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Correlated responses in sow appetite, residual feed intake, body composition, and reproduction after divergent selection for residual feed intake in the growing pig¹

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ABSTRACT: Residual feed intake (RFI) has been explored as an alternative selection criterion to feed conversion ratio to capture the fraction of feed intake not explained by expected production and maintenance requirements. Selection experiments have found that low RFI in the growing pig is genetically correlated with reduced fatness and feed intake. Selection for feed conversion ratio also reduces sow appetite and fatness, which, together with increased prolificacy, has been seen as a hindrance for sow lifetime performance. The aims of our study were to derive equations for sow RFI during lactation (SRFI) and to evaluate the effect of selection for RFI during growth on sow traits during lactation. Data were obtained on 2 divergent lines selected for 7 generations for low and high RFI during growth in purebred Large Whites. The RFI was measured on candidates for selection (1,065 pigs), and sow performance data were available for 480 sows having from 1 to 3 parities (1,071 parities). Traits measured were sow daily feed intake (SDFI); sow BW and body composition before farrowing and at weaning (28.4 ± 1.7 d); number of piglets born total, born alive, and surviving at weaning; and litter weight, average piglet BW, and within-

litter SD of piglet BW at birth, 21 d of age (when creep feeding was available), and weaning. Sow RFI was defined as the difference between observed SDFI and SDFI predicted for sow maintenance and production. Daily production requirements were quantified by litter size and daily litter BW gain as well as daily changes in sow body reserves. The SRFI represented 24% of the phenotypic variability of SDFI. Heritability estimates for RFI and SRFI were both 0.14. The genetic correlation between RFI and SRFI was 0.29 ± 0.23 . Genetic correlations of RFI with sow traits were low to moderate, consistent with responses to selection; selection for low RFI during growth reduced SDFI and increased number of piglets and litter growth, but also increased mobilization of body reserves. No effect on rebreeding performance was found. Metabolic changes previously observed during growth in response to selection might explain part of the better efficiency of the low-RFI sows, decreasing basal metabolism and favoring rapid allocation of resources to lactation. We propose to consider SRFI as an alternative to SDFI to select for efficient sows with reduced input demands during lactation.

Key words: correlated responses to selection, lactating sow, pig, residual feed intake, sow residual feed intake

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INTRODUCTION

Improving the use of feed during the growth period remains a major goal in pig production in order to reduce feed costs and waste. Selection experiments have envisioned residual feed intake (**RFI**) as an alternative selection criterion to feed conversion ratio (**FCR**) to improve feed efficiency in pigs (Gilbert et al., 2007; Hoque et al., 2007; Cai et al., 2008). Residual feed intake captures feed intake unexplained by expected production and maintenance requirements (e.g., related

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to physical activity; Herd and Arthur, 2009), whereas FCR quantifies the efficiency of the conversion of feed into BW gain. They have been shown to be moderately to highly correlated. Selection for low RFI and low FCR also reduces fatness and feed intake during growth (Gilbert et al., 2007; Hoque et al., 2007; Cai et al., 2008).

Selection for feed efficiency during growth has been assumed to lead to faster growing, leaner pigs with reduced appetite relative to protein deposition (Fowler et al., 1976; Webb, 1989). It has also resulted in leaner sows with increased prolificacy and reduced appetite (Eissen et al., 2003; Tribout et al., 2003). Lactation is a period of major energy requirements (Noblet et al., 1990); if sows have low feed intake compared with requirements, the litter nutrient supply is provided by depleting body resources, thus impairing rate of rebreeding (Dourmad et al., 1994). Selection for feed efficiency during growth is thus questioned with respect to its effect on sow reproduction ability (Prunier et al., 2010). Veerkamp et al. (1995) and Rauw et al. (2002) proposed the concept of RFI for lactating animals to comprehend female strategies to meet the litter demand, but it is yet to be studied in lactating sows. Using data from lines selected for RFI during growth, the aims of this study were to propose a model to derive sow RFI during lactation and to evaluate the effect of selection for RFI during growth on sow appetite, body composition, and reproductive performances.

MATERIALS AND METHODS

The data collected for this analysis cover the first 7 generations (from G0 to G6) of selection for high RFI or low RFI in growing pigs, in 2 purebred Large White (LW) lines, in accordance with the national regulations for humane care and use of animals in research.

Source of Data

The selection process is described in detail in Gilbert et al. (2007). In brief, from a unique LW population (F0) comprising 30 sires and 30 dams, 2 divergent lines were built: at each generation G0 to G6, 6 sires with the greatest (and least) RFI values (referred to as index) were selected, and a herd of 35 to 40 dams/line was maintained with no selection on females, a gilt randomly replacing its dam at each generation. Initially, pairs of full sisters were randomly selected in each F0 litter, and 1 was assigned to each line to limit the genetic difference between the nonselected founder dams. Sows from the 2 lines were bred in 2 different facilities (Rouillé, Vienne, France, and Le Magneraud, Charente-Maritime, France) and had from 1 to 3 litters. The first- and second-parity litters were purebred. The third-parity litter was from a mating with boars of different genotypes (LW × Piétrain or Duroc) for all generations except G6, where third-parity litters were

purebred. During gestation, sows were housed in groups and twice daily were fed 2.5 to 3 kg of a commercial sow diet containing 12.3 to 13.2 MJ of DE, a minimum of 135 g of CP, and 4.7 g of total lysine/kg. To control variation in body fatness at the time of farrowing, feed supply was more restricted during the 2 wk before farrowing for the visibly fattest sows from 2006, affecting the last 3 generations of the experiment. The breeding process determined by the age of sexual maturity of boars and availability of facilities created experimental constraints in the management of gilt reproduction. As a consequence, the age (439 ± 17 d) and BW (246 ± 25 kg) at first farrowing were greater than usually reported for commercial sows in the French commercial populations (378 ± 20 d in 2008; IFIP, 2010) or in other studies (Bunter et al., 2008). Feed distributed during lactation contained a minimum of 13.8 MJ of DE, 160 g of CP, and 7.6 g of total lysine/kg. Sows were fed semirestrictively on the basis of their feed consumption during the previous day. The daily allowance was gradually increased from 0.3 kg on d 1 after farrowing to a maximum of 9.9 kg in later stages of lactation.

Traits

In this study, RFI recorded during growth on boar candidates to selection and sow performance traits recorded on unselected sows were jointly considered to measure the effect of selection during growth on later sow lifetime performance. The selection criterion “index” was analyzed on a total of 1,065 candidates for selection. The details for the calculation of index are given in Gilbert et al. (2007). In brief, index was defined as the difference between actual and predicted feed intakes of group-housed males fed ad libitum between 35 and 95 kg of BW. Actual daily feed intake (DFI) was recorded with single-place electronic feeders (ACEMA 64, ACEMO, Pontivy, France; Labroue et al., 1994). Predicted feed intake was assessed by linear multiple regression on ADG from 35 to 95 kg of BW, and backfat thickness (BFT) was measured by ultrasonic scanning at 95 kg of BW using an Aloka SSD 500 (Aloka, Cergy Pontoise, France) echograph (average of 6 measurements). The coefficients of index were derived from a previous population of French LW boars (Labroue et al., 1999). The prediction equation for RFI was $DFI (g) - 1.06 \times ADG (g) - 37 \times BFT (mm)$. Index was obtained after standardization to a mean of 100 and SD of 20. Note that results were not significantly different from those presented in the subsequent sections for index when RFI computed de novo based on the selection experiment data set was used instead of index. The results relative to the new computation of RFI are therefore not detailed in this paper.

Reproduction traits were available for all of the 480 sows of the selection experiment for parity 1; 332 and 259 sows had records in parity 2 and 3, respectively. A total of 20 unsuccessful rebreeding events, equally

distributed between the lines, were observed after parity 1. Other culling events were the result of herd-management decisions to adjust for availability of facilities. Sow feed intake was recorded volumetrically from farrowing to weaning at 28.4 ± 1.7 d. Sow daily feed intake (**SDFI**) over the whole lactation was computed when more than 80% of the DFI records were available in the database [e.g., 23 records for a lactation length of 28 d (86% of the lactations)]. The average number of missing DFI records in a lactation length was 1.5 ± 1.3 in the resulting data file, usually due to 1 or 2 d of fasting after farrowing. The percentage of data deleted after data control was similar in the 2 lines. Sow BW and BFT (average of 6 ultrasonic measurements, on each side of the spine at the shoulder, the mid back, and the hip joint) were recorded during the week before farrowing and on the day of weaning to quantify sow body composition.

Piglets were individually weighed at birth and at weaning. Cross-fostering was applied when piglet or sow survival was threatened (5% of the piglets in both lines). Creep feeding was available for the fourth week after birth (from 20.7 ± 2.0 d to weaning), but creep feed intake of the litter was not recorded. To eliminate the nuisance effect of creep feeding on the estimation of milk production obtained from the growth of the litter (Renaudeau and Noblet, 2001), piglets were also individually weighed the day when creep feeding became available. This stage of lactation was called 21 d after farrowing in the following definitions of traits.

The sow traits retained for the analysis were as follows: average SDFI from farrowing to weaning (**SDFIw**); average SDFI from farrowing to 7 d after farrowing (**SDFI-1**), from 8 to 14 d after farrowing (**SDFI-2**), from 15 to 21 d after farrowing (**SDFI-3**), and from 21 d after farrowing to weaning (**SDFI-4**); BW and BFT of the sow before farrowing (**BWf** and **BFTf**, respectively); BW and BFT of the sow at weaning (**BWw** and **BFTw**, respectively); change in BW and change in BFT during lactation (**Δ BW** and **Δ BFT**, respectively) approximated by the change in BW (Δ BW = BWw - BWf) and BFT (Δ BFT = BFTw - BFTf) of the sow from the entrance in the farrowing facility to weaning; total number of piglets born (**TB**), born alive (**BA**), and surviving biological piglets of the sow at weaning (**NS**); weight of the litter at birth including stillborn piglets (**LWb**), at 21 d (**LW21**), and at weaning (**LWw**); litter BW gain between birth and 21 d of age (**Δ LW21**) and between birth and weaning (**Δ LWw**); average piglet BW at birth (**APWb**), at 21 d (**APW21**), and at weaning (**APWw**); and within-litter SD of piglet BW at birth (**SDWb**), at 21 d (**SDW21**), and at weaning (**SDWw**).

Data checking was applied using SAS software (SAS Inst. Inc., Cary, NC), and records differing by more than 3 phenotypic SD from the mean were considered outliers and were systematically excluded. The resulting number of records for each trait is given in Table 1.

Computation of Sow RFI

Similarly to RFI measured during growth (Kennedy et al., 1993), sow RFI (**SRFI**) was defined as the difference between the observed DFI and the predicted daily feed intake required for maintenance of the sow and her production (Rauw et al., 2002). The maintenance requirements of the sow were derived from sow metabolic BW ($BWw^{0.75}$; Noblet et al., 1990). The daily production requirements are driven by the milk demand of the growing litter, usually quantified by the size and the BW gain of the litter (Noblet and Etienne, 1989). In this study, NS and $d\Delta LW21 = \Delta LW21 \times (\text{lactation length})^{-1}$ were used to obtain a daily estimate. In addition, nutrient requirements for litter growth met by changes in body reserves of the sow must be considered in the definition of predicted daily sow feed intake. Because BW and BFT at 21 d were not available to predict the exact changes related to milk production, daily changes were approximated as $d\Delta BW = (BWw - BWf - LWb) \times (\text{lactation length})^{-1}$ and $d\Delta BFT = (\Delta BFT) \times (\text{lactation length})^{-1}$. The prediction of DFI was obtained by multiple regression of SDFIw on $d\Delta BW$, $d\Delta BFT$, $d\Delta LW21$, NS, and $BWw^{0.75}$ following the procedure used for the growing pig in Gilbert et al. (2007). Because sows were bred in 2 farms, fixed effects retained as nuisance parameters in the model were the farm effect (Le Magneraud or Rouillé) and the contemporary group effect, defined as the farrowing group within farm (144 levels), which included parity and season effects.

Analysis

Estimating Variance Components. Variance-covariance components were estimated using REML methodology (Patterson and Thompson, 1971) applied to a multiple-trait individual animal model with version 6.0 of the VCE software package (Neumaier and Groeneveld, 1998). Two- or 3-trait analyses were performed systematically including the trait index to properly account for the effects of selection for this trait in the divergent RFI lines (Hofer, 1998). The pedigree file comprised 4,367 individuals, including G0 to G6 individuals and up to 9 generations of ancestors. The fixed effects for index were growing batch (29 levels), birth farm (2 levels), and pen size (5 levels: ≤ 7 , 8 or 9, 10, 11, and 12 animals/pen). For reproduction traits, contemporary group was based on sow parity, birth farm, and farrowing batch (144 levels). The age of the sow at farrowing was used as a linear covariate. Direct additive genetic value and permanent environment of the sow were fitted as random effects. Individual estimates of additive genetic values were obtained from the variance components estimations for further analyses.

Quantifying Responses to Selection. Responses to selection were computed from individual additive genetic values via differences in LSMEANS (GLM

Table 1. Number of records, mean, phenotypic SD, minimum, and maximum of the traits investigated

Trait ¹	No. of records	Mean	Phenotypic SD	Minimum	Maximum
Index, points	1,118	100	19	44	166
SRFIw, kg/d	852	0.00	0.49	-1.74	2.17
SDFIw, kg/d	1,029	4.70	0.62	2.12	7.39
SDFI-1, kg/d	920	2.75	0.51	0.77	4.97
SDFI-2, kg/d	921	4.61	0.69	1.80	7.13
SDFI-3, kg/d	916	5.38	0.98	1.45	8.77
SDFI-4, kg/d	915	5.70	1.08	1.47	9.52
BWf, kg	981	262	20	175	348
BWw, kg	993	228	20	146	314
ΔBW, kg	948	-34	15	-95	26
BFTf, mm	1,026	25.5	2.8	12.7	40.7
BFTw, mm	1,012	20.4	2.4	7.6	32.3
ΔBFT, mm	997	-5.1	1.0	-15.0	5.2
TB	1,071	12.4	4	1	22
BA	1,064	11.6	3	1	21
NS	1,052	9.7	3	3	15
LWb, kg	1,066	18	5	2	34
LW21, kg	988	63	12	20	108
LWw, kg	923	82	14	29	132
ΔLW21, kg	980	45	12	7	89
ΔLWw, kg	922	64	14	15	115
APWb, kg	1,056	1.49	0.25	0.63	2.4
APW21, kg	1,023	6.8	1.0	3	12.3
APWw, kg	1,002	8.9	1.1	5	12.9
SDWb, kg	1,064	0.29	0.09	0.02	0.59
SDW21, kg	1,022	1.02	0.36	0.06	2.73
SDWw, kg	993	1.26	0.41	0.22	2.73

¹Index = criterion of selection; SRFIw = sow residual daily feed intake during lactation; SDFIw = sow daily feed intake during lactation; SDFI-1 = sow daily feed intake from farrowing to 7 d after farrowing; SDFI-2 = sow daily feed intake from 8 to 14 d after farrowing; SDFI-3 = sow daily feed intake from 15 to 21 d after farrowing; SDFI-4 = sow daily feed intake from 21 d after farrowing to weaning; BWf = BW of the sow before farrowing; BWw = BW of the sow at weaning; ΔBW = change of BW of the sow during lactation; BFTf = backfat thickness of the sow before farrowing; BFTw = backfat thickness of the sow at weaning; ΔBFT = change of backfat thickness of the sow during lactation; TB = total number of piglets born; BA = number born alive; NS = number of surviving biological piglets at weaning; LWb = weight of the litter at birth, including stillborn piglets; LW21 = weight of the litter at 21 d; LWw = weight of the litter at weaning; ΔLW21 = litter weight gain between birth and 21 d of age; ΔLWw = litter weight gain between birth and weaning; APWb = average piglet BW at birth; APW21 = average piglet BW at 21 d; APWw = average piglet BW at weaning; SDWb = within-litter SD of piglet BW at birth; SDW21 = within-litter SD of piglet BW at 21 d; SDWw = within-litter SD of piglet BW at weaning.

procedure of SAS) of the high-RFI line vs. the low-RFI line at each generation. The model included the fixed effects of the line, generation, and line × generation interaction. An approximated Bonferroni correction was applied to the nominal *P*-values of the test to account for the testing of multiple traits. Therefore, only tests corresponding to nominal *P*-values <0.005 were considered significant.

RESULTS AND DISCUSSION

Computation of SRFI

The R^2 of the multiple regression used to predict sow DFI during lactation was 0.76. In this regression, the effect of the contemporary group accounted for about 20% of the phenotypic variation of SDFIw. Calculation resulted in the following equation for SRFI: SRFIw (kg/d) = SDFIw (kg/d) + 0.590 × dΔBW (kg/d) + 0.404 × dΔBFT (mm/d) - 0.429 × dΔLW21 (kg/d) -

0.015 × NS (piglets) - 0.015 × BWw^{0.75} (kg). Among the predictors of sow feed intake, dΔBW and dΔLW21 were highly significant ($P < 0.0001$) and BWw^{0.75} was significant ($P = 0.0051$), whereas dΔBFT and NS were marginally significant ($P = 0.063$ and 0.077, respectively).

Sow Characteristics

Phenotypic characteristics of sow and litter traits were in accordance with the values reported in the literature. During lactation, SDFIw was 4.70 kg/d, which was at the low end of the range of 4.64 to 6.08 kg/d reported previously for multiparous sows of similar breeds (Eissen et al., 2003; Hermes, 2007; Hermes et al., 2010). However, a direct comparison of average values is difficult because DFI depends heavily on energy concentration of the diet and parity (Dourmad et al., 1994). Sows were on average heavier and fatter before farrowing than reported in previous studies

(e.g., Hermesch et al., 2010). However, sow BW losses (including the litter weight at birth) expressed as a proportion of the BW before farrowing were in accordance with those observed in recent studies; sows in our study lost on average 13% of their initial BW, compared with 11% (Hermesch et al., 2010) and 17% (Bergsma et al., 2008) in multiparous sows, 12% (Bunter et al., 2008) and 13% (Guillemet et al., 2006) in primiparous sows, and 11% in first- and second-parity sows (Grandison et al., 2005). The average loss of backfat was 5.1 ± 2.8 mm (i.e., 20% of BFT before farrowing), compared with 5% in Guillemet et al. (2006), 8% in Hermesch et al. (2010), 10% in Bunter et al. (2008), and 20% in Grandison et al. (2005). Contrary to BW loss, the proportion of backfat loss during lactation observed across studies was directly related to the amount of backfat available at the beginning of lactation. The CV of backfat loss observed in this study (20%) was considerably less than the value of 90% reported by Grandison et al. (2005) and the values of 149 and 210% found in 2 Australian studies (Bunter et al., 2008, and Hermesch et al., 2010, respectively). This may be related to the greater and more homogeneous levels of backfat at farrowing in our study.

Prolificacy was 1.3 and 1.5 piglets less for TB and NS, respectively, than litter size measures observed in the French LW population in 2008 (IFIP, 2010). Sows in our experiment were all young and purebred, whereas 90% of French sows have 5 parities on average and are crossbred, taking advantage of heterosis for prolificacy. Moreover, the recent genetic improvement of prolificacy in the French commercial population was not present in our lines, which originated from LW pigs born at the end of the 1990s. In comparison, sows and piglets in our study had characteristics similar to those reported by Quesnel et al. (2008) for purebred LW sows with data collected between 2001 and 2004.

Genetic Parameters

Heritabilities. The heritability of index was 0.14 (Table 2), similar to the estimate reported for an earlier stage of the experiment including 4 generations of selection (Gilbert et al., 2007). The heritability estimate for SRFI was moderate (0.14 ± 0.06), similar to the estimate reported for lactation efficiency by Bergsma et al. (2008). The heritability estimate for SDFI was close to 0 for the first week after farrowing, confirming that SDFI during the first days after farrowing is more highly driven by farrowing conditions than genetic potential for intake capacity. The heritability estimates for weekly measures of SDFI ranged from 0.14 to 0.20 in the following weeks, increasing between wk 2 and 3, and were similar to values found by Hermesch (2007) and Bunter et al. (2010).

Heritability estimates for traits related to sow BW and body composition were low to moderate. The estimate obtained for BW before farrowing was close to the least values previously reported, ranging from 0.19

(Grandison et al., 2005) to 0.45 (Bergsma et al., 2008). Despite the voluntary limitation of greater levels of fatness at farrowing mentioned previously, our estimate of heritability for backfat before farrowing was in the range of values previously reported, ranging from 0.35 (Bunter et al., 2008) to 0.52 (Bergsma et al., 2008). Heritability estimates reported previously (Grandison et al., 2005; Bergsma et al., 2008; Bunter et al., 2008, 2010) for BW change (0.20 to 0.23) and backfat change (0.05 to $0.10 \pm$) during lactation were close to the values found in the present study. However, contrary to our results, the estimate of heritability for BW loss was usually greater than that for backfat loss in the other studies.

Heritability estimates for TB, BA, and NS were moderate to low, as reported in Bidanel (2011). Heritability estimates for total litter weight were low, in accordance with those reported previously (e.g., Bergsma et al., 2008), whereas those for average piglet BW were moderate, ranging from 0.23 ± 0.06 to 0.31 ± 0.04 , as reported in the literature (Bunter et al., 2008), and tended to increase with age of piglets. Heritability estimates for the within-litter SD of piglet BW were low (around 0.10) but significantly different from 0, contrary to those reported by Bergsma et al. (2008).

Genetic Correlations. Despite the relatively large SE of our estimates, general trends can be outlined. Genetic correlations between index and sow feed intake traits were consistently positive, but not significant, in accordance with low to moderate estimates of genetic correlations (range: -0.13 to 0.39) presented recently (Bergsma et al., 2010; Bunter et al., 2010) between DFI or RFI recorded in the growing pig and feed intake of lactating sows. All genetic correlations estimated between SRFI and SDFI traits were highly positive and close to the upper limit of the parameter space. Similarly, Hermesch (2007) found genetic correlations close to unity between weekly measures of sow feed intake during lactation. Index showed genetic correlations close to 0.40 with the change in sow BW and fat depth during lactation, indicating that greater BW and fat losses were associated with smaller index values. The genetic correlations between sow BW and SRFI or SDFI were positive and high, ranging from 0.75 to 0.91. In comparison, no significant genetic associations between comparable trait combinations were found in the studies by Bergsma et al. (2010) and Bunter et al. (2010). On the other hand, no significant correlations were estimated between sow BFT and SRFI or SDFI.

Overall, litter characteristics showed weak genetic associations with index, although lesser index tended to be genetically correlated with greater APW21, supporting favorable genetic associations between early piglet growth and measures of feed efficiency and leanness (Hermesch et al., 2001). In contrast, all trait definitions of SRFI or SDFI had moderate to high positive genetic correlations with average piglet BW and within-litter SD of APW21 and APWw, indicating that a greater proportion of resources available from SDFI was direct-

Table 2. Estimates of heritability (h^2), SD for the animal effects (σ_A), direct (r_A), and permanent environment of the sow (σ_{pe}) correlations with the selection index, sow residual daily feed intake up to weaning (SRFIw), and sow daily feed intake to weaning (SDFIw) for the traits related to reproduction

Trait ¹	h^2 (SE)	σ_A	σ_{pe}	r_A		
				Index (SE)	SRFIw (SE)	SDFIw (SE)
Index, points	0.14 (0.03)	7.3				
SRFIw, kg/d	0.14 (0.06)	0.19	0.20	0.29 (0.23)		
SDFIw, kg/d	0.26 (0.07)	0.32	0.22	0.28 (0.20)	1.00 ²	
SDFI-1, kg/d	0.03 (0.04)	0.08	0.14	0.91 (0.83)	0.94 (0.13)	0.98 (0.04)
SDFI-2, kg/d	0.14 (0.05)	0.26	0.18	0.36 (0.22)	1.00 ²	1.00 ²
SDFI-3, kg/d	0.20 (0.06)	0.43	0.23	0.28 (0.21)	1.00 ²	1.00 ²
SDFI-4, kg/d	0.19 (0.07)	0.47	0.34	0.26 (0.22)	1.00 ²	1.00 ²
BWf, kg	0.16 (0.07)	8.2	14.0	0.07 (0.22)	0.75 (0.35)	0.86 (0.27)
BWw, kg	0.23 (0.07)	9.5	14.1	0.24 (0.21)	0.76 (0.36)	0.91 (0.18)
Δ BW, kg	0.13 (0.05)	5.5	6.6	0.35 (0.21)	0.29 (0.33)	0.38 (0.22)
BFTf, mm	0.40 (0.07)	2.8	2.0	-0.10 (0.16)	-0.08 (0.20)	0.00 (0.17)
BFTw, mm	0.38 (0.02)	2.4	2.3	0.07 (0.17)	0.06 (0.23)	0.09 (0.18)
Δ BFT, mm	0.14 (0.04)	1.0	0.8	0.39 (0.19)	0.24 (0.21)	0.16 (0.19)
TB	0.17 (0.05)	1.5	1.0	0.02 (0.19)	-0.09 (0.30)	0.11 (0.18)
BA	0.16 (0.05)	1.4	0.9	-0.06 (0.21)	-0.28 (0.32)	0.05 (0.23)
NS	0.11 (0.05)	1.1	1.0	-0.08 (0.23)	-0.88 (0.57)	0.01 (0.26)
LWb, kg	0.16 (0.03)	2.0	1.7	-0.06 (0.20)	0.18 (0.26)	0.30 (0.19)
LW21, kg	0.09 (0.04)	3.4	4.7	-0.16 (0.26)	0.25 (0.26)	0.65 (0.15)
LWw, kg	0.09 (0.04)	4.4	5.6	0.02 (0.20)	0.50 (0.21)	0.77 (0.11)
Δ LW21, kg	0.09 (0.05)	3.4	4.6	-0.19 (0.23)	0.16 (0.28)	0.51 (0.15)
Δ LWw, kg	0.01 ²	0.06	0.04	—	0.44 (0.34)	—
APWb, kg	0.23 (0.06)	0.12	0.10	-0.05 (0.18)	0.34 (0.23)	0.21 (0.20)
APW21, kg	0.31 (0.04)	0.53	0.00	-0.27 (0.16)	0.77 (0.12)	0.66 (3.97)
APWw, kg	0.31 (0.07)	0.60	0.26	-0.08 (0.18)	0.75 (0.17)	0.67 (0.15)
SDWb, kg	0.12 (0.05)	0.03	0.03	-0.27 (0.22)	-0.14 (0.32)	-0.08 (0.27)
SDW21, kg	0.08 (0.04)	0.10	0.11	-0.17 (0.23)	0.73 (0.31)	0.52 (0.21)
SDWw, kg	0.11 (0.05)	0.14	0.04	-0.14 (0.20)	0.58 (0.23)	0.37 (0.22)

¹Index = criterion of selection; SRFIw = sow residual daily feed intake during lactation; SDFIw = sow daily feed intake during lactation; SDFI-1 = sow daily feed intake from farrowing to 7 d after farrowing; SDFI-2 = sow daily feed intake from 8 to 14 d after farrowing; SDFI-3 = sow daily feed intake from 15 to 21 d after farrowing; SDFI-4 = sow daily feed intake from 21 d after farrowing to weaning; BWf = BW of the sow before farrowing; BWw = BW of the sow at weaning; Δ BW = change of BW of the sow during lactation; BFTf = backfat thickness of the sow before farrowing; BFTw = backfat thickness of the sow at weaning; Δ BFT = change of backfat thickness of the sow during lactation; TB = total number of piglets born; BA = number born alive; NS = number of surviving biological piglets at weaning; LWb = weight of the litter at birth, including stillborn piglets; LW21 = weight of the litter at 21 d; LWw = weight of the litter at weaning; Δ LW21 = litter weight gain between birth and 21 d of age; Δ LWw = litter weight gain between birth and weaning; APWb = average piglet BW at birth; APW21 = average piglet BW at 21 d; APWw = average piglet BW at weaning; SDWb = within-litter SD of piglet BW at birth; SDW21 = within-litter SD of piglet BW at 21 d; SDWw = within-litter SD of piglet BW at weaning.

²Reached the end of parameter space.

ed toward high litter growth until 21 d and weaning. Comparable genetic correlations could not be found in the literature. With the exception of a negative correlation between SRFIw and NS, traits referring to litter size showed generally no genetic association with SDFI or SRFI, as was found previously for similar trait combinations (Bergsma et al., 2008; Hermes et al., 2008; Bunter et al., 2010).

Responses to Selection. Because the correlations between individual breeding values were ignored in the computation of responses to selection, nominal significance of the responses might be overestimated and only P -values < 0.005 are reported as significant. Test values for the effect of the generation \times line interaction for individual breeding values estimated during the 7 generations of selection were significant at $P < 0.005$ for all traits except LWb ($P < 0.076$). Figure 1 presents the line differences, expressed in genetic SD (σ_A) units of the trait, at each generation for index, SRFIw, and

the traits used to compute SRFIw. To our knowledge, no comparable responses to selection were available in the literature.

Table 3 gives the least squares means of breeding values for each line in G6. The line difference in least squares means for index reached $2.7 \sigma_A$ in G6, corresponding to an average divergence of $0.39 \sigma_A$ /generation. The line difference for SRFIw was reduced ($0.58 \sigma_A$ in G6), corresponding to 109 g/d of SRFIw. In comparison, the line difference was $0.84 \sigma_A$ in G6 for SDFIw (i.e., 280 g/d). This line difference was related to differences in SDFI at the weekly level, with 220 g/d more SDFI in wk 1 after farrowing up to 440 g/d in wk 3 after farrowing. Differences in sow BW were greater at weaning than before farrowing (4.1 vs. 9.1 kg in G6). This resulted in increasing line differences between G0 and G6 for changes in BW during lactation, with the low-RFI line sows losing on average 5.7 kg more BW than the high-RFI line sows in G6. Similar trends were

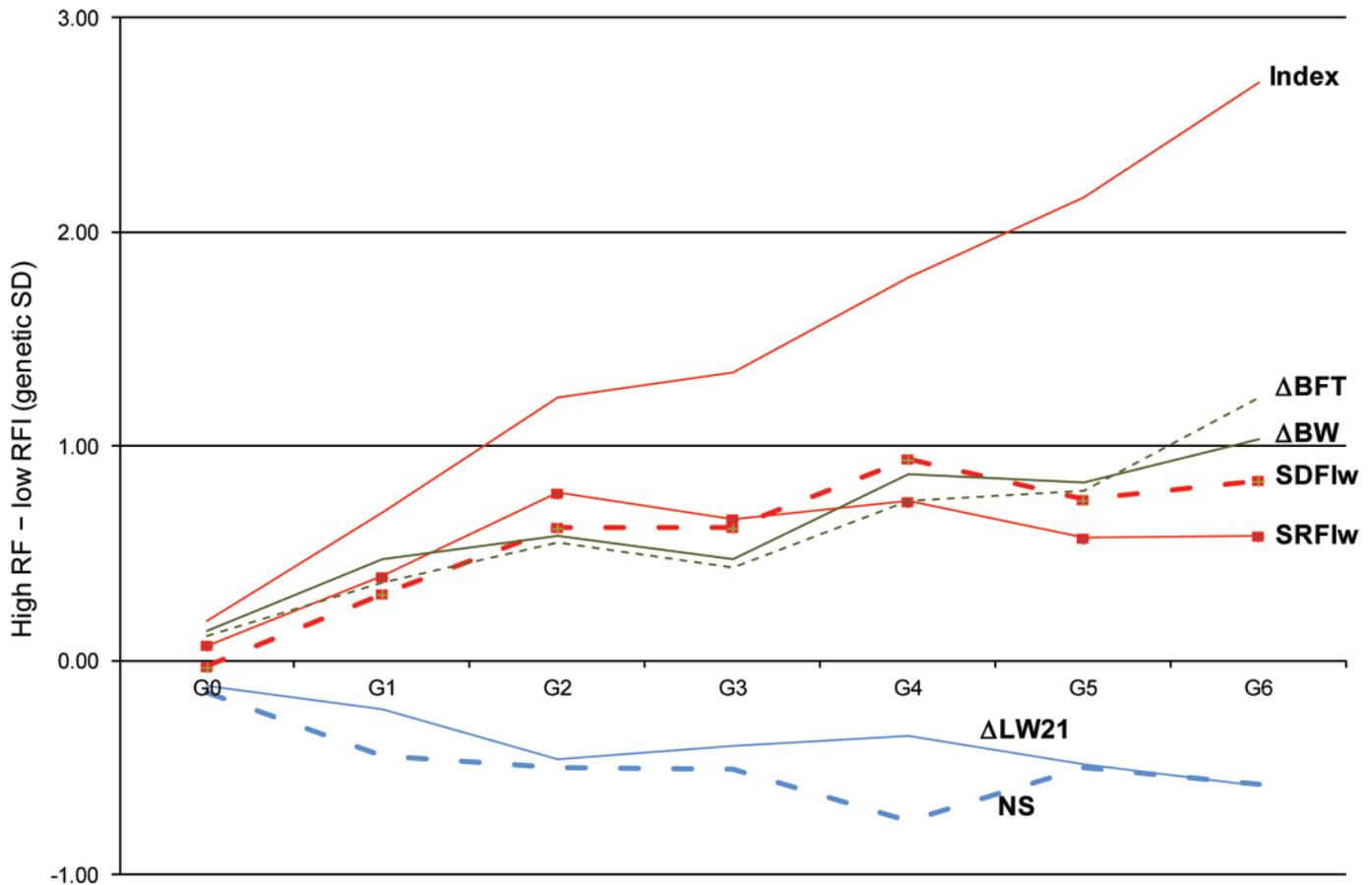


Figure 1. Difference of LSMEANS between the high residual feed intake (RFI) and the low-RFI lines for each generation expressed in genetic SD of the traits, for RFI of growing pigs (index), and for RFI of the lactating sow (SRFIw) and its components [daily feed intake of the lactating sow (SDFIw), change of BW during lactation (Δ BW), change of backfat thickness during lactation (Δ BFT), litter growth (Δ LW21), and number of piglets (NS)]. Except differences at generation 0 (G0), all values are significant at $P < 0.0001$. In G0, only index is significantly different ($P = 0.04$). Color version available in the online PDF.

observed for BFT, resulting in sows of the low-RFI line losing 1.3 mm ($1.23 \sigma_A$) more BFT than sows of the high-RFI line despite no significant line difference between the lines in G6 for BFT before farrowing. The similar level of backfat before farrowing in both lines was potentially attributable to a change in the feeding strategy of sows at the end of gestation implemented in the last 3 generations of selection to achieve even fatness levels before farrowing.

Line differences for TB, BA, and NS corresponded approximately to an additional 0.5 piglet at birth, 21 d, and weaning in the low-RFI line. Concerning litter weights, the line difference for Δ LW21 increased in favor of the low-RFI line, reaching $0.59 \sigma_A$ (2.0 kg) in G6. However, the difference for LWb and LWw did not increase from G4 to G6 (not shown), and no significant line difference was found in G6 for Δ LWw. Despite greater average piglet BW at birth in the high-RFI line ($0.42 \sigma_A$; i.e., 47 g in G6) than in the low-RFI line, the smaller growth rate of litters from the high-RFI line resulted in average piglet BW being slightly less at 21 d ($-0.55 \sigma_A$; i.e., -287 g in G6) and no significant difference for APWw ($0.05 \sigma_A$; i.e., 29 g in G6). Line differences for within-litter SD of birth weights tended to increase as a result of selection; the low-RFI line was

more heterogeneous ($0.95 \sigma_A$; i.e., 25 g in G6). Because APWb was less in the low-RFI line, this increased within-litter SD was not attributable to a scaling effect. No clear line difference was observed for within-litter SD of APW21 or APWw.

The variance due to genetic drift within each line was not taken into account when assessing the level of significance of the line differences in G6. This drift variance can be approximated from the average inbreeding coefficient within each line (around 0.15 in G6) and the genetic additive variance of the trait (Hill, 1972). The estimated genetic drift variance of the line difference was $0.29 \sigma_A^2$ in this study. Some of the differences reported for reproduction traits might thus be partly attributable to genetic drift.

General Discussion

Reproduction Trait Characteristics. Age, BW, and fatness of the sows at first farrowing were greater in our study than usually observed in commercial pig herds. On average, first farrowing occurred at 377 ± 20 d of age in 2008 in France (IFIP, 2010; i.e., 2 mo earlier than in our experiment). It can thus be suspected that the sows in our experiment were more mature and had

Table 3. Least squares means of individual breeding values in generation 6 in the low residual feed intake (RFI; more efficient) and high-RFI (less efficient) lines (plus the mean of the trait), and *P*-value for the differences

Trait ¹	Low RFI	High RFI	<i>P</i> -value
Index, points	89.9	108.1	<0.0001
SRFIw, kg/d	-0.05	0.06	<0.0001
SDFIw, kg/d	4.54	4.82	<0.0001
SDFI-1, kg/d	2.63	2.85	<0.0001
SDFI-2, kg/d	4.44	4.75	<0.0001
SDFI-3, kg/d	5.12	5.56	<0.0001
SDFI-4, kg/d	5.51	5.86	<0.0001
BWf, kg	259.4	263.5	<0.0001
BWw, kg	222.0	231.1	<0.0001
ΔBW, kg	-36.1	-30.5	<0.0001
BFTf, mm	26.1	26.2	0.63
BFTw, mm	19.9	21.4	<0.0001
ΔBFT, mm	-5.6	-4.3	<0.0001
TB	12.7	12.1	<0.0001
BA	12.1	11.4	<0.0001
NS	10.2	9.6	<0.0001
LWb, kg	18.5	18.0	0.0004
LW21, kg	64.2	62.2	<0.0001
LWw, kg	82.0	82.2	0.5
ΔLW21, kg	46.1	44.1	<0.0001
ΔLWw, kg	63.9	64.1	<0.0001
APWb, kg	1.48	1.52	<0.0001
APW21, kg	6.96	6.67	<0.0001
APWw, kg	8.92	8.95	0.6
SDWb, kg	0.30	0.27	<0.0001
SDW21, kg	1.00	0.98	0.01
SDWw, kg	1.22	1.24	0.16

¹Index = criterion of selection; SRFIw = sow residual daily feed intake during lactation; SDFIw = sow daily feed intake during lactation; SDFI-1 = sow daily feed intake from farrowing to 7 d after farrowing; SDFI-2 = sow daily feed intake from 8 to 14 d after farrowing; SDFI-3 = sow daily feed intake from 15 to 21 d after farrowing; SDFI-4 = sow daily feed intake from 21 d after farrowing to weaning; BWf = BW of the sow before farrowing; BWw = BW of the sow at weaning; ΔBW = change of BW of the sow during lactation; BFTf = backfat thickness of the sow before farrowing; BFTw = backfat thickness of the sow at weaning; ΔBFT = change of backfat thickness of the sow during lactation; TB = total number of piglets born; BA = number born alive; NS = number of surviving biological piglets at weaning; LWb = weight of the litter at birth, including stillborn piglets; LW21 = weight of the litter at 21 d; LWw = weight of the litter at weaning; ΔLW21 = litter weight gain between birth and 21 d of age; ΔLWw = litter weight gain between birth and weaning; APWb = average piglet BW at birth; APW21 = average piglet BW at 21 d; APWw = average piglet BW at weaning; SDWb = within-litter SD of piglet BW at birth; SDW21 = within-litter SD of piglet BW at 21 d; SDWw = within-litter SD of piglet BW at weaning.

less difficulty coping with the challenge of nursing the piglets while still growing compared with sows in commercial herds. However, estimates of heritability for traits related to reproduction were in the usual ranges for these traits.

RFI and Female Reproductive Performances. The generally low but favorable genetic correlation of RFI during growth with reproduction traits suggests the absence of genetic antagonism between feed use during growth and an adequate feed intake of lactating sows to supply piglet demand and rebreed in

good shape. Moreover, despite low to moderate genetic correlations of index with sow feed intake and body characteristics and weak correlations with litter traits, we obtained significant responses to divergent selection for RFI during growth for almost all sow traits. When significant, correlations and responses to selection were consistent between traits. During lactation, the sows from the low-RFI line had reduced SDFI, greater changes in body reserves, and larger litter weight gain, along with slightly lighter BW and a tendency to be leaner at farrowing. These differences in strategies of the lactating sow to respond to piglet demand have been previously documented, showing that sows tend to either eat more and mobilize their body reserves to a lesser extent or eat less and mobilize their reserves to a larger extent. As a consequence, feed intake of sows during lactation is usually described as an adaptive trait (Dourmad et al., 1996). Similar differences between RFI lines were reported at the phenotypic level by Young et al. (2010) in a similar selection experiment conducted at Iowa State University. Bunter et al. (2010), using FCR to assess feed efficiency, reported genetic correlations between reproduction and performance traits. They found nonsignificant genetic correlations between FCR and feed intake or changes of body composition during lactation, despite positive genetic correlations between FCR and BFT before farrowing and at weaning. In addition to the criterion retained to describe feed efficiency, sow maturity at first farrowing is a major difference between the studies; Bunter et al. (2010) reported first mating at 29 wk of age, with lighter and leaner sows than in our study. Additionally, our estimates of line differences for litter growth reflect both the growth potential of the piglets to use feed more efficiently, as a correlated response to selection during the growing period, and the milk production of sows (quantity and quality). These 2 components could be separated by cross-fostering a significant amount of the piglets to sows from the other line. In the present data set, cross-fostering was less than 5%, so the respective influence of growth potential of the piglets and milk production of sows could not be evaluated.

Rather unexpected favorable responses to selection were observed for prolificacy traits; an additional 0.6 piglet in the G6 low-RFI litters was obtained for TB, BA, and NS. However, the APWb was significantly reduced in the low-RFI line but positively associated with a greater litter weight gain during lactation. As a result, no significant line difference in APWw was found. Similar trends were reported by Young et al. (2010) at the phenotypic level, but with a larger number of stillborn piglets in the low-RFI litters that was not observed in our genetic study. We observed a greater SD of within-litter APWb in the low-RFI line, associated with an increased number of piglets of lighter individual BW. Similar correlations between litter traits have been previously reported by Canario et al. (2006). Piglet survival did not seem to be affected (data not shown).

Results obtained in other species reported similar favorable responses to selection for RFI during growth on female reproductive traits. For example, Arthur et al. (2005) found no significant correlative response on cow maternal ability traits after 1 to 3 generations of divergent selection for RFI, despite slightly greater fatness in cows from the high-RFI line. In the same experiment, responses to selection for growth traits (Arthur and Herd, 2008) were reported to be similar to the responses obtained in pigs, in particular for body composition. On the other hand, in a divergent selection experiment for postweaning net feed intake in mice, Hughes and Pitchford (2004a) reported greater growth rate and fatness in the low line during growth. In addition, Hughes and Pitchford (2004b) reported a smaller number of pups in the most efficient line, along with individual BW at birth and at weaning similar to that in this experiment. During lactation, they found no significant line difference on net feed intake despite significantly greater rates of BW gain (mouse + litter) in the low line. The disparities between the results of the pig and mouse experiments suggest that different metabolic pathways were recruited in response to selection for residual or net feed intake during growth in mice and pigs. Responses to selection for RFI in mature animals, as applied in laying hens by Bordas and Minvielle (1999), essentially affected (residual) feed consumption after sexual maturity, suggesting recruitment of different metabolic pathways when selecting for reduced RFI during growth or maturity.

SRFI and Lactation Efficiency. In our study, the reduced SDFI in the low-RFI line was not totally compensated by a greater body reserve mobilization of the sows to meet the demands of larger litter weight gain, resulting in significantly reduced SRFI at the genetic level. As a consequence, approximately 60% of the line difference for SDFI during lactation was attributable to differences in SRFI. This is by construction not attributable to differences in litter growth or body reserve mobilization. It is worth noting that the line difference at the phenotypic level in SRFI was not significant in G6 ($P = 0.17$) despite a consistently positive increase of SRFI difference over generations. Young et al. (2010) reported no significant observed line differences in lactation efficiency (**LE**; as defined by Bergsma et al., 2009) despite a 4.4% line difference in LE mostly driven by a line difference in terms of amount of energy used for output during lactation (piglet growth and maintenance and sow maintenance). In this study, sow feed efficiency was computed as the ratio of the energy required for outputs to the energy required for inputs (sow feed intake and mobilization of body resources). This computation gives an indicator of feed efficiency similar to G:F, which relates to feed efficiency during growth. Some differences between LE and SRFI during lactation are thus expected; similarly to differences between G:F and RFI during growth, LE computes the efficiency of the use of feed relative to the production level of the lactating animals, whereas

SRFI separates out requirements of feed for production from requirements of feed for the residual components, allowing a comparison of the use of feed independent from performance differences. However, the results in the 2 experiments indicate similar trends for sow feed efficiency during lactation, with sows from low-RFI lines being more efficient in the use of feed.

RFI and SRFI: Effect on Metabolism. Sow residual feed intake accounted for about 25% of the phenotypic variation of SDFI, which is less than the proportion of DFI (30 to 35%) usually accounted for by RFI during growth in pigs (Dekkers and Gilbert, 2010). Moreover, genetic correlations between SRFI and SDFI were not significantly different from 1 in this study, whereas they usually range from 0.64 to 0.82 during growth (Hoque et al., 2007). Similarly but to a lesser extent, Bergsma et al. (2008) reported a negative genetic correlation between ad libitum sow feed intake during lactation and lactation efficiency (i.e., a tendency for reduced feed intake in efficient sows during lactation).

Previous studies of traits recorded during growth and at the abattoir showed that in response to selection for RFI during growth, pigs from the low-RFI lines have reduced DFI, are leaner, and tend to have slower growth (Gilbert et al., 2007; Cai et al., 2008). After slaughter, they have greater dressing percentage, lesser ultimate pH, which is usually correlated to greater muscle glycogen content, greater reflectance values, and drip loss (Boddicker et al., 2011; Lefaucheur et al., 2011). It has been hypothesized that selection for low RFI in these lines has driven metabolism of energy toward short-term mechanisms during growth. These differences in metabolism are expected to be maintained in later stages of production. They might explain the favorable responses to selection obtained for reproduction traits in this study. In the literature on resource allocation, the residual part of the feed intake is generally understood as a buffer compartment that is available when the animal is facing challenges (e.g., physiological modifications caused by changes in feed, alteration of immune environment, or reproduction; Rauw, 2009). However, reproduction can be considered a long-term stress, and a switch of resources toward short-term mechanisms during growth should not directly explain the observed responses. On the other hand, Barea et al. (2010) showed that the low-RFI line of the current study had decreased requirements for basal metabolism (10% less) than the high-RFI line during growth. This difference might also be maintained during later stages and might explain part of the loss of energy in the sows of the high-RFI line, inducing greater maintenance requirements for both the sow and her piglets. Further, Bunter et al. (2010) proposed that heavier sows are beneficial in the first parities but tend to show difficulties in later parities because requirements for greater BW of the sow competed with requirements for lactation. These results also suggest a better adjustment of feed intake to the metabolic requirements of the litter

in the low-RFI line. It is possible that sows in the study of Bunter et al. (2010) had less body reserves than sows in our experiment because they were younger and leaner at first insemination. In the present data set the lack of line difference for rebreeding success after first parity suggested that in the particular conditions of this experiment rebreeding abilities of primiparous sows were not affected by selection for RFI in the growing pig.

Despite these divergences between lines, SDFI was shown to be genetically uncorrelated with prolificacy traits, in accordance with results of Mullan and Close (1989) at the phenotypic level and Bunter et al. (2010) at the genetic level. These authors showed that sow feed intake during lactation does not depend on litter size, implying that when a lactating sow is inadequately fed, or does not have enough appetite or ingestion capacity, she will use her body resources to provide adequate nutrients to the litter. Similarly, genetic correlation estimated in our study pointed out increased use of body resources (BW of the sow) when SDFI is low. However, for longer lactation periods, Bunter et al. (2010) reported positive relationships between sow fatness at weaning and sow feed intake during lactation. In modern genetic types of sows, Eissen et al. (2003) reported similar tendencies, associated with deleterious effects of greater body losses on weaning-to-estrus interval and litter size of the following parity. In the present study, no data were available to investigate weaning-to-estrus interval, but study of failure of insemination after weaning of first parity (2% of the data set) provided no evidence of differences between the selected lines. It must be noted that despite greater fat losses in the low-RFI line during lactation, low-RFI sows still have 19.9 mm backfat at weaning, which corresponds to a good status for rebreeding.

SDFI vs. SRFI: Which Is the Better Choice to Maintain Sow Performance? The genetic correlations between SRFI and other traits recorded during lactation provide knowledge about the selection of efficient sows with high reproductive performances. Genetic correlations between SRFI and the explicative variables used in the phenotypic regression were not significantly different from 0 except for the number of piglets weaned. The latter point suggested a greater early efficiency of the sow when the number of suckling piglets is greater, potentially because of better stimulation of the lactating process in the mid-term lactation, but a reduced influence of number of piglets at birth, potentially due to greater difficulty of coping with longer farrowing events. However, SRFI showed relatively strong and positive relationships with litter weight, litter weight gain, and piglet BW traits, suggesting decreased efficiency of the sow when litters or piglets are heavier. This questions the role of piglet maintenance requirements on the efficiency of the sow. Hughes and Pitchford (2004b) included the average metabolic BW of the litter in the estimation of net feed intake of the lactating mouse. In the present study, following the suggestion by Noblet and Etienne (1987), we retained

a simpler alternative, the number of piglets fed by the sow, considering that the number of piglets and the litter weight gain accounted jointly for the average BW of the piglets in the predictive equation of SDFI because piglet BW shows low variation at farrowing. Additionally, we estimated positive correlations between SRFI and SD of within-litter APW21 or APWw, suggesting that greater within-litter variability of piglet weights might result in less efficiency of the sow, potentially because it is difficult for the sow to cope with individual requirements of the piglets.

In our context (piglets weaned at 28 d of age, creep feeding available at 21 d), it seems reasonable to compute SRFI between d 5 after birth and weaning, avoiding the nongenetic effects of DFI just after birth but accounting for the ability of the sows to start restoring their resources as soon as piglets are less demanding. Previous studies recommend selecting for greater SDFI during lactation to ensure piglet growth and sow longevity (Eissen et al., 2000). However, in terms of economic value, the feed costs for lactating sows can be significantly modified depending on the strategy retained. In our study, differences between lines corresponded on average to a difference of feed intake of 7 kg for lactation lengths of 28 d, which can be related to a gain of 0.14 €/piglet for a feed price of 240 €/ton and assuming 12 piglets/litter. As a consequence, the concept of SRFI, basically representing SDFI variation corrected for sow body condition and litter growth, questions the increase of SDFI as a safe objective for selection as proposed by Eissen et al. (2000). As outlined previously, we demonstrated the absence of genetic antagonism between feed use during growth and adequate feed intake during lactation to supply piglet demand and rebreed in good shape when measured by means of SRFI. In comparison, lactation efficiency per se would not be recommended as an objective for selection because similar increase of LE would be obtained by either reducing lactation feed intake or increasing litter weight gain. Further studies need to evaluate longevity in more stressful conditions (first insemination at younger age) to confirm the reduced effect of the selection for SRFI on rebreeding abilities. However, an index combining SRFI and a minimum level of BFT of the sows at weaning might efficiently counterselect sows that would tend to lose too much fatness during lactation. Alternatively, accounting for both feed intake up to time of insemination and success of the insemination might provide the necessary knowledge to select for efficient sows with high standards of longevity and low input demands.

Conclusions

Selecting for low RFI during growth, leading to an increased number of piglets and a better litter growth, did not impair sow performance levels at the expense of a greater mobilization of body reserves. No effect on rebreeding performances was found. Differences

between lines in DFI during lactation related to differences in sow strategies to meet litter requirements. This resulted in differences in SRFI during lactation, which are independent from litter growth or mobilization of body reserves. Metabolic changes observed during growth, decreasing basal metabolism and favoring rapid allocation of resources to lactation, might explain part of the better efficiency of the low-RFI sows. Larger studies are required to extensively evaluate the effect of selection for RFI on sow longevity and piglet survival in herds with high sow productivity, where sows may face more stress. To improve sow selection criteria, we propose to consider SRFI as an alternative to SDFI to select for efficient sows with reduced input demands during lactation.

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