alive out of the total number farrowed (born alive + dead at birth + mummies). Farrowing and weaning dates were recorded for all piglets, along with date of death for piglets that died during ~~lactation~~ the suckling period. Individual weights were recorded at birth for all non-mummified piglets and at weaning for all piglets alive at weaning. Pre-weaning survivability, as a trait of the sow, was calculated as the

percentage of piglets weaned out of the number of piglets ~~nursing~~ nursed by the sow after cross-fostering. Litter weaning weight, average weaning weight, and number weaned were calculated either based on all piglets born to a sow regardless of whether she nursed them or not (referred to hereafter as by litter) or based on all piglets actually nursed by a sow regardless of whether she farrowed them or not (referred to hereafter as by sow). Piglet growth was defined as the difference between weaning and birth weights. The ADG of piglets that survived to weaning was calculated as piglet growth divided by age at weaning. Weights of piglets that died were estimated using the growth rate of their littermates and the age at mortality as:

*Mortality weight (kg)* = Birth weight (kg) + [(Fraction  $\times$  ADG<sub>littermates</sub>)/1000]  $\times$  Age at mortality (d),

where Fraction is the relative piglet growth during each week of lactation as defined by Bergsma et al. (2009):

$$Fraction = 0.583333 + 0.270833 \times WM - 0.058333 \times WM^2 + 0.004167 \times WM^3,$$

where **WM** = week of mortality (1, 2, 3, 4). Piglet energy gain from birth to weaning was calculated using estimated fat and protein deposition and piglet maintenance requirements, following Bergsma et al. (2009):

*Fat deposition, **FD** (kg)* = (Weaning weight – Birth weight)  $\times$  (0.135 + 0.00014  $\times$  ADG),

$$Protein\ deposition,\ \mathbf{PD}\ (kg) = (Weaning\ weight - Birth\ weight) \times 0.16,$$

$$Piglet\ maintenance\ (MJ\ ME/d) = 0.440 \times [(Weaning\ weight + Birth\ weight) / 2]^{0.75},$$

$$Piglet\ energy\ gain\ (MJ\ ME/d) = [(FD \times 39.5 + PD \times 23.8) / Age\ at\ weaning] +$$

Maintenance.

The litter traits of ADG, growth, and energy gain were calculated by summing the respective piglet traits across piglets nursed by a sow.

#### *Sow traits*

Sows were weighed upon entering and exiting the farrowing house. Ultrasonic backfat was obtained at farrowing and at weaning by averaging measurements taken at the 10<sup>th</sup> rib and the last rib. Sow weight at farrowing was calculated by adjusting the weight at entrance into the farrowing house for the estimated weight of the piglets, placentas, and intra-uterine fluid, following Noblet et al. (1985):

$$\text{Total fetal weight (g), } \mathbf{TFW} = e^{(8.72962 - 4.07466 * e^{(-0.03318 * (d - 45))} + 0.000154 * f * d + 0.06774 * n)},$$

$$\text{Placental weight (g), } \mathbf{PW} = e^{(7.02746 - 0.95164 * e^{(-0.06879 * (d - 45))} + 0.000085 * f * d + 0.09335 * n)},$$

$$\text{Intra-uterine fluid weight (g), } \mathbf{IUFW} = e^{(-0.2636 + 0.18805 * d - 0.001189 * d^2 + 0.13194 * n)},$$

where  $d$  = days of pregnancy;  $f$  = energy intake during gestation (MJ ME/d); and  $n$  = number of fetuses. Parameter  $f$  was set equal to 35 MJ ME/d for this study based on sows being fed 2.8 kg each morning during gestation and an energy content of the diet of 12.5 MJ ME/kg. Total fetal weight was estimated separately for the day of pregnancy at weighing and for the day of pregnancy at parturition in order to convert the observed litter birth weight to an estimated weight of the litter, placenta, and intra-uterine fluid at time of weighing, which was used to adjust the recorded weight of the sow as follows (Noblet et al., 1985):

$$\text{Sow weight at farrowing (kg)} = \text{recorded weight (kg)} - \text{litter birth weight (kg)} \times \times$$

$$[(\text{TFW at weighing} + \text{PW at weighing} + \text{IUFW at weighing}) / \text{TFW at parturition}].$$

Sow weight at weaning was adjusted for the change in water composition of the body, given the estimated milk production, from the start to the end of lactation. Equations used were derived from Kim et al. (1999a, 1999b, 2000) by Bergsma et al. (2009):

*Sow weight at weaning (kg)* = Recorded weight (kg) – [(*Water*<sub>weaning</sub> – *Water*<sub>farrowing</sub>)/1000],

$$\text{Water}_{\text{weaning}} (g) = (\text{NFG} - \text{NWBS}) \times 73 + (\text{NWBS} \times 146.15 + 2.17 \times \text{ADG}) \times (1 - \text{DM}_{\text{weaning}}/100),$$

$$\text{Water}_{\text{farrowing}} (g) = \text{NFG} \times 431.5 \times (1 - \text{DM}_{\text{farrowing}}/100),$$

$$\% \text{ dry tissue } (\text{DMDM}) = 31.805 - 0.6027 \times \text{DL} + 0.011 \times \text{DL}^2,$$

$$\text{Litter ADG } (g) = [(\text{Litter weaning weight of piglets} / \text{NWBS} - \text{Total birth weight of piglets to be nursed by sow} / \text{Number to be nursed by sow}) \times 1000] / \text{Lactation length},$$

where NFG = number of functional glands at parturition (assumed to equal the number of piglets to be nursed + 1 with a maximum value of 15), NWBS = number of piglets weaned by sow, and DL = day of lactation. Protein mass and fat mass of sows at farrowing and weaning were estimated using equations derived by Bergsma et al. (2009) from Everts et al. (1994):

$$\text{Protein mass } (kg) = 1.90 + 0.1711 \times \text{body weight } (kg) - 0.3113 \times \text{backfat } (mm),$$

$$\text{Fat mass } (kg) = -11.58 + 0.1027 \times \text{body weight } (kg) + 1.904 \times \text{backfat } (mm).$$

Weight loss, fat mass loss, protein mass loss, and backfat loss were calculated as the value at farrowing minus the value at weaning. Thus, positive values refer to a loss. Sow maintenance was estimated using the same equation as used for piglet maintenance:

$$\text{Sow maintenance } (MJ \text{ ME}/d) = 0.440 \times [((\text{Weight at weaning} + \text{Weight at farrowing})/2)^{0.75}],$$

Feed intake was recorded on sows while they were in the farrowing house as described above and summed across the lactation period. The lactation diet contained 13.64 MJ ME and 172 g crude protein per kg of feed.

The efficiency of the sow during lactation was quantified using lactation efficiency, lactation RFI, and energy balance. Lactation efficiency was defined as the ratio of energy output (in the form of piglet growth and maintenance) to energy input (energy from feed and body tissue mobilization above maintenance requirements of the sow) based on the diagram of energy flow during lactation shown in Figure 1 (Bergsma et al., 2008, 2009). Lactation RFI was calculated by estimating regression coefficients of total lactation feed intake on ~~sow maintenance times lactation length~~ the total maintenance requirement of the sow during lactation, litter growth, sow weight loss, and sow backfat loss using the mixed procedure in SAS (SAS Institute Inc., Cary, NC). The model used was based on the model used by Gilbert et al. (2010) which, in addition to the aforementioned covariates across all line, generation, and parity combinations, included the fixed effects of line, generation, and parity and the random effect of sow. Using regression coefficients estimated from our data, the equation for lactation RFI was:

*Lactation RFI (kg/lactation) = Sow feed intake - (6.1934 + 0.2255 × (Sow maintenance × Lactation length) + 0.000231 × Litter growth + 7.404 × Sow weight loss + 0.8728 × Sow backfat loss).*

Energy balance was defined as the difference between energy retained by the sow at weaning and at farrowing, which were estimated using protein mass and fat mass at weaning and farrowing. The energy contents of protein and fat were set as 23.8 MJ ME/kg protein and 39.5 MJ ME/kg fat, respectively (Bergsma et al., 2009).

*Energy retained by the sow at farrowing (MJ ME) = Sow protein mass at farrowing × 23.8 + Sow fat mass at farrowing × 39.5.*

*Energy retained by the sow at weaning (MJ ME) = Sow protein mass at weaning × 23.8 + Sow fat mass at weaning × 39.5.*

*Energy balance (MJ ME/d)* = (Energy retained by the sow at weaning – Energy retained by the sow at farrowing) / Lactation length.

The above equations for piglet and sow traits were assumed to be equally applicable to both lines, which may not be valid. Previous studies have shown differences in lean growth between the two lines (Cai et al., 2008; Smith et al., 2011; Young and Dekkers, 2012). Boddicker et al. (2011) showed that the LRFI line consumed slightly less feed when assigned to a weight stasis protocol, which would suggest slightly lower maintenance requirements.

### *Statistical analyses*

Numbers of records available for analyses are presented in Table 1. Due to missing data and culling after the first parity, not all sows had data for both parities. Simple means and standard deviations of traits analyzed are presented in Table 2. To estimate line differences, data were analyzed using the mixed procedure of SAS. Fixed effects included in the model were line and the interactions of line with generation and generation with parity. The random effect of sow was included for all traits to account for repeated measures on a sow. Covariates depended on the trait analyzed (Table 23). Table 3 only includes traits for which the model included a covariate. Lactation length was used as a covariate for several traits because, although average lactation length did not differ between lines, it did vary between sows. Since SAS adjusts least squares means (LS Means) to the overall mean of the covariate and covariate means differed between generations, LS Means for Generation 9 were adjusted to the mean of covariates in that generation as follows: LS Mean – covariate estimate × (overall covariate mean – generation 9 covariate mean). Heritabilities of sow traits were estimated using an animal model in AS-REML (Gilmour et al., 1995), both across and within lines. The pedigree included 14,169 individuals from generation -1 through generation 8, plus the parents of generation -1. Sow was fitted as a

permanent environmental effect to account for repeated measures on the same sow. Fixed effects and covariates for sow traits were the same as used to estimate line differences.

## Results and Discussion

### *Line differences*

After 97 generations, the lines that were divergently selected for  $RFI_{G/F}$  differed in selection for  $RFI_{G/F}$  impacted sow reproductive performance and lactation efficiency. The LRFI line had 1.0 more total piglets farrowed per litter ( $P = 0.11$ ), 1.3 more piglets born alive ( $P < 0.05$ ), and 0.43 fewer mummies per litter ( $P < 0.01$ ) (Table 3). While not statistically significant, the LRFI line had 1.0 more total piglets farrowed per litter (11.6 vs. 10.6 piglets/litter;  $P = 0.11$ ) and a greater farrowing survival rate (92.8 vs. 90.2 %;  $P = 0.26$ ), which resulted in a significant increase in piglets born alive ( $P = 0.04$ ) (Table 4). The LRFI line had 0.43 fewer mummies per litter ( $P < 0.01$ ) while there was no difference in the number of piglets dead at birth between the two lines ( $P = 0.45$ ). The LRFI line weaned more piglets, both by sow (9.7 vs. 8.6,  $P < 0.01$ ) and by litter (9.8 vs. 8.2,  $P < 0.01$ ). Differences in numbers weaned by sow and by litter are due to use of some cross-fostering across lines and a higher pre-weaning survival in the LRFI line (91.8 vs. 87.8%,  $P = 0.18$ ). Although not significant, the LRFI line had greater average birth weights was higher in the LRFI than in the HRFI line (1.26 vs. 1.20 kg,  $P = 0.11$ ) and a tendency there was a trend for greater total birth weight (13.4 vs. 13.0 kg,  $P = 0.32$ ) after adjusting for total number born. Although the LRFI line still also had heavier piglets when considering only piglets born alive, after adjusting for number born alive, these differences were not significant on either a piglet (1.28 vs. 1.22 kg,  $P = 0.14$ ) or litter basis (12.6 vs. 12.3 kg,  $P = 0.39$ ). When adjusting for number weaned (total weaning weights) and lactation length, weaning weights did not differ between lines by litter (total for LRFI vs. HRFI = 63.1 vs. 63.2 kg,  $P = 0.93$ ; average

for LRFI vs. HRFI = 6.3 vs. 6.5 kg,  $P = 0.36$ ) or by sow (total for LRFI vs. HRFI = 57.8 vs. 57.4 kg,  $P = 0.85$ ; average for LRFI vs. HRFI = 6.9 vs. 7.1 kg,  $P = 0.50$ ). Growth rates on a piglet or a litter basis did not differ between lines ( $P > 0.7$ ).

While performance of piglets during lactation did not differ, the manner in which sows supported growth of their nursed piglets did differ substantially between the two lines (Table 4 5). At farrowing, LRFI sows tended to have slightly greater body mass than HRFI sows (166.9 vs. 160.1 kg,  $P = 0.21$ ), slightly lower fat mass (42.1 vs. 45.1 kg,  $P = 0.12$ ), and slightly greater protein mass (23.9 vs. 23.4 kg,  $P = 0.12$ ). However, sows from the LRFI line lost more weight during lactation (9.3 vs. -0.5 kg,  $P < 0.01=0.002$ ), which was due to both a greater fat mass depletion (12.3 vs. 5.3 kg,  $P < 0.0001$ ) and a greater protein mass depletion (1.6 vs. -0.0 kg,  $P < 0.01$ ). LRFI sows had similar estimated maintenance costs compared to HRFI sows (19.9 vs. 19.8 MJ ME/d,  $P = 0.83$ ) but consumed 25 kg less feed ( $P < 0.0001$ ) and had a greater negative energy balance (-19.8 vs. -8.0 MJ ME/d,  $P < 0.001$ ) than sows from the HRFI line. The LRFI sows had tended to have greater energy output during lactation than the HRFI sows (34.1 vs. 32.1 MJ ME/d,  $P = 0.09$ ) but similar energy input from feed intake and tissue mobilisation (56.0 vs. 57.5 MJ ME/d,  $P = 0.66$ ). This resulted in the LRFI line having a higher lactation efficiency than the HRFI line (61.3 vs. 57.8%,  $P = 0.47$ ) although this difference was not statistically significant. Lactation RFI was, however, lower in the LRFI line than in the HRFI line (-28.6 vs. 8.2 kg,  $P < 0.0001$ ).

A concurrent study in France has also evaluated the effects of divergent selection for RFI<sub>G/F</sub> on sow reproduction (Dekkers and Gilbert, 2010; Gilbert et al., 2010, 2012). Similar to our study, number born alive and born total, sow weight loss during lactation, and sow backfat loss during lactation were greater in their LRFI line than in their HRFI line. Sow feed intake and

lactation RFI were lower in the LRFI line than the HRFI line, similar to our study. While no differences litter birth weight were found in our lines, in the lines in France, litter birth weight was greater in the LRFI line than in the HRFI line.

Selection for decreased  $RFI_{G/F}$  has resulted in leaner pigs (Cai et al., 2008; Smith et al., 2011) and, as shown in this study, this has resulted in sows that have better reproductive performance in terms of litter size and equal piglet growth, while eating less and mobilizing more tissue resources during lactation. Several studies have selected for lean growth in pigs and evaluated the effects on reproduction. Correlated responses to selection for lean growth have varied and depended on the method of selection for lean growth, either direct selection for lean growth or selection for components of lean growth (Kersey DeNise et al., 1983; Kerr and Cameron, 1996; Cameron et al., 2002). Response to selection for lean growth resulted in greater (Vangen, 1980), equal (Kerr and Cameron, 1996), or fewer (Kersey DeNise et al., 1983; Cleveland et al., 1988) piglets born. Our results of more piglets farrowed agree with those by Vangen (1980), who also found that number born alive increased with selection for lean growth. However, Kersey DeNise et al. (1983) and Cleveland et al. (1988) found that number born alive decreased with selection for lean growth. Similar to our results, response of litter birth weight to selection for lean growth was positive (Vangen, 1980; Cleveland et al., 1988; Kerr and Cameron, 1996), although not always significant (Kerr and Cameron, 1996; Cameron et al., 2002). Unlike our study, number weaned was lower (Kersey DeNise et al., 1983; Cleveland et al., 1988) or equal (Kerr and Cameron, 1996) in lines selected for lean growth. Results for weaning weight varied from heavier (Cleveland et al., 1988) to equal (Kerr and Cameron, 1996) to lighter (Kerr and Cameron, 1996) for lines selected for lean growth. Sow weight at farrowing was either equal or greater in lines selected for components of lean growth (Kerr and Cameron, 1996; Cameron et

al., 2002), which is opposite to what we found in our study. However, similar to our study, sow backfat depth at farrowing was less in lines selected for components of lean growth than in control lines (Kerr and Cameron, 1996; Cameron et al., 2002) but weight loss and backfat loss tended to be equal between lines (McKay, 1992; Kerr and Cameron, 1996; Cameron et al., 2002). Kerr and Cameron (1996) and Cameron et al. (2002) found that sow feed intake was lower in lines selected for reduced feed intake during grow finish and in lines selected for lean food conversion but greater in lines selected for improved lean growth rate compared with control lines. As a result, the energy balance was more negative in lines selected for reduced daily feed intake and lean food conversion, whereas the lines selected for lean growth rate had similar energy balances compared to control lines (Cameron et al., 2002). These results show that response to selection for lean growth will depend on the selection method used. Results may also be population dependent. Since we selected for  $RFI_{G/F}$  and had a correlated response in leanness, the underlying selection pressure on reproductive performance appears to be different when selecting for  $RFI_{G/F}$  compared to selecting for lean growth or components of lean growth.

### *Heritabilities*

Heritabilities of piglet traits varied greatly, from 0.04 for number of mummies within the LRFI line to 0.51 for litter birth weight in the LRFI line (Table 56). Heritabilities estimated across and within lines were similar, with the exception of a few traits. Number of piglets dead at birth and number of mummies had heritabilities within the HRFI line (0.22 and 0.23, respectively) that were 3 to 4 times larger than in the LRFI line (0.08 and 0.04, respectively) or across lines (0.08 and 0.06, respectively). Farrowing survival and number weaned by sow had greater heritabilities in the LRFI line (0.14 for both traits) than in the HRFI line (0.08 and 0.03, respectively) or across lines (0.10 and 0.08, respectively). Traits pertaining to piglet birth weight

tended to be highly heritable, ranging from 0.36 for total and average live piglet birth weight in the HRFI line to 0.51 for litter birth weight in the LRFI line. Traits pertaining to number of piglets tended to be lowly heritable, ranging from 0.04 for number of mummies within the LRFI line to 0.25 for total born and number fully formed in the HRFI line, with heritability for most traits being around 0.2. ~~Number of mummies was not significantly heritable.~~ Traits pertaining to growth of piglets during lactation were moderately heritable, ranging from 0.14 for litter growth across lines and litter average daily gain and growth in the HRFI line to 0.28 for piglet energy gain in the HRFI line.

Traits pertaining to sow weight and body composition at farrowing and at weaning were highly heritable (Table 67), ranging from 0.34 for sow protein mass at weaning in the LRFI line to 0.72 for sow weight at weaning in the LRFI line. Sow weight loss, fat mass loss, and protein loss were moderately to highly heritable, ranging from 0.19 for backfat loss across lines and in the HRFI line to 0.42 for sow protein mass loss in the HRFI line. Sow maintenance was highly heritable (0.70 across lines, 0.71 in the HRFI line, and 0.74 in the LRFI line). Sow feed intake was only moderately heritable (0.23 in the LRFI line, 0.27 across lines, and 0.28 in the HRFI line). Traits pertaining to different measures of efficiency during lactation had a wide range of heritabilities, ranging from 0.08 for energy input in the HRFI line to 0.44 for lactation RFI in the HRFI line. Lactation RFI was moderately to highly heritable (0.23 in the LRFI line, 0.32 across lines, and 0.44 in the HRFI line). Energy balance was lowly to moderately heritable (0.08 in the LRFI line, 0.12 across lines, and 0.22 in the HRFI line).

Heritabilities of total born across and within lines (0.21 to 0.25, Table 56) were higher than the estimate of 0.13 by Bergsma et al. (2008). Previous reports of heritabilities for number born alive range from 0.08 to 0.16 (Tholen et al., 1996; Chen et al., 2003; Ehlers et al., 2005;

Holm et al., 2005; Bunter et al., 2007), which is lower than our range of 0.17 to 0.19. Our heritabilities for litter birth weight of 0.40 to 0.51 are much higher than those previously reported by Ehlers et al. (2005), which ranged from 0.162 to 0.20. Our heritabilities for average litter birth weight (0.39 to 0.50) were also much higher than previous reports of heritabilities by Tholen et al. (1996), which were 0.30 and 0.28 in their herd 1 and 0.15 and 0.11 in their herd 2 for first and second parity sows, respectively, and the estimate of 0.30 by Bunter et al. (2007). Previous reports of the heritability of number weaned by sow ranged from 0.02 to 0.09 (Chen et al., 2003; Serenius and Stalder, 2004; Serenius et al., 2008), which is lower than the heritability found in the LRFI line (0.14) in our population. Although not significantly different from zero, the heritability of 0.04 for number weaned by sow in the HRFI line falls within the range of heritabilities previously reported, as does the heritability of 0.08 across lines. Our heritabilities for pre-weaning survival (0.15 to 0.16) were much higher than the heritability of 0.04 reported by Bergsma et al. (2008).

Our estimates of heritabilities of weaning weight by sow across lines (0.19), in the LRFI line (0.20), and in the HRFI line (0.22) are slightly higher than the previously reported range of 0.07 to 0.17 (Tholen et al., 1996; Chen et al., 2003). Our heritability estimates for litter growth (0.14 across lines and in the LRFI line and 0.19 in the HRFI line) were similar to the heritabilities of 0.19 and 0.16 reported by Bergsma et al. (2008) and Bergsma (2011), respectively. The estimates of heritability of sow weight at farrowing were higher in our population (0.60 to 0.65) than the 0.50 reported by Bergsma (2011). However, the estimates of heritability of sow fat mass at farrowing were similar in our population (0.42 to 0.46) as in the population evaluated by Bergsma (2011) (0.42). The estimates of heritability of sow weight loss were higher in our population (0.36 to 0.39) than the 0.14 reported by Bergsma (2011). However,

the estimates of heritability of sow feed intake were similar in our population (0.23 to 0.28) as in the population evaluated by Bergsma (2011) (0.23) and estimates in both studies were greater than the 0.11 reported by Bunter et al. (2007). Estimated heritabilities for lactation efficiency of 0.12 and 0.10 reported by Bergsma et al. (2008) and Bergsma (2011), respectively, fall within our range of heritabilities for lactation efficiency of 0.07 to 0.16.

### **Conclusions and implications**

Results from this study show that selection for decreased  $RFI_{G/F}$  has had no detrimental effect on sow reproductive performance ~~and, in fact, resulted in increased litter size and equal piglet performance. The equal piglet performance, however, came from a greater loss of body condition for sows from the LRFI line.~~ However, sows from the LRFI line had a greater loss of body condition during lactation. The greater loss of body condition for sows from the LRFI line was accounted for in part by their lower feed intake during lactation. Nevertheless, sows from the LRFI line were more efficient at converting energy from feed intake and body tissue mobilization into piglet growth, which also could be affected by differences in piglet efficiency. These results indicate that pigs selected for increased efficiency during grow-finish are better able to direct resources where needed during other life history phases, i.e. early growth, reproduction, and lactation.

The greater loss of body condition for sows from the LRFI line may, however, have an impact on rebreeding. The greater loss of body condition may also result in a greater wean to first estrus interval. In this population, sows were not bred at first estrus post-weaning but to fit the farrowing and finishing schedule of the research farm, so rebreeding success could not be evaluated. The impact on sow longevity could also not be evaluated in this study because all sows were culled after two parities. Also, only sows that had offspring selected to go onto the

FIRE feeders for parity 1 were rebred to produce parity 2; therefore, some sows were culled after only 1 parity.

The efficiency of sows transforming feed into piglet gain was heritable, whether it was measured as lactation efficiency or lactation RFI. Heritability estimates were consistent across and within lines and with literature. Therefore, it would be possible to select sows that are more efficient during lactation and this appears to coincide with efficiency during the grow/finish phase. Sows used in this study were not evaluated for feed efficiency during grow-finish. Although this does not prevent genetic correlations between efficiency during lactation and grow-finish to be estimated, these analyses unfortunately did not converge. The LRFI line, however, had better efficiency regardless of how it was measured, suggesting that grow/finish efficiency and sow efficiency coincided. This was particularly true for lactation RFI, which showed a 20.4 kg difference in residual intake between the lines which was ~15 % of total lactation feed intake in the HRFI line. With the industry moving towards total efficiency across production phases, it is desirable that grow/finish efficiency and sow efficiency coincide, which the results of this study support.

Sows from the LRFI line consumed less feed during lactation and produced more (in terms of piglets) than sows from the HRFI line, which are both beneficial from a producer standpoint (less input and greater output). Because gilts/sows were managed equally between lines and the LRFI gilts/sows had better feed efficiency and tended to be smaller, there may have been indirect preferential feeding of the LRFI gilts/sows compared to the HRFI gilts/sows. However, sows from the LRFI line ~~but~~ lost more body reserves, which may detrimentally impact rebreeding performance and longevity. Therefore, when selecting for pigs that are more feed

efficient during the grow/finish phase, sow feed intake and body condition change during lactation must be taken into consideration.

### **Acknowledgements**

The authors would like to thank the farm staff at the Lauren Christian Swine Breeding Research Center and the multiple ultrasound technicians that made data collection possible. The authors would also like to acknowledge Anoosh Rakhshandeh for his help in developing the equation used to estimate energy balance. Funding was provided by the National Pork Board, Iowa Pork Producers Association, and USDA National Needs Graduate Fellowship Competitive Grant No. 2007-38420-17767 from the National Institute of Food and Agriculture.

### **Literature Cited**

- Bergsma, R., E. Kanis, M. W. A. Verstegen, and E. F. Knol. 2008. Genetic parameters and predicted selection results for maternal traits related to lactation efficiency in sows. *J. Anim. Sci.* 86:1067-1080.
- Bergsma, R., E. Kanis, M. W. A. Verstegen, C. M. C. van der Peet-Schwering, and E. F. Knol. 2009. Lactation efficiency as a result of body composition dynamics and feed intake in sows. *Livest. Sci.* 125:208-222.
- Bergsma, R. 2011. Genetic aspects of feed intake in lactating sows. PhD Thesis. Wageningen University, Wageningen, the Netherlands.
- Boddicker, N., N. K. Gabler, M. E. Spurlock, D. Nettleton, and J. C. M. Dekkers. 2011. Effects of *ad libitum* and restricted feeding on early production performance and body composition of Yorkshire pigs selected for reduced residual feed intake. *Animal* 5:1344-1353.

- Bunter, K. L., B. G. Luxford, and S. Hermes. 2007. Associations between feed intake of growing gilts, lactating sows and other reproductive or performance traits. *Proc. Assoc. Advmt. Breed. Genet.* 17:57-60.
- Bunter, K. L., W. Cai, D. J. Johnston, and J. C. M. Dekkers. 2010. Selection to reduce residual feed intake in pigs produces a correlated response in juvenile insulin-like growth factor-I concentration. *J. Anim. Sci.* 88:1973-1981.
- Cai, W., D. S. Casey, and J. C. M. Dekkers. 2008. Selection response and genetic parameters for residual feed intake in Yorkshire swine. *J. Anim. Sci.* 86:287-298.
- Cameron, N. D., J. C. Kerr, G. B. Garth, R. Fenty, and A. Peacock. 2002. Genetic and nutritional effects on lactational performance of gilts selected for components of efficient lean growth. *Anim. Sci.* 74:25-38.
- Chen, P., T. J. Baas, J. W. Mabry, K. J. Koehler, and J. C. M. Dekkers. 2003. Genetic parameters and trends for litter traits in U.S. Yorkshire, Duroc, Hampshire, and Landrace pigs. *J. Anim. Sci.* 81:46-53.
- Cleveland, E. R., R. K. Johnson, and P. J. Cunningham. 1988. Correlated responses of carcass and reproductive traits to selection for rate of lean growth in swine. *J. Anim. Sci.* 66:1371-1377.
- Clowes, E. J., F. X. Aherne, G. R. Foxcroft, and V. E. Baracos. 2003. Selective protein loss in lactating sows is associated with reduced litter growth and ovarian function. *J. Anim. Sci.* 81:753-764.
- Dekkers, J. C. M., and H. Gilbert. 2010. Genetic and biological aspect of residual feed intake in pigs. *Proc 9<sup>th</sup> WCGALP. Paper # 287.*

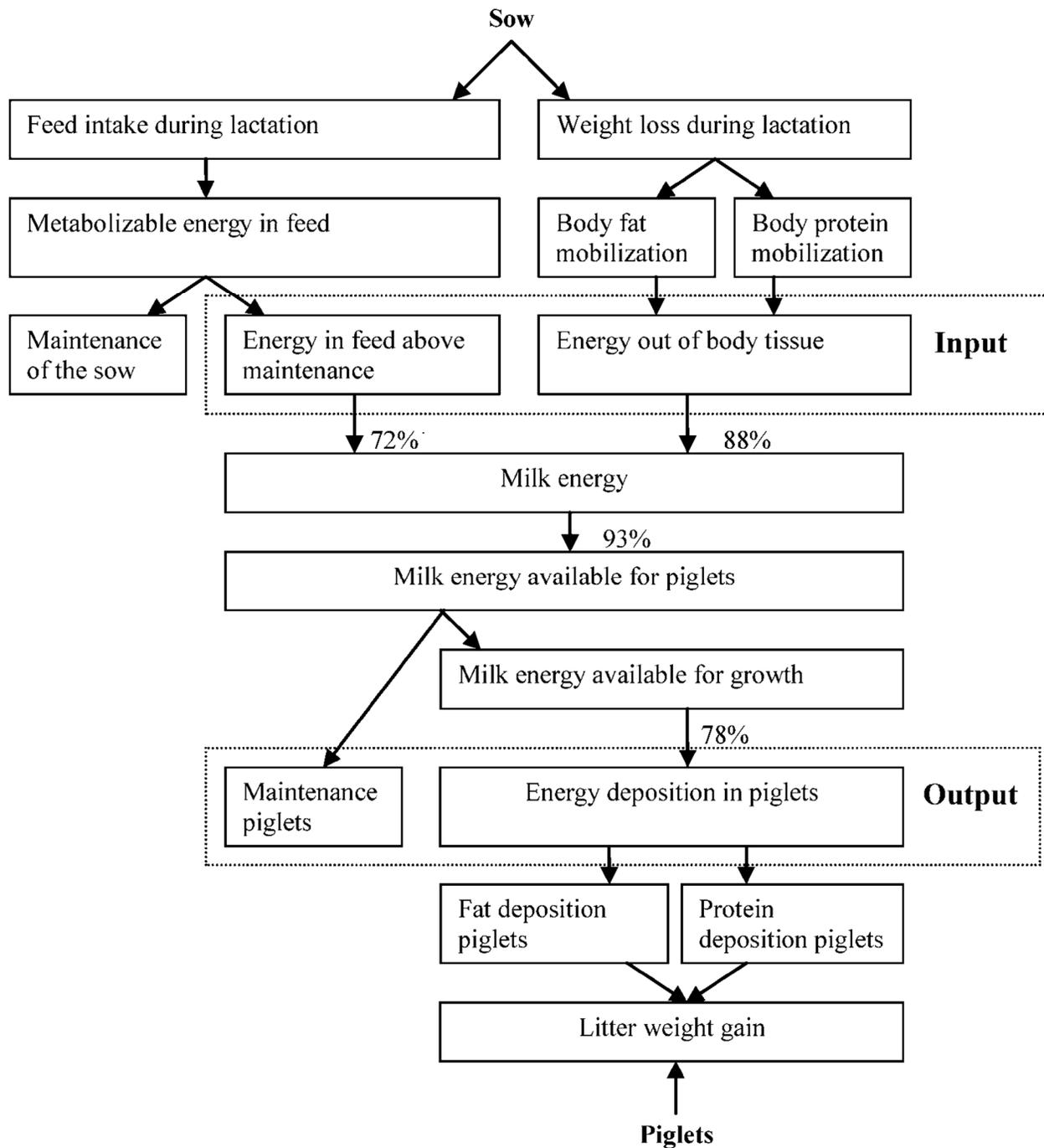
- Ehlers, M. J., J. W. Mabry, J. K. Bertrand, and K. J. Stalder. 2005. Variance components and heritabilities for sow productivity traits estimated from purebred versus crossbred sows. *J. Anim. Breed. Genet.* 122:318-324.
- Everts, H., and R. A. Dekker. 1994. Balance trials and comparative slaughtering in breeding sows: description of techniques and observed accuracy. *Livest. Prod. Sci.* 37:339-352.
- Formigoni, A., and E. Trevisi. 2003. Transition cow: interaction with fertility. *Vet. Res. Commun.* 27 Suppl 1:143-152.
- Gilbert, H., Y. Billon, H. Lagant, J. A. Calderon, P. Guillouet, J.-P. Bidanel, J. Noblet, P. Sellier, and S. Hermesch. 2010. Correlated responses in sow feed intake, body composition and reproduction after divergent selection for residual feed intake in the growing pig. *Proc 9<sup>th</sup> WCGALP. Paper # 293.*
- Gilbert, H., J.-P. Bidanel, Y. Billon, H. Lagant, P. Guillouet, P. Sellier, J. Noblet, and S. Hermesch. 2012. Correlated response in sow appetite, residual feed intake, body composition and reproduction after divergent selection for residual feed intake in the growing pig. *J. Anim. Sci.* 90:1097-1108.
- Gilmour, A. R., R. Thompson, and B. R. Cullis. 1995. Average Information REML, an efficient algorithm for variance parameter estimation in linear mixed models. *Biometrics.* 51:1440-1450.
- Holm, B., M. Bakken, O. Vangen, and R. Rekaya. 2005. Genetic analysis of age at first service, return rate, litter size, and weaning-to-first service interval of gilts and sows. *J. Anim. Sci.* 83:41-48.
- Kennedy, B. W., J. H. van der Werf, and T. H. Meuwissen. 1993. Genetic and statistical properties of residual feed intake. *J. Anim. Sci.* 71:3239-3250.

- Kerr, J. C., and N. D. Cameron. 1996. Responses in gilt post-farrowing traits and pre-weaning piglet growth to divergent selection for components of efficient lean growth rate. *Anim. Sci.* 63:523-531.
- Kersey DeNise, R. S., K. M. Irvin, L. A. Swiger, and R. F. Plimpton. 1983. Selection for increased leanness of Yorkshire swine. IV. Indirect responses of the carcass, breeding efficiency and preweaning litter traits. *J. Anim. Sci.* 56:551-559.
- Kim, S. W., W. L. Hurley, I. K. Han, and R. A. Easter. 1999a. Changes in tissue composition associated with mammary gland growth during lactation in sows. *J. Anim. Sci.* 77:2510-2516.
- Kim, S. W., I. Osaka, W. L. Hurley, and R. A. Easter. 1999b. Mammary gland growth as influenced by litter size in lactating sows: impact on lysine requirement. *J. Anim. Sci.* 77:3316-3321.
- Kim, S. W., W. L. Hurley, I. K. Hant, and R. A. Easter. 2000. Growth of nursing pigs related to the characteristics of nursed mammary glands. *J. Anim. Sci.* 78:1313-1318.
- Llewellyn, S., R. Fitzpatrick, D. A. Kenny, J. J. Murphy, R. J. Scaramuzzi, and D. C. Wathes. 2007. Effect of negative energy balance on the insulin-like growth factor system in pre-recruitment ovarian follicles of *post partum* dairy cows. *Repro.* 133:627-639.
- McKay, R. M. 1992. Effect of index selection for reduced backfat thickness and increased growth rate on sow weight changes through two parities in swine. *Can. J. Anim. Sci.* 72:403-408.
- Morisson, M., A. Bordas, J. M. Petit, C. Jayat-Vignoles, R. Julien, and F. Minvielle. 1997. Associated effects of divergent selection for residual feed consumption on reproduction, sperm characteristics, and mitochondria of spermatozoa. *Poult. Sci.* 76:425-431.

- Noblet, J., W. H. Close, R. P. Heavens, and D. Brown. 1985. Studies on the energy metabolism of the pregnant sow: 1. Uterus and mammary tissue development. *Br. J. Nutr.* 53:251-265.
- Serenius, T., and K. J. Stalder. 2004. Genetics of length of productive life and lifetime prolificacy in the Finnish Landrace and Large White pig populations. *J. Anim. Sci.* 82:3111-3117.
- Serenius, T., K. J. Stalder, and R. L. Fernando. 2008. Genetic associations of sow longevity with age at first farrowing, number of piglets weaned, and wean to insemination interval in the Finnish Landrace swine population. *J. Anim. Sci.* 86:3324-3329.
- Shaffer, K. S., P. Turk, W. R. Wagner, and E. E. D. Felton. 2011. Residual feed intake, body composition, and fertility in yearling beef heifers. *J. Anim. Sci.* 89:1028-1034.
- Smith, R. M., N. K. Gabler, J. M. Young, W. Cai, N. J. Boddicker, M. J. Anderson, E. Huff-Lonergan, J. C. M. Dekkers, and S. M. Lonergan. 2011. Effects of selection for decreased residual feed intake on composition and quality of fresh pork. *J. Anim. Sci.* 89:192-200.
- Tholen, E., K. L. Bunter, S. Hermes, and H-U. Graser. 1996. The genetic foundation of fitness and reproduction traits in Australian pig populations 2. Relationships between weaning to conception interval, farrowing interval, stayability, and other common reproduction and production traits. *Aust. J. Agric. Res.* 47:1275-1290.
- Vangen, O. 1980. Studies on a two trait selection experiment in pigs. V. Correlated responses in reproductive performance. *Acta Agric. Scand.* 30:309-319.
- Veerkamp, R. F., E. P. C. Koenen, and G. De Jong. 2001. Genetic correlations among body condition score, yield, and fertility in first-parity cows estimated by random regression models. *J. Dairy Sci.* 84:2327-2335.

Whittemore, C. T., and C. A. Morgan. 1990. Model components for the determination of energy and protein requirements for breeding sows: a review. *Livest. Prod. Sci.* 26:1-37.

Young, J. M., and J. C. M. Dekkers. 2012. The genetic and biological basis of residual feed intake as a measure of feed efficiency. Pages 153-166 in *Feed efficiency of swine*. J. F. Patience, ed. Wageningen Academic Publishers, The Netherlands.



**Figure 1.** Schematic flow chart of the energy metabolism of sows during lactation (From Bergsma et al., 2008, 2009).

**Table 1:** Number of sows with reproductive data available for analysis within the LRFI and HRFI lines by generation.

Generation	Line	Sows <sup>1</sup>		
		Parity 1 only	Both Parity 1 & 2	Parity 2 only
-1		22 (26)	52 (46)	0 (0)
0	LRFI	17 (15)	35 (34)	0 (0)
	HRFI	24 (22)	.	.
1	LRFI	9 (8)	36 (34)	1 (1)
	HRFI	17 (17)	.	.
2	LRFI	29 (34)	25 (17)	6 (3)
	HRFI	11 (13)	15 (9)	5 (7)
3	LRFI	16 (45)	33 (0)	0 (0)
	HRFI	11 (23)	17 (0)	0 (0)
4	LRFI	22 (40)	37 (8)	0 (2)
	HRFI	12 (24)	34 (6)	0 (3)
5	LRFI	16 (20)	40 (26)	0 (2)
	HRFI	24 (28)	34 (22)	0 (4)
6	LRFI	9 (0)	41 (1)	3 (41)
	HRFI	14 (2)	37 (2)	1 (34)
7	LRFI	29 (28)	27 (22)	0 (1)
	HRFI	23 (20)	31 (25)	0 (1)
8	LRFI	45 (41)	.	.
	HRFI	52 (41)	.	.
Total	LRFI	214 (257)	326 (188)	10 (50)
	HRFI	188 (190)	168 (64)	6 (49)

<sup>1</sup> Sow counts are given as two numbers  $a$  ( $b$ ), where  $a$  is the number of sows with reproductive data and  $b$  is the number of sows that have all the information necessary to calculate lactation efficiency for parity 1 only, parity 2 only, or both parity 1 and 2. Sows produced piglets belonging to the next generation. I.e. a generation 0 sow produced generation 1 piglets.

**Table 2.** Simple statistics for piglet and sow traits for sows that produced generation 9 piglets.

Trait	Mean			SD		
	Overall	LRFI <sup>1</sup>	HRFI <sup>1</sup>	Overall	LRFI <sup>1</sup>	HRFI <sup>1</sup>
Total born (n)	11.08	11.61	10.57	2.55	2.33	2.66
Number fully formed piglets (n)	10.68	11.43	9.96	2.47	2.26	2.47
Number born alive (n)	10.11	10.77	9.48	2.46	2.41	2.36
Number of piglets dead at birth (n)	0.57	0.66	0.48	0.84	0.91	0.75
Number of mummies (n)	0.40	0.18	0.61	0.88	0.50	1.11
Farrowing survival (%)	91.43	92.76	90.16	9.51	8.65	10.20
Litter birth weight (kg)	13.04	14.05	12.07	2.93	2.66	2.89
Average litter birth weight (kg)	1.24	1.24	1.23	0.18	0.18	0.18
Total live piglet birth weight (kg)	12.44	13.34	11.59	2.91	2.74	2.83
Average live piglet birth weight (kg)	1.25	1.26	1.24	0.18	0.19	0.18
Number weaned by litter (n)	9.00	9.82	8.22	2.51	2.20	2.56
Number weaned by sow (n)	9.13	9.70	8.59	1.68	1.39	1.77
Pre-weaning survival by sow (%)	89.78	91.82	87.83	13.59	9.19	16.63
Weaning weight by litter (kg)	63.14	67.19	59.27	19.67	16.32	21.89
Average weaning weight by litter (kg)	7.00	6.88	7.12	1.05	0.97	1.11
Weaning weight by sow (kg)	63.8	66.5	61.2	14.6	11.4	16.8
Average weaning weight by sow (kg)	6.99	6.89	7.08	1.10	1.00	1.19
Piglet average daily gain (g/d)	210	208	211	29	25	32
Piglet growth (kg)	5.49	5.44	5.54	1.15	0.98	1.30
Piglet energy gain (MJ ME)	3.40	3.38	3.42	0.47	0.41	0.53
Litter average daily gain (g/d)	2016	2087	1949	346	262	402
Litter growth (kg)	52.87	54.50	51.31	12.17	9.79	14.01
Litter energy gain (MJ ME)	32.72	33.92	31.57	5.65	4.29	6.54
Sow weight at farrowing (kg)	163.5	166.9	160.1	18.9	18.0	19.3
Sow fat mass at farrowing (kg)	43.58	43.16	44.02	11.58	12.24	10.99
Sow protein mass at farrowing (kg)	23.61	24.31	22.89	3.05	2.96	3.01
Sow backfat depth at farrowing (mm)	20.15	19.75	20.56	5.63	6.01	5.25
Sow weight at weaning (kg)	159.06	156.68	161.50	18.42	17.66	19.07
Sow fat mass at weaning (kg)	34.73	31.07	38.49	9.81	7.96	10.18
Sow protein mass at weaning (kg)	22.84	22.56	23.13	3.32	3.55	3.08
Sow backfat depth at weaning (mm)	15.74	13.95	17.59	4.66	3.92	4.69
Sow weight loss (kg)	4.47	10.20	-1.40	16.03	14.46	15.58
Sow fat mass loss (kg)	8.85	12.09	5.53	8.64	8.01	8.05
Sow protein mass loss (kg)	0.76	1.74	-0.24	2.74	2.47	2.66
Sow backfat loss (mm)	4.41	5.80	2.98	3.96	3.64	3.80
Sow maintenance (MJ/d)	19.89	19.94	19.85	1.56	1.52	1.62
Sow feed intake (kg)	122.8	108.7	137.2	31.1	29.4	25.9
Energy output (MJ ME/d)	33.12	33.87	32.36	5.50	4.39	6.42
Energy input (MJ ME/d)	56.74	56.05	57.46	11.54	9.78	13.19
Lactation efficiency (%)	59.57	61.32	57.77	9.57	7.58	11.06
Sow residual feed intake (kg)	-10.44	-28.65	8.23	40.68	38.54	34.15
Energy balance (MJ ME/d)	-13.97	-19.93	-7.85	15.19	13.97	14.05

<sup>1</sup>LRFI = low residual feed intake line; HRFI = high residual feed intake line.

**Table 23:** Covariates used for data analysis

Traits <sup>1</sup>	TB	NBA	LL	NWBL	NWBS	SFWT	SWWT	SFFM	SFPM	SFBF	IN
Litter birth weight	X										
Average litter birth weight	X										
Total live piglet birth weight		X									
Average live piglet birth weight		X									
Weaning weight by litter			X	X							
Average weaning weight by litter			X	X							
Weaning weight by sow			X		X						
Average weaning weight by sow			X		X						
Piglet average daily gain			X								
Piglet growth			X								
Piglet energy gain			X								
Litter average daily gain			X		X						
Litter growth			X		X						
Litter energy gain			X		X						
Sow fat mass at farrowing						X					
Sow protein mass at farrowing						X					
Sow weight at weaning			X								
Sow fat mass at weaning			X				X				
Sow protein mass at weaning			X				X				
Sow backfat depth at weaning			X								
Sow weight loss			X			X					
Sow fat mass loss			X					X			
Sow protein mass loss			X						X		
Sow backfat loss			X							X	
Sow feed intake			X								
Energy output			X								X
Energy input			X								
Energy balance			X								

<sup>1</sup> Traits down the side are the traits being analyzed, traits across the top are used as covariates.

Abbreviations are TB = total born, NBA = number born alive, LL = lactation length, NWBL = number weaned by litter, NWBS = number weaned by sow, SFWT = sow weight at farrowing, SWWT = sow weight at weaning, SFFM = sow fat mass at farrowing, SFPM = sow protein mass at farrowing, SFBF = sow backfat depth at farrowing, IN = energy input. No covariates were used for traits not in the left column.

**Table 34:** Line differences for piglet traits for sows that produced generation 9.

Traits	Least squares means		
	LRFI	HRFI	P-value <sup>1</sup>
Total born (n)	11.6	10.6	0.11
Number fully formed piglets (n)	<b>11.4</b>	<b>10.0</b>	<b>0.02</b>
Number born alive (n)	<b>10.8</b>	<b>9.5</b>	<b>0.04</b>
Number of piglets dead at birth (n)	0.66	0.48	0.45
Number of mummies (n)	<b>0.18</b>	<b>0.61</b>	<b>0.003</b>
Farrowing survival (%)	92.8	90.2	0.26
Litter birth weight, adjusted for total born (kg)	13.4	13.0	0.32
Average litter birth weight, adjusted for total born (kg)	1.26	1.20	0.11
Total live piglet birth weight, adjusted for number born alive (kg)	12.6	12.3	0.39
Average live piglet birth weight, adjusted for number born alive (kg)	1.28	1.22	0.14
Number weaned by litter (n)	<b>9.8</b>	<b>8.2</b>	<b>0.004</b>
Number weaned by sow (n)	<b>9.7</b>	<b>8.6</b>	<b>0.003</b>
Pre-weaning survival by sow (%)	91.8	87.8	0.18
Weaning weight by litter, adjusted for lactation length and number weaned by litter (kg)	63.1	63.2	0.93
Average weaning weight by litter, adjusted for lactation length (kg)	6.9	7.1	0.36
Weaning weight by sow, adjusted for lactation length and number weaned by sow (kg)	64.0	63.6	0.85
Average weaning weight by sow, adjusted for lactation length (kg)	6.9	7.1	0.50
Piglet average daily gain, adjusted for lactation length (g/d)	208	211	0.72
Piglet growth, adjusted for lactation length (kg)	5.46	5.52	0.77
Piglet energy gain, adjusted for lactation length (MJ ME)	3.39	3.41	0.81
Litter average daily gain, adjusted for lactation length and number weaned by sow (g/d)	2017	2017	0.99
Litter growth, adjusted for lactation length and number weaned by sow (kg)	52.9	52.9	1.00
Litter energy gain, adjusted for lactation length and number weaned by sow (MJ ME)	32.7	32.7	0.98

<sup>1</sup>Traits with P-values in bold are significantly different between the two lines.

**Table 4-5:** Line differences in sow traits in sows producing generation 9 piglets.

Traits	Least squares means		
	LRFI	HRFI	P-value <sup>1</sup>
Sow weight at farrowing (kg)	166.9	160.1	0.21
Sow fat mass at farrowing, adjusted for sow weight at farrowing (kg)	42.1	45.1	0.12
Sow protein mass at farrowing, adjusted for sow weight at farrowing (kg)	23.9	23.4	0.12
Sow backfat depth at farrowing (mm)	19.7	20.6	0.49
Sow weight at weaning, adjusted for lactation length (kg)	156.5	161.7	0.29
Sow fat mass at weaning, adjusted for lactation length and sow weaning weight (kg)	<b>31.7</b>	<b>37.8</b>	<b>0.0003</b>
Sow protein mass at weaning, adjusted for lactation length and sow weaning weight (kg)	22.9	22.8	0.70
Sow backfat depth at weaning, adjusted for lactation length (mm)	<b>13.9</b>	<b>17.6</b>	<b>0.0002</b>
Sow weight loss, adjusted for lactation length and sow weight at farrowing (kg)	<b>9.3</b>	<b>-0.5</b>	<b>0.002</b>
Sow fat mass loss, adjusted for lactation length and sow fat mass at farrowing (kg)	<b>12.3</b>	<b>5.3</b>	<b>&lt;0.0001</b>
Sow protein mass loss, adjusted for lactation length and sow protein mass at farrowing (kg)	<b>1.6</b>	<b>-0.0</b>	<b>0.004</b>
Sow backfat loss, adjusted for lactation length and sow backfat depth at farrowing (mm)	<b>6.0</b>	<b>2.8</b>	<b>&lt;0.0001</b>
Sow maintenance (MJ/d)	19.9	19.8	0.83
Sow feed intake, adjusted for lactation length (kg)	<b>110.5</b>	<b>135.5</b>	<b>&lt;0.0001</b>
Energy output, adjusted for lactation length and energy input (MJ ME/d)	34.1	32.1	0.09
Energy input, adjusted for lactation length (MJ ME/d)	56.0	57.5	0.66
Lactation efficiency (%)	61.3	57.8	0.47
Sow residual feed intake (kg)	<b>-28.6</b>	<b>8.2</b>	<b>&lt;0.0001</b>
Energy balance, adjusted for lactation length (MJ ME/d)	<b>-19.9</b>	<b>-8.0</b>	<b>0.0003</b>

<sup>1</sup>Traits with P-values in bold are significantly different between the two lines.

**Table 56:** Heritabilities and permanent environmental effects<sup>1</sup> of piglet traits of the sow, estimated across or within lines.

Traits	Across lines	Within lines	
		LRFI	HRFI
Total born	<b>0.21 ± 0.04</b>	<b>0.21 ± 0.05</b>	<b>0.25 ± 0.06</b>
Number fully formed	<b>0.20 ± 0.04</b>	<b>0.20 ± 0.05</b>	<b>0.25 ± 0.06</b>
Number born alive	<b>0.17 ± 0.04</b>	<b>0.19 ± 0.05</b>	<b>0.19 ± 0.06</b>
Number of piglets dead at birth	<b>0.08 ± 0.04</b>	0.08 ± 0.04	<b>0.22 ± 0.07</b>
		(0.12 ± 0.10)	(0.02 ± 0.11)
Number of mummies	0.06 ± 0.03	0.04 ± 0.04	<b>0.23 ± 0.07</b>
	<b>(0.17 ± 0.07)</b>		
Farrowing survival	<b>0.10 ± 0.04</b>	<b>0.14 ± 0.05</b>	0.08 ± 0.06
	(0.06 ± 0.07)	(0.16 ± 0.09)	<b>(0.26 ± 0.13)</b>
Litter birth weight	<b>0.45 ± 0.04</b>	<b>0.51 ± 0.05</b>	<b>0.40 ± 0.05</b>
Average litter birth weight	<b>0.46 ± 0.04</b>	<b>0.50 ± 0.05</b>	<b>0.39 ± 0.06</b>
	(0.03 ± 0.05)		(0.02 ± 0.09)
Total live piglet birth weight	<b>0.39 ± 0.04</b>	<b>0.44 ± 0.05</b>	<b>0.36 ± 0.06</b>
Average live piglet birth weight	<b>0.41 ± 0.04</b>	<b>0.45 ± 0.05</b>	<b>0.36 ± 0.06</b>
	(0.04 ± 0.05)		
Number weaned by litter	<b>0.13 ± 0.04</b>	<b>0.16 ± 0.05</b>	<b>0.15 ± 0.06</b>
Number weaned by sow	<b>0.08 ± 0.03</b>	<b>0.14 ± 0.05</b>	0.03 ± 0.05
		(0.03 ± 0.09)	
Pre-weaning survival by sow	<b>0.16 ± 0.04</b>	<b>0.16 ± 0.06</b>	<b>0.15 ± 0.06</b>
	(0.05 ± 0.06)		
Weaning weight by litter	<b>0.08 ± 0.03</b>	<b>0.12 ± 0.05</b>	<b>0.11 ± 0.05</b>
Average weaning weight by litter	<b>0.10 ± 0.04</b>	<b>0.17 ± 0.05</b>	0.09 ± 0.05
			(0.06 ± 0.12)
Weaning weight by sow	<b>0.19 ± 0.04</b>	<b>0.20 ± 0.05</b>	<b>0.22 ± 0.06</b>
Average weaning weight by sow	<b>0.17 ± 0.04</b>	<b>0.20 ± 0.05</b>	<b>0.22 ± 0.06</b>
	(0.06 ± 0.07)	(0.09 ± 0.09)	(0.07 ± 0.12)
Piglet average daily gain	<b>0.23 ± 0.04</b>	<b>0.24 ± 0.06</b>	<b>0.27 ± 0.06</b>
	(0.01 ± 0.06)	(0.06 ± 0.08)	(0.03 ± 0.10)
Piglet growth	<b>0.20 ± 0.04</b>	<b>0.21 ± 0.06</b>	<b>0.19 ± 0.06</b>
			(0.05 ± 0.12)
Piglet energy gain	<b>0.25 ± 0.04</b>	<b>0.26 ± 0.06</b>	<b>0.28 ± 0.06</b>
		(0.02 ± 0.08)	(0.03 ± 0.10)
Litter average daily gain	<b>0.16 ± 0.04</b>	<b>0.14 ± 0.05</b>	<b>0.22 ± 0.06</b>
Litter growth	<b>0.14 ± 0.04</b>	<b>0.14 ± 0.05</b>	<b>0.19 ± 0.06</b>
Litter energy gain	<b>0.18 ± 0.04</b>	<b>0.17 ± 0.05</b>	<b>0.24 ± 0.06</b>

<sup>1</sup> Estimates of the proportion of variance explained by permanent environmental effects with non-zero estimates in ( ) below the heritability estimates. Estimates in bold are significantly different from zero.

**Table 67:** Heritabilities and permanent environmental effects<sup>1</sup> of sow traits, estimated across or within lines.

Traits	Across lines	Within lines	
		LRFI	HRFI
Sow weight at farrowing	<b>0.60 ± 0.03</b> ( <b>0.10 ± 0.04</b> )	<b>0.65 ± 0.04</b> (0.04 ± 0.05)	<b>0.65 ± 0.04</b> (0.03 ± 0.07)
Sow fat mass at farrowing	<b>0.43 ± 0.05</b> ( <b>0.17 ± 0.06</b> )	<b>0.46 ± 0.06</b> ( <b>0.18 ± 0.07</b> )	<b>0.42 ± 0.07</b>
Sow protein mass at farrowing	<b>0.43 ± 0.05</b> ( <b>0.17 ± 0.06</b> )	<b>0.46 ± 0.06</b> ( <b>0.18 ± 0.07</b> )	<b>0.42 ± 0.07</b>
Sow backfat depth at farrowing	<b>0.43 ± 0.05</b> (0.09 ± 0.06)	<b>0.39 ± 0.06</b> (0.06 ± 0.07)	<b>0.46 ± 0.06</b>
Sow weight at weaning	<b>0.69 ± 0.03</b> (0.01 ± 0.04)	<b>0.72 ± 0.03</b> (0.01 ± 0.05)	<b>0.69 ± 0.04</b>
Sow fat mass at weaning	<b>0.46 ± 0.04</b>	<b>0.42 ± 0.06</b>	<b>0.45 ± 0.06</b>
Sow protein mass at weaning	<b>0.42 ± 0.05</b> ( <b>0.12 ± 0.06</b> )	<b>0.34 ± 0.06</b> (0.09 ± 0.08)	<b>0.48 ± 0.06</b> (0.08 ± 0.11)
Sow backfat depth at weaning	<b>0.47 ± 0.04</b>	<b>0.43 ± 0.06</b>	<b>0.50 ± 0.06</b>
Sow weight loss	<b>0.36 ± 0.05</b> (0.01 ± 0.06)	<b>0.39 ± 0.06</b>	<b>0.39 ± 0.07</b>
Sow fat mass loss	<b>0.24 ± 0.05</b>	<b>0.29 ± 0.06</b>	<b>0.24 ± 0.07</b>
Sow protein mass loss	<b>0.35 ± 0.05</b>	<b>0.33 ± 0.06</b>	<b>0.42 ± 0.07</b>
Sow backfat loss	<b>0.19 ± 0.05</b>	<b>0.24 ± 0.06</b>	<b>0.19 ± 0.07</b>
Sow maintenance	<b>0.70 ± 0.03</b> (0.04 ± 0.04)	<b>0.74 ± 0.03</b> (0.01 ± 0.05)	<b>0.71 ± 0.04</b> (0.01 ± 0.07)
Sow feed intake	<b>0.27 ± 0.05</b>	<b>0.23 ± 0.06</b> (0.18 ± 0.10)	<b>0.28 ± 0.06</b>
Energy output	<b>0.11 ± 0.03</b>	<b>0.12 ± 0.05</b>	0.09 ± 0.05
Energy input	<b>0.09 ± 0.04</b>	<b>0.12 ± 0.06</b>	0.08 ± 0.07
Lactation efficiency	0.07 ± 0.04	0.09 ± 0.06	<b>0.16 ± 0.07</b>
Lactation residual feed intake	<b>0.32 ± 0.05</b> ( <b>0.19 ± 0.07</b> )	<b>0.23 ± 0.07</b> (0.09 ± 0.11)	<b>0.44 ± 0.07</b> (0.03 ± 0.14)
Energy balance	<b>0.12 ± 0.05</b>	<b>0.08 ± 0.06</b>	<b>0.22 ± 0.07</b>

<sup>1</sup> Estimates of the proportion of variance explained by permanent environmental effects with non-zero estimates in ( ) below the heritability estimates. Estimates in bold are significantly different from zero.