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Analysis of 28 generations of selection for reproduction, growth, and carcass traits in swine

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ABSTRACT: Selection (28 generations, G) in a Large White–Landrace composite population for traits aimed at increasing live pigs born per litter (BA), with additional selection for increased 180-d weight (WT180) and longissimus muscle area (LMA) and decreased back fat (BF10) in the last 8 generations, was practiced. Objectives herein were to estimate genetic and phenotypic responses and genetic parameters ($n = 1,883$ to 54,174) and to investigate whether a plateau in response for BA occurred. Line 2 (L2) was selected for an index of ovulation rate and embryo survival (G0 to G11), fully formed pigs (FF) per litter (G12 to 14), and BA and pig birth weight (PBW, G15 to G19), and its control line (LC1) was selected randomly (G0 to G21). Line 4 (L4), derived from L2, and line 5 (L5), derived from LC1, at G8 were selected in 2 stages for ovulation rate and FF (G9 to G16) and BA and PBW (G17 to G19), and their control (LC6) was selected randomly. At G20, L4 and L5 were crossed to form L45, and L4 and L2 were crossed to continue L2; L2 and L45 were subsequently selected for BA, WT180, LMA, and BF10 (G21 to G28). At G21, LC1 and LC6 were reciprocally crossed to form LC16, control for L2, and LC61, control for L45. Selection in L2 and L45 was first for BA and then for other traits

among pigs selected for BA. Line sizes were 40 to 60 litters by 15 to 20 sires/G. Cumulative selection differentials (CSD) were calculated. MTDFREML was used to estimate variance components, EBV, and responses. Genetic changes at G28 in L2 were 4.63 FF and 3.66 BA, with 72% (FF) and 86% (BA) of the change occurring after G11. Two-stage selection produced similar responses ($P < 0.01$) in FF in L4 and L5 (0.27 and 0.29 pigs/G) but a greater response in BA in L5 (0.19 vs. 0.28 pigs/G). Genetic change in L45 from G20 to G28 was 0.17 pigs/G for both FF and BA ($P < 0.01$). Genetic changes at G28 in L45 were 4.16 FF and 3.68 BA. Genetic correlations of reproductive and growth traits were near zero, ranging from -0.43 (stillborn pigs/litter with BF10) to 0.21 (mummies/litter with LMA). Selection for growth traits along with litter size selection during G19 to G28 resulted in responses consistent with the selection applied and the heritability of the trait. No evidence for a selection plateau existed; selection differentials and variances of FF and BA in selection lines during G20 to G28 were similar to those in earlier generations. Over all generations, heritability of BA was 0.20 ± 0.03 and remained at approximately 0.17 in selection lines in later generations.

Key words: genetic parameters, growth, long-term selection, pig, reproduction

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INTRODUCTION

Several litter size selection experiments in pigs have been conducted, but most were short term (12 generations or less), practiced in relatively small populations, and resulted in insignificant or little response (Ollivier, 1982; Haley et al., 1988; Bolet et al., 1989; Estany et al., 2002; Holl and Robison, 2003). Pérea-Enciso and Bidanel

(1997) concluded that direct selection in small populations may not be practical. However, selection using the hyperprolific breeding scheme in large populations was effective (Sorensen et al., 2000; Noguera et al., 2002; Tribout et al., 2003). Today, most maternal line populations maintained by breeding organizations are quite large, and positive genetic trends in litter size from its inclusion in their maternal line indexes have been realized.

We initiated an experiment in 1981 with the aim of increasing litter size by selection on an index of ovulation rate and embryo survival to 50 d of gestation. After 11 generations (G), responses in litter size

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were less than predicted (Johnson et al., 1984); fetal losses after 50 d partially offset the response in ovulation rate (Johnson et al., 1999). On the basis of the work of Bennett and Leymaster (1989, 1990a,b), 2 additional selection lines, one from the index selection line and one from the control line, were created at G8. Two-stage selection for ovulation rate and litter size at term as a measure of uterine capacity was practiced for 8 G within each line (Ruiz-Flores and Johnson, 2001). Subsequently, lines were maintained with selection for increased litter size at birth through G28 with additional selection for growth traits from G19 to G28. Responses through G19 are reported (Petry and Johnson, 2004).

The objective of our experiment was to increase litter size by selecting for its components (ovulation rate, embryonic survival, and uterine capacity) and by direct selection. Results from different phases through G19 have been reported. Selection continued through G28, but results from all selection procedures have not been integrated into 1 coherent report, nor have results from G20 to G28 been reported. Therefore, the objectives herein are to integrate the results of all lines into 1 analysis describing the selection applied, estimating responses from G0 to G28, estimating genetic and phenotypic parameters among traits, and investigating whether a selection plateau for litter size occurred.

MATERIALS AND METHODS

This research was approved by the University of Nebraska Institutional Animal Care and Use Committee.

Population and Data

Data were collected at the University of Nebraska Agricultural and Research Development Center Swine Research Farm. The primary selection objective in all selection lines was increased litter size (**LS**) and included selection for ovulation rate and embryonic survival, 2-stage selection for ovulation rate and **LS**, or direct selection for **LS**. In later generations, after selection for **LS**, additional selection for growth traits including birth weight or weight, back fat, and longissimus muscle area at 180 d of age was practiced.

The pedigree file contained 61,081 animals beginning with parents of litters born in 1979. Generation interval in all lines was 1 yr. Records analyzed were for first-parity females and their litters from 1981 through 2009. Reproductive traits included age at puberty (**AP**), ovulation rate (**OR**), number of embryos at 50 d of gestation (**E**), embryo survival rate as a percentage of ovulation rate (**ES**), and numbers of fully formed (**FF**), live (**BA**), stillborn (**SB**), and mummified (**MUM**) pigs per litter at birth. Traits recorded on pigs and litters from

birth through weaning included individual pig weight at birth (**PBW**), litter birth weight (**LBW**), number of pigs weaned per litter (**NW**), individual pig weight at weaning (**WW**), and litter weight at weaning (**LWW**). Traits recorded on pigs at 180 d of age included weight (**WT180**), longissimus muscle area at the 10th rib (**LMA**), and either the average of 3 back fat depths recorded at the first rib, last rib, and last lumbar vertebrae (**ABF**) or a single back fat depth recorded at the 10th rib (**BF10**). Methods for measurement of **LMA**, **ABF**, and **BF10** are described in Petry et al. (2004) and Hsu et al. (2010).

Lines

The origins of pigs for this experiment were samples of pure line English Large White (**LW**) and Landrace (**LR**) obtained in 1976 from PIC USA. Pregnant females of each line were shipped to the University of Nebraska (**UNL**) and to the U.S. Meat Animal Research Center (**MARC**). Baby pigs were taken by cesarean section at both sites and placed on their respective research farms. The **UNL** samples were too small for closed-population genetic research. Thus, the lines were crossed at **UNL**, but first, additional pregnant sows carrying pure line litters were obtained from **MARC**. Litters were obtained by cesarean section, and pigs were moved to the **UNL** research farm, where boars and gilts of the **UNL** and **MARC** sources were randomly mated to produce F1 pigs (both **LW** × **LR** and **LR** × **LW**) that were born in 1979.

There were 54 litters by 21 boars in the F1 base population. Two generations of random selection and mating were practiced before selection and control lines were formed and selection was initiated. Evolution of the lines is illustrated in Fig. 1. The selection lines are denoted as **L2**, **L4**, **L5**, and **L45**, and the control lines are denoted as **LC1**, **LC6**, **LC16**, and **LC61**. All lines were derived from the **LW-LR** composite population formed in 1979.

Index selection for increased **OR** and **ES** was initiated in **L2** in 1981 (**G0**) and continued for 11 generations. Selection in **L2** was for only **FF** during **G12** to **G14**. Thereafter, selection in **L2** was first for increased **BA** (**G15** to **G28**) and then included selection for increased **PBW** during **G15** to **G19** and increased **WT180**, decreased **BF10**, and increased **LMA** among pigs selected for **BA** during **G20** to **G28**. Random selection was practiced in **LC1** (**G0** to **G21**) and **LC16** (**G21** to **G28**), control lines that farrowed contemporary with **L2**.

At **G8**, **L4** was derived from **L2**, and **L5** and **LC6** were both derived from **LC1** by remating selected females and males to produce parity 2 litters that were born 6 mo later than **LC1** and **L2** litters. Pigs within litters by **LC1** dams were randomly assigned to **L5** or **LC6**. Beginning with the female progeny, **L4** and **L5** were selected in 2 stages for **OR** and **FF** (**G9** to **G16**).

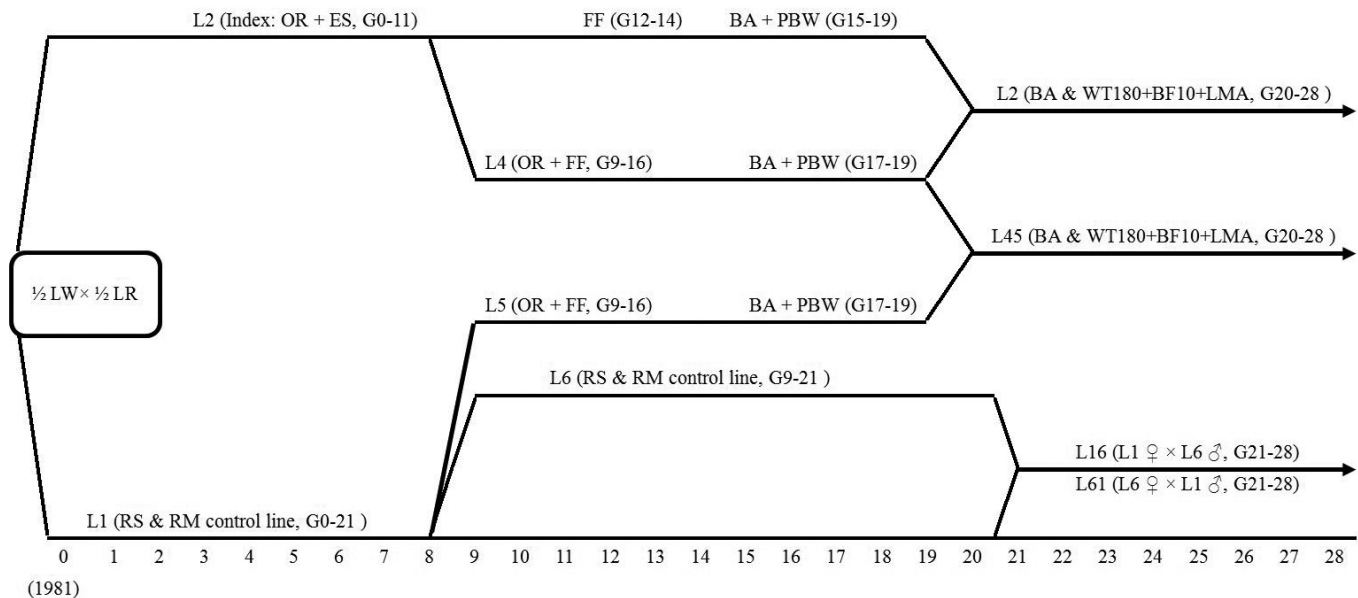


Figure 1. Description of selected and control lines by generation. LW = Large White breed; LR = Landrace breed; LC1, LC6, LC16, and LC61 = control lines; L2, L4, L5, and L45 = selection lines; G = generations; OR and ES = ovulation rate and number of surviving embryos at 50 d of gestation; FF and BA = number of fully formed and born alive pigs; PBW = birth weight; WT180, BF, and LMA = body weight, back fat of the 10th rib, and longissimus muscle area at 180 d of age; RS = random selection; RM = random mating; ♀ = gilts; ♂ = boars.

Subsequent selection in L4 and L5 was first for increased BA and then within litter selection for PBW (G17 to G19). Selected L4 and L5 males from G19 were reciprocally crossed (L4 males \times L5 females and L5 males \times L4 females) to produce L45, which was subsequently selected for the same criteria as L2 from G20 to G28. Line 6 was selected randomly (G9 to G21) and served as a control for L4 and L5. Lines 1 and 6 were reciprocally crossed to form LC16 (LC6 males \times LC1 females) and LC61 (LC1 males \times LC6 females), which were contemporary controls to L2 and L45, respectively, and selected randomly from G21 to G28.

During G17 to G19, after selection of replacement females in LC1 and L2, additional females of each line were retained as breeders. These females were mated with an unrelated maternal line to produce crossbred pigs for another project. Data for these litters ($n = 226$) through weaning were included in analyses reported herein. Details of the design and results of that project are in Petry and Johnson (2004) and Petry et al. (2004).

Selection Criteria and Mating

Line sizes were maintained with approximately 40 to 60 litters by 15 to 20 sires in most generations. Mating of full-sibs and half-sibs was avoided throughout all generations in all lines. Otherwise, random mating was practiced. In control lines, in each generation, 2 sons per sire (a primary breeder and an alternate) and 1 or 2 gilts per litter were randomly selected at 60 d of age, resulting in selection of approximately 30 boars, 15 of which were used as breeders, and 55 gilts per generation.

Johnson et al. (1999) give the procedures for index selection in L2 from G0 to G11, and Ruiz-Flores and Johnson (2001) provide details of the 2-stage selection practiced in L4 and L5 from G9 to G16. Therefore, only a brief overview of those procedures is provided here.

From G0 to G11, all gilts from all L2 litters were retained as candidates for selection. Random selection of LC1 replacement gilts and boars occurred at approximately 60 d of age, and only selected pigs were retained.

Estrus detection in the presence of a boar commenced at approximately 140 d of age, and AP was recorded in all LC1 and L2 females retained as candidates for breeding. Those expressing a pubertal estrus were mated at a subsequent estrus, and laparotomy was performed at 50 d of gestation on those that were pregnant; OR, E, and ES were recorded. Females in L2 were ranked on an index of OR and ES, and high-indexing females, approximately 30%, were farrowed. Sons of dams in the upper 10% of the distribution were selected.

After G11, selection for FF or BA in L2 was accomplished by ranking litters for these traits and selecting boars from the upper 20% to 30% of the distribution and gilts from approximately the upper 40% of the distribution. Selection for PBW or for WT180, BF10, and LMA was then based on pig performance for these traits among individuals previously selected for BA. Depending on generation, 15 to 20 boars, with the restriction of no more than 2 boars per litter, were selected as breeders; 5 alternates were identified and used as breeders only if a primary boar died or failed to breed. Gilts first selected for BA were then ranked for performance traits, and the highest-ranking gilts were selected. In generations when

WT180, BF10, and LMA were the secondary selection traits, approximately 50% of the selection emphasis was on WT180, with the remainder approximately equally on BF10 and LMA. In practice, selection decisions were somewhat arbitrary as the number of individuals selected per family was also considered. For example, rarely were more than 2 males per full-sib family selected. Thus, in some instances, boars with lesser trait deviations from line means were selected to maintain a broader genetic base. These traits also were recorded in LC1 and LC16 males and females, which continued to be selected randomly at approximately 60 d of age.

Selection in L4 and L5 during G9 to G16 was practiced in 2 stages. In stage 1, all gilts in the 50% of the litters with the greatest FF, approximately 100 gilts per line per generation, were retained, their AP was recorded, and laparotomy was used to record OR at second estrus. The 50% with the greatest OR were mated, and the cycle was repeated. Two boars, a primary breeder and an alternate, were selected from the 15 largest litters and mated with selected gilts. After 2-stage selection, selection in L4, L5, and L45 was as described above for L2. In all generations, selection in control lines, LC6 and LC61, was as described above for LC1 and LC16.

Management

Weight of all FF pigs was recorded at birth; PBW of all FF pigs in the litter were summed and recorded as LBW. Pigs were transferred among litters within and across lines within approximately 1 d after birth in an attempt to create nursing cohorts of 8 to 12 piglets. This management practice could be implemented only if matched pairs or sets of sows farrowing within a 2-d interval were available. Approximately 88% of pigs were raised in litters of 8 to 12 pigs.

Pigs were weaned and placed in nursery pens at approximately 28 (G0 to G12), 12 (G13 to G22), or 18 d of age (G23 to G28). Age, NW, and WW were recorded for each nursing cohort; WW was summed to produce LWW for each sow. Pigs were selected and moved from nurseries to grower pens at approximately 56 d of age. Boars and gilts were assigned to different buildings or rooms so as to not share a common air space. In generations during which AP was recorded, beginning when the oldest gilt in the pen was 140 d of age, gilts were moved daily from their living quarters to a separate heat-check area, exposed to a mature boar, and observed for symptoms of estrus for approximately 15 min. Age of first expressions of estrus was considered AP. Pens of pigs were weighed and scanned when mean age was approximately 180 d and weight, back fat, and LMA were recorded. Average back fat was recorded through G17; thereafter, BF10 was recorded. More details about this experiment from gen-

eration of founder animals to G19 were given by Johnson et al. (1999), Ruiz-Flores and Johnson (2001), Petry and Johnson (2004), Petry et al. (2004), and Hsu et al. (2010).

Realized and Cumulative Selection Differential

Cumulative selection differentials (CSD) of all traits included in selection objectives were calculated to describe the selection history within each line. For reproductive traits recorded for females and their litters (OR, E, ES, FF, and BA) the selection differential for those individuals that left offspring, the realized selection differential, of males or females in generation n (G_n) was

$$S_n^m = S_n^f = \frac{1}{\sum D_k} \sum_{k=1}^k [(P_{n_k} - \bar{P}_n) \times D_k]$$

where S_n^m and S_n^f are the selection differential of males and females in G_n , respectively; P_{n_k} is the phenotypic value of the k th selected dam born in G_n having granddaughters through sons measured in G_{n+2} for S_n^m or having daughters measured in G_{n+1} for S_n^f ; \bar{P}_n is the phenotypic mean of G_n , $n = 0, 1, \dots, n$; for S_n^m , D_k is the number of granddaughters through sons measured in G_{n+2} of selected dam k ; and for S_n^f , D_k is the number of daughters measured in G_{n+1} of selected dam k , $n = 0, 1, \dots, n$, $k = 1, 2, \dots, k$. The realized CSD was

$$CSD_0 = 0, \quad CSD_1 = \frac{1}{2} S_0^f,$$

$$CSD_n = \frac{1}{2} S_{n-1}^f + \frac{1}{4} \sum_{i=0}^{n-2} (S_i^m + S_i^f)$$

where CSD_0 , CSD_1 , and CSD_n are the cumulative selection differentials on females of G_0 , G_1 , and G_n , $n = 2, \dots, n$, respectively; S_0^f and S_{n-1}^f are the selection differentials of females in G_0 and G_{n-1} , $n = 2, \dots, n$, respectively; and S_i^m and S_i^f are the selection differentials of males and females in G_i , $i = 0, 1, \dots, n-2$, respectively.

The realized selection differential for traits recorded in both males and females (PBW, WT180, ABF, BF10, and LMA) in G_n was

$$S_n^m \text{ or } S_n^f = \frac{1}{\sum D_k} \sum_{k=1}^k [(P_{n_k} - \bar{P}_n) \times D_k]$$

where S_n^m and S_n^f are the selection differentials of males and females in G_n , respectively; P_{n_k} is the phenotypic value of selected parent k born in G_n having progeny measured in G_{n+1} ; \bar{P}_n is the phenotypic mean of G_n ; D_k is the number of progeny measured in G_{n+1} of selected parent k , $n = 0, 1, \dots, n$, $k = 1, 2, \dots, k$. The realized CSD was

$$CSD_m = 0, \quad CSD_n = \frac{1}{2} \sum_{i=0}^{n-1} (S_i^m + S_i^f)$$

where CSD_m is the cumulative selection differential on pigs of G-1, CSD_n is the cumulative selection differential on pigs of Gn, and S_i^m and S_i^f are the selection differentials of males and females in Gi, $n = 0, 1, \dots, n, i = 0, 1, \dots, n - 1$.

Statistical Models and Analyses

The MTDFREML program (Boldman et al., 1995) was used to obtain estimates of genetic parameters and EBV. Models are given in Table 1. Depending on the trait, the mixed model for a single trait is

$$y = X\beta + Z_a a + Z_m m + Z_{lit} lit + Z_{pen} pen + e$$

where y is the $N \times 1$ vector of observations; β is the vector of fixed effects (i.e., contemporary group, sex, and linear and quadratic regression coefficients for age, 180-d weight, and number of pigs nursed); a, m, lit, pen and e are the vectors of direct additive genetic, maternal genetic, independent random litter, independent random pen, and independent random residual effects, respectively; and X, Z_a, Z_m, Z_{lit} and Z_{pen} are known incidence matrices relating observations to $\beta, a, m, lit,$ and pen . The symbols in matrix notation for 2-trait models are the same as those for a single-trait model. For single-trait and 2-trait models, the expectation of y is $X\beta$. The expectations of trait i of $a_i, m_i, lit_i, pen_i,$ and $e_i, i = 1$ or $2,$ and the (co)variance matrix for mixed models are

$$E \begin{bmatrix} a_i \\ m_i \\ lit_i \\ pen_i \\ e_i \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix};$$

$$Var \begin{bmatrix} a_1 \\ m_1 \\ a_2 \\ m_2 \\ lit_1 \\ pen_1 \\ lit_2 \\ pen_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma_{a_1}^2 & A\sigma_{a_1 m_1} & A\sigma_{a_1 a_2} & A\sigma_{a_1 m_2} & 0 & 0 & 0 & 0 & 0 & 0 \\ & A\sigma_{m_1}^2 & A\sigma_{m_1 a_2} & A\sigma_{m_1 m_2} & 0 & 0 & 0 & 0 & 0 & 0 \\ & & A\sigma_{a_2}^2 & A\sigma_{a_2 m_2} & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & A\sigma_{m_2}^2 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & I\sigma_{lit_1}^2 & 0 & I\sigma_{lit_1 lit_2} & 0 & 0 & 0 \\ & & & & & I\sigma_{pen_1}^2 & 0 & I\sigma_{pen_1 pen_2} & 0 & 0 \\ & & & & & & I\sigma_{lit_2}^2 & 0 & 0 & 0 \\ & & & & & & & I\sigma_{pen_2}^2 & 0 & 0 \\ & & & & & & & & I\sigma_{e_1}^2 & I\sigma_{e_1 e_2} \\ & & & & & & & & & I\sigma_{e_2}^2 \end{bmatrix}$$

Symmetric

where $\sigma_{a_i}^2, \sigma_{m_i}^2, \sigma_{lit_i}^2, \sigma_{pen_i}^2,$ and $\sigma_{e_i}^2$ are the variances due to direct additive genetic, maternal genetic, litter, pen, and residual effects, respectively, for trait $i, i = 1$ or $2;$ $\sigma_{a_i m_j}$ is the covariance between direct genetic effect for trait i and maternal genetic effect for trait $j, i = 1$ and $j = 2;$ $\sigma_{a_i a_j}, \sigma_{m_i m_j}, \sigma_{lit_i lit_j}, \sigma_{pen_i pen_j},$ and $\sigma_{e_i e_j}$ are the covariance between direct genetic, maternal genetic, litter, pen, and residual effects, respectively, for traits i and $j, i = 1$ and $j = 2;$ A

Table 1. Models used to obtain REML estimates of genetic parameters¹

Trait ¹	Fixed effects and covariates ²					Random effects ³				
	CG	Sex	Age	Wt	NN	A	M	Lit	Pen	E
OR	X					X		X		X
E	X					X		X		X
ES	X					X		X		X
AP	X					X		X		X
BA	X					X		X		X
FF	X					X		X		X
MUM	X					X		X		X
SB	X					X		X		X
LBW	X					X		X		X
LWW	X		Q		Q	X		X		X
NW	X		Q		Q	X		X		X
PBW	X	X				X	X	X		X
WW	X	X	Q			X	X	X		X
WT180	X	X	L			X	X	X	X	X
ABF(age)	X	X	L			X		X	X	X
ABF(wt)	X	X		L		X		X	X	X
BF10(age)	X	X	L			X		X	X	X
BF10(wt)	X	X		L		X		X	X	X
LMA(age)	X	X	L			X		X	X	X
LMA(wt)	X	X		L		X	X	X	X	X

¹OR = ovulation rate; E = number of embryos; ES = embryo survival rate; AP = age at puberty; BA, FF, MUM, and SB = number of live, fully formed, mummified, and stillborn pigs per litter, respectively; LBW = litter birth weight; LWW = litter weaning weight, NW = number of pigs weaned per litter; PBW = pig birth weight; WW = pig weaning weight; WT180 = weight at 180 d of age; ABF(age), BF10(age), and LMA(age) = average of back fat at first rib, last rib, and last lumbar vertebrae, back fat at 10th rib, and longissimus muscle area at 10th rib, respectively, with age in model as a covariate; ABF(wt), BF10(wt), and LMA(wt) = average back fat, back fat at 10th rib, and longissimus muscle area at 10th rib, respectively, adjusted for weight.

²X = included in model; Q = linear and quadratic regression coefficients included; L = only linear regression included; CG = contemporary group; Wt = weight at 180 d of age; Age = weaning age for weaning weight and age when weighed for Wt, ABF(age), BF10(age), and LMA(age); NN = number of pigs nursed.

³A = direct additive genetic effect; M = maternal additive genetic effect; Lit = litter of birth effect; Pen = pen effect; E = residual environmental effect.

is the augmented numerator relationship matrix; and the I are identity matrices of appropriate order.

Linear and quadratic regressions of LWW, NW, and WW on weaning age and number nursed in the litter were included in models. Although the quadratic regression coefficient for age was not significant for LWW, NW, and WW at all sets of weaning ages, it was for some, and to be consistent, the quadratic regression was included in analysis of LWW, NW, and WW at all ages.

Estimates of variance components and genetic responses for BF, ABF, and LMA in models with a covariate of age were similar to those in models with a covariate of WT180. Only results for models including a covariate of WT180 are reported for BF10, ABF, and LMA.

The difference between models with and without maternal genetic effects was significant for PBW and WW at 28 and 12 d and for WT180 ($P < 0.01, \chi_{2,0.01}^2 =$

9.21) and approached significance for LMA. Maternal genetic effects were included in the models for PBW, WW for all data sets, WT180, and LMA.

The convergence criterion was set at 1×10^{-6} for a variance of -2 times the logarithms of the likelihood in the simplex. The number of simplex rounds was set to 500 for models without maternal genetic effects and to 800 to 3,500 for other models. After convergence was obtained, several additional restarts were executed until -2 times the logarithms of the likelihood did not change at the third decimal place. Restarts ended when estimates of variance components were similar or the same for the last 3 restarts.

The MTDFREML program with OPTION 4 and with final estimates of variance components was used to obtain means of EBV and phenotypes by generation for each line. A fixed factor of line \times generation was added to the original model of all traits. Genetic and phenotypic trends were estimated with the GLM procedure of SAS (SAS Inst. Inc., Cary, NC) by linear and quadratic regression of mean EBV and phenotype on generation. Both genetic and phenotypic trends in control lines (LC1, LC6, LC16, and LC61) were similar and did not differ significantly; thus, trends for control lines (denoted LC) were averaged to illustrate responses.

Adjustment of SE of Estimates of Responses for Random Genetic Drift

Inbreeding for each pig was calculated within the MTDFREML analyses. Covariates for inbreeding were not included in statistical models because selection was made without regard to a pig's inbreeding coefficient. However, considerable inbreeding occurred during the experiment, which could have resulted in genetic drift within lines across generations. The practice of avoiding the mating of full-sibs and half-sibs together reduced the within-generation variation in inbreeding and caused most of the variation to be among generations. Inbreeding increased at a rate of 0.81% per generation in L2 and averaged 23.7% in G28. Mean inbreeding coefficients in L4 and L5 at G9, when these lines were formed from second-parity progeny of G8 L2 and LC1 parents, were 10.5% and 8.4%, respectively. Inbreeding increased at rates of 1.22% and 1.09% per generation in L4 and L5 and averaged 22.9% and 16.4% at G19. The mean inbreeding coefficient decreased sharply to 3.7% when L4 and L5 were crossed to produce L45 and then increased at a greater rate than in other lines to a mean value of 20.5% at G27. Inbreeding in LC1 and LC6 increased at rates of 0.69% and 0.73% per generation, respectively. When LC1 and LC6 were crossed to form LC16 and LC61, inbreeding decreased sharply in the progeny, averaging 56.5% of the mean of LC1 and LC6.

Thereafter, inbreeding increased at more rapid rates in these lines (LC16 = 1.19% and LC61 = 1.26% per generation). Mean inbreeding in LC16 in G28 was 17.9%, and mean inbreeding in LC61 in G27 was 16.4%.

Standard errors of estimates of genetic and phenotypic trends within lines coinciding with changes in selection objectives were adjusted for genetic drift. Approximate variance due to random genetic drift was calculated from mean inbreeding coefficients and estimates of genetic variance as described by Falconer (1981). Approximate random drift variance of total change from G_0 to G_n within a line is $F_n \sigma_a^2$, where F_n is the mean inbreeding at G_n (assuming $F_0 = 0$) and σ_a^2 is the additive genetic variance of the trait. This formula applies strictly to randomly selected control lines but is also approximately correct for selection lines (Hill and Thompson, 1977). Estimates of trends herein are expressed per generation. Therefore, for trends per generation estimated from G_i to G_j ($j - i$ generations), drift variance was calculated as $(F_j - F_i) \sigma_a^2 / (j - i)^2$. Approximate random genetic drift variance was calculated for each trait and generation interval for which responses were estimated and added to the variance of trends obtained by regression analyses. Standard errors of regression coefficients for testing whether trends differed from zero were obtained from this total variance.

RESULTS

Cumulative Selection Differential

The CSD for OR, E, and ES increased at rates of 2.21 ova, 1.53 embryos, and 0.01%, respectively, per generation in L2 during G1 to G11 and were 24.61 ova, 15.90 embryos, and 0.07% at G11 compared with CSD of -0.77 ova, 0.33 embryos, and 0.16% survival in LC1 (Table 2). The CSD for OR in L4 and L5 increased 0.68 and 0.45 ova per generation during G9 to G16 and averaged 22.44 and 2.79 ova at G16, respectively.

The CSD for FF and BA increased linearly with generation number (Table 3). The CSD for FF in L2 increased at rates of 0.44, 1.70, 1.15, and 1.31 pigs/G, and the CSD for BA increased at rates of 0.46, 1.33, 1.15, and 1.47 pigs/G during G0 to G11, G12 to G14, G15 to G19, and G20 to G27, respectively. After G14, selection differentials in L2 were greater for BA than for FF in most generations. Thus, at G27, CSD were slightly greater for BA (26.62 pigs) than for FF (25.85 pigs). Some unintended selection for increased litter size occurred in control lines as CSD for FF and BA averaged 3.46 and 3.84 pigs at G27.

The CSD for FF in L4 and L5 from G9 to G16 increased at rates of 1.52 and 1.21 pigs per generation, respectively, whereas CSD for BA increased at rates of

Table 2. Realized cumulative selection differentials for ovulation rate (OR), number of embryos (E), and embryo survival rate (ES) by line and generation (G)¹

G	OR		OR			E		ES, E/OR	
	LC1	L2	L4	L5	LC6	LC1	L2	LC1	L2
1	0.00	1.10	—	—	—	0.00	1.13	0.00	0.02
2	-0.36	2.89	—	—	—	-0.01	2.47	0.02	0.02
3	-0.66	4.92	—	—	—	-0.08	3.63	0.03	0.01
4	-0.41	6.97	—	—	—	-0.35	5.33	0.01	0.02
5	-0.36	8.88	—	—	—	0.21	6.95	0.04	0.03
6	-0.27	10.40	—	—	—	-0.14	8.20	0.01	0.04
7	-0.82	12.27	—	—	—	0.36	9.90	0.10	0.06
8	-0.89	14.38	—	—	—	0.36	11.66	0.11	0.08
9	-0.60	17.22	17.22	-0.60	-0.60	0.59	13.15	0.16	0.07
10	-0.47	20.57	18.75	-0.03	—	0.56	15.05	0.14	0.07
11	-0.77	24.61	19.02	0.48	—	0.33	15.90	0.16	0.07
12	—	—	20.10	1.00	—	—	—	—	—
13	—	—	20.24	1.00	-0.48	—	—	—	—
14	—	—	20.97	1.60	-0.45	—	—	—	—
15	—	—	21.66	2.11	-0.01	—	—	—	—
16	—	—	22.44	2.79	-0.14	—	—	—	—

¹LC1 = control line 1, contemporary with selection line L2; L4 = selection line 4 derived from L2; L5 = selection line 5 derived from LC1; LC6 = control line 6 derived from LC1, contemporary with L4 and L5.

1.30 and 1.12 pigs/G. Rates of increase in CSD during G17 to G19 for FF in L4 and L5 were 1.37 and 1.16 pigs, respectively, and rates of increase in BA in these lines during that period were 1.61 and 1.55 pigs/G. The CSD for FF and BA in L45 increased at rates of 1.25 and 1.37 pigs/G, respectively, during G20 to G26 and averaged 24.37 and 25.21 pigs, respectively, at G26.

Although not directly intended, selection for earlier age at puberty occurred in both selection and control lines. The CSD decreased at rates of -1.07, -1.50, -1.67, and -1.67 d/G in LC, L2, L4, and L5 ($P < 0.01$), respectively. This selection was the result of the management and selection protocols. The breeding and farrowing periods were approximately 5 wk, and each year populations farrowed during the same time period. In all lines, gilts were not mated at their pubertal estrus. Thus, puberty was recorded for most gilts, but those that expressed estrus late in the observation period could not be mated at their second or later estrus and still fit the programmed breeding period and were culled. The phenotypic standard deviation of AP was 26.6 d, and the CSD at G16 ranged from $0.72\sigma_p$ in LC to $1.06\sigma_p$ in L5.

Indirect selection for increased birth weight occurred in all lines, including control lines (Table 3). The increase in CSD in LC, the average of control lines, was 0.06 kg/G, resulting in a CSD of 1.62 kg ($5.7\sigma_p$) at G27. Some additional selection for birth weight occurred in selection lines. The CSD for L2, L4, L5, and L45 increased at rates of 0.06, 0.09, 0.04, and 0.14 kg/G and averaged 1.89 ($6.7\sigma_p$, L2), 1.59, 1.03, and 2.29 kg ($8.1\sigma_p$, L45) at G27, G20, G20, and G27, respectively.

Even though a small amount of within-litter selection for birth weight occurred from G15 to G19, nearly all of the increase in CSD occurred after G19 as a correlated response to selection for 180-d weight, which had a phenotypic correlation with birth weight of 0.33.

Cumulative selection differentials for WT180, ABF (G0 to G17), BF10 (G19 to G27), and LMA (G19 to G27) are given in Table 4. Some selection for WT180 occurred in control lines, with most of it accumulating from G20 to G28. At G27, the CSD in LC was 16.8 kg ($1.46\sigma_p$). Negligible selection for back fat thickness and LMA occurred in LC.

During generations of index selection for OR and ES in L2 and in subsequent generations of selection for litter size, there was unintended negative selection for WT180. The CSD decreased at a rate of -1.00 kg/G through G19. However, the opposite occurred in L4 and L5, for which CSD for WT180 increased at rates of 1.60 and 2.22 kg/G, respectively, from G9 to G19. As in L2, selection for back fat thickness was negligible in L4 and L5 during this period.

Estimates of Variance Components

Estimates of (co)variance components are given in Table 5. Considerable phenotypic variation existed for all reproductive traits, and their direct heritabilities ranged from 0.11 for ES to 0.57 for AP, indicating substantial genetic variation also existed. Heritabilities of FF and BA, the traits directly selected for over all generations of the experiment, were 0.20.

Direct heritabilities of LBW, LWW, and NW, which are measures of sow productivity, ranged from 0.11 for NW at 28 d of age to 0.34 for LWW. In all cases, maternal heritability of PBW and WW were as great or greater than direct heritability, indicating a greater role for the dam's genes than the pig's genes on variation in these traits. Correlations between direct and maternal genetic effects on pig weights at birth and weaning were small, with the exception of pig weaning weight at 12 d of age, for which the correlation was 0.98. However, this is a relatively unimportant relationship as the direct heritability of WW at 12 d of age was 0.01 and phenotypic variance was only 0.47 kg^2 , substantially less than for weaning weights at older ages, indicating very little additive genetic variation for the trait.

Variation due to litter of birth was very small and unimportant for all reproductive and sow productivity traits but, excluding residual variation, was the greatest source of variation, explaining 17% to 24% of the phenotypic variation, in pig weights at birth and weaning. Thus, in this population and management system, environmental variation between litters affected pig weights to weaning but did not affect subsequent reproduction of gilts in these litters.

Table 3. Realized cumulative selection differentials for birth weight (PBW), number of fully formed (FF) and live (BA) pigs per litter by line and generation (G)¹

G	PBW					FF					BA				
	LC	L2	L4	L5	L45	LC	L2	L4	L5	L45	LC	L2	L4	L5	L45
0	-0.04	0.07	—	—	—	-0.21	0.13	—	—	—	-0.24	0.11	—	—	—
1	0.04	0.05	—	—	—	-0.22	0.50	—	—	—	-0.20	0.52	—	—	—
2	0.09	0.13	—	—	—	-0.33	0.98	—	—	—	-0.33	0.84	—	—	—
3	0.18	0.20	—	—	—	-0.44	1.18	—	—	—	-0.39	1.06	—	—	—
4	0.22	0.19	—	—	—	-0.32	1.99	—	—	—	-0.31	1.51	—	—	—
5	0.25	0.28	—	—	—	0.04	2.42	—	—	—	-0.01	2.19	—	—	—
6	0.37	0.39	—	—	—	-0.00	2.37	—	—	—	-0.01	2.53	—	—	—
7	0.44	0.42	—	—	—	0.46	2.85	—	—	—	0.46	3.02	—	—	—
8	0.41	0.43	—	—	—	0.54	3.78	—	—	—	0.33	3.90	—	—	—
9	0.48	0.55	0.55	0.48	—	0.88	4.33	4.33	0.88	—	0.76	4.34	4.34	0.76	—
10	0.51	0.58	0.54	0.48	—	1.18	4.79	5.62	2.16	—	1.04	4.81	5.62	2.06	—
11	0.55	0.67	0.57	0.45	—	1.02	4.42	7.12	3.83	—	0.99	4.46	7.15	3.85	—
12	0.60	0.70	0.65	0.46	—	1.21	5.89	9.14	4.67	—	1.10	6.01	8.30	4.36	—
13	0.63	0.69	0.76	0.47	—	1.32	7.65	10.96	5.90	—	1.22	7.26	9.62	5.60	—
14	0.72	0.70	0.83	0.55	—	1.50	9.28	11.87	7.10	—	1.46	8.67	10.49	6.57	—
15	0.76	0.72	0.90	0.56	—	1.49	10.84	13.27	8.23	—	1.49	10.12	12.23	7.59	—
16	0.79	0.76	1.00	0.58	—	1.58	12.35	14.78	9.47	—	1.59	11.66	13.61	8.85	—
17	0.85	0.77	1.10	0.61	—	2.18	13.07	16.82	11.41	—	2.24	12.33	15.47	10.83	—
18	0.94	0.84	1.24	0.71	—	2.53	14.62	18.47	12.95	—	2.54	13.82	17.09	12.46	—
19	1.05	0.98	1.40	0.86	—	2.30	15.45	19.55	13.73	—	2.33	14.78	18.68	13.92	—
20	1.09	1.13	1.59	1.03	1.31	2.55	16.87	20.48	14.48	17.48	2.60	16.67	19.87	14.81	17.34
21	1.19	1.26	—	—	1.45	2.67	18.46	—	—	19.04	2.58	18.22	—	—	19.19
22	1.28	1.32	—	—	1.55	2.73	19.13	—	—	19.64	3.05	19.41	—	—	20.36
23	1.35	1.45	—	—	1.75	2.86	20.31	—	—	21.22	3.31	20.62	—	—	22.21
24	1.42	1.54	—	—	1.90	3.07	21.74	—	—	22.96	3.67	22.60	—	—	23.47
25	1.51	1.67	—	—	2.02	3.46	23.21	—	—	24.56	3.89	24.22	—	—	24.93
26	1.58	1.77	—	—	2.17	3.70	25.11	—	—	24.37	4.02	25.71	—	—	25.21
27	1.62	1.89	—	—	—	3.46	25.85	—	—	—	3.84	26.62	—	—	—

¹LC = control line LC1 for G0–G8, average of controls LC1 and LC6 for G9–G21, and average of control lines LC16 and LC61 for G21–G27; L2, L4, L5, and L45 = selection lines.

Correlations among Traits

Genetic and phenotypic correlations among traits recorded on females and litters through weaning are given in Table 6. Ovulation rate was positively correlated with number of embryos at 50 d of gestation (0.32) but was negatively correlated with the proportion of ova represented by an embryo (-0.81). Although the number of live pigs per litter was positively correlated with both number of embryos and embryo survival rate, the genetic relationships were not strong (0.49 and 0.30, respectively). A very weak genetic relationship (-0.05) existed between OR and BA. With the exception of LBW, which had a genetic correlation of 0.68 with BA, genetic correlations of BA with other traits were low. Relatively low correlations of AP with all other traits existed. Because BA and FF were highly correlated ($r_g = 0.89$, $r_p = 0.84$), relationships of BA and FF with other traits were similar.

Genetic and phenotypic correlations among traits recorded at 180 d of age and of these traits with traits recorded on females, pigs, and litters through weaning

are given in Table 7. Genetic correlations between traits recorded at 180 d of age and traits recorded on females from 50 d of gestation through weaning were quite low, ranging from -0.43 (BF10 with SB) to 0.33 (WT180 with LWW at 18 d). Phenotypic relationships tended to be even weaker as most were between -0.10 and 0.12. Thus, little change in postweaning growth traits is expected from selection for the reproductive traits recorded in this experiment.

Genetic and phenotypic correlations of WT180 with PBW and WW were positive ($r_g = 0.24$ to 0.46, $r_p = 0.33$ to 0.41); however, correlations of PBW with BF10, ABF, and LMA tended to be low. Correlations with LMA were also low and were inconsistent across weaning ages.

Control Line Responses

Estimates of average phenotypic and genetic changes in LC are given in Table 8. Although some estimates

Table 4. Realized cumulative selection differentials by generation (G) for weight (WT, kg), back fat (BF, cm), and longissimus muscle area recorded at 10th rib (LMA, cm²) at 180 d of age for control lines (LC) and selection lines L2, L4, L5, and L45¹

G	LC			L2			L4			L5			L45		
	WT	BF ²	LMA	WT	BF ²	LMA	WT	BF ²	LMA	WT	BF ²	LMA	WT	BF ²	LMA
-1	0.0	0.000	—	0.0	0.000	—	—	—	—	—	—	—	—	—	—
0	0.5	-0.003	—	0.2	-0.017	—	—	—	—	—	—	—	—	—	—
1	0.7	0.002	—	0.2	-0.034	—	—	—	—	—	—	—	—	—	—
2	2.8	-0.019	—	-3.1	-0.176	—	—	—	—	—	—	—	—	—	—
3	3.3	-0.021	—	-2.3	-0.335	—	—	—	—	—	—	—	—	—	—
4	0.8	-0.097	—	-5.0	-0.138	—	—	—	—	—	—	—	—	—	—
5	-0.8	-0.078	—	-8.8	-0.205	—	—	—	—	—	—	—	—	—	—
6	-3.4	-0.071	—	-9.2	-0.060	—	—	—	—	—	—	—	—	—	—
7	-1.8	0.003	—	-10.8	-0.028	—	—	—	—	—	—	—	—	—	—
8	-2.3	0.015	—	-13.8	-0.034	—	—	—	—	—	—	—	—	—	—
9	-3.1	-0.043	—	-16.1	0.128	—	-16.1	0.128	—	-3.1	-0.043	—	—	—	—
10	-1.6	-0.041	—	-20.1	0.086	—	-14.0	0.198	—	-0.1	0.055	—	—	—	—
11	-0.3	-0.038	—	-22.7	0.182	—	-13.0	0.183	—	2.5	0.088	—	—	—	—
12	0.1	-0.064	—	-22.7	0.337	—	-8.3	0.262	—	6.4	0.064	—	—	—	—
13	0.8	-0.029	—	-21.8	0.466	—	-4.6	0.295	—	8.3	0.039	—	—	—	—
14	2.1	0.000	—	-20.0	0.482	—	-3.4	0.275	—	10.3	0.087	—	—	—	—
15	3.0	-0.002	—	-20.2	0.504	—	-3.9	0.128	—	12.5	0.103	—	—	—	—
16	2.9	-0.029	—	-16.6	0.827	—	-3.6	0.029	—	14.7	-0.059	—	—	—	—
17	4.0	-0.073	—	-16.7	0.730	—	-1.8	0.029	—	16.4	-0.186	—	—	—	—
18	6.9	—	—	-12.6	—	—	-0.4	—	—	18.4	—	—	—	—	—
19	8.0	-0.001	-0.3	-12.0	-0.007	-0.7	-0.6	-0.058	-0.2	18.4	-0.042	0.7	—	—	—
20	7.3	-0.034	-0.5	-9.5	0.021	-0.1	0.0	-0.080	0.2	18.8	-0.099	0.3	9.4	-0.090	0.3
21	8.7	-0.045	0.1	-5.7	0.085	0.8	—	—	—	—	—	—	13.6	-0.253	1.2
22	10.5	-0.037	-0.3	-1.3	-0.005	2.3	—	—	—	—	—	—	21.3	-0.369	3.3
23	12.4	0.021	-0.1	1.3	-0.191	3.1	—	—	—	—	—	—	31.4	-0.475	5.9
24	13.7	0.040	-0.3	8.5	-0.109	6.0	—	—	—	—	—	—	35.2	-0.731	6.6
25	15.4	0.002	0.1	12.5	-0.352	7.8	—	—	—	—	—	—	40.7	-0.943	8.1
26	17.7	0.034	0.6	23.2	-0.402	10.1	—	—	—	—	—	—	50.6	-0.965	10.1
27	16.8	0.046	-0.1	33.7	-0.325	12.6	—	—	—	—	—	—	61.2	-0.942	11.5

¹LC = control line LC1 for G0–G8, average of controls LC1 and LC6 for G9–G21, and average of control lines LC16 and LC61 for G21–G27; L2, L4, L5, and L45 = selection lines.

²BF = average of back fat thickness at first rib, last rib, and first lumbar vertebrae, generations -1 to 17, and back fat thickness recorded at the 10th rib, G18 to G27.

of changes over generations differed significantly from zero, these changes were, for the most part, quite small. An exception was age at puberty, for which genetic and phenotypic changes per generation during G0 to G16 were -0.57 d ($P < 0.01$) and -0.71 d ($P < 0.05$), respectively. The genetic trend in AP is completely explained by the CSD that decreased at a rate of -1.06 d/G and a heritability of 0.57.

Genetic and phenotypic changes in litter size traits and weight traits at birth and weaning were relatively small; only the change in LWW at 28 d during G0 to G11 (0.15 kg/G; $P < 0.05$) was significant after adjustment for random drift variance. The only other significant changes that occurred in LC were in 180-d weight, for which both direct and maternal genetic effects declined from G0 to G19 and then increased from G19 to G28. Overall, there was a phenotypic increase in WT180 of 0.27 kg/G ($P < 0.01$) from G0 to G28.

Selection Line Responses

Genetic and phenotypic responses in L2 are given in Table 9. During index selection for OR and ES (G0 to G11) linear genetic increases per generation of 0.53 ± 0.07 ova and 0.26 ± 0.04 embryos (Fig. 2) and phenotypic increases of 0.77 ± 0.09 ova and 0.29 ± 0.04 embryos per generation occurred. Even though the index included embryo survival rate, the CSD for ES relative to that for OR was relatively small (Table 2), and a strong negative genetic correlation of -0.81 existed between them. Thus, there were negative genetic and phenotypic trends in ES (-0.002 ± 0.001 and -0.010 ± 0.003 embryos per ova per generation for genetic and phenotypic). Genetic increases in litter size (0.12 ± 0.04 fully formed pigs and 0.05 ± 0.04 live pigs per generation) from index selection for OR and ES were small relative to the increase in OR. These changes did

Table 5. Numbers of observations for each trait (n); REML estimates of phenotypic variances (σ_p^2); and proportions due to direct (h_a^2), maternal (h_m^2), litter, pen, and residual effects and direct-maternal genetic correlations (r_{am})

Trait ¹	n	σ_p^2	h_a^2	h_m^2	r_{am}	Litter	Pen	Residual
OR, ova	3,298	19.11	0.27	—	—	0.06	—	0.67
E, embryo number	1,883	8.43	0.17	—	—	0.03	—	0.80
ES, %	1,883	0.04	0.11	—	—	0.02	—	0.87
AP, d	4,842	710.82	0.57	—	—	0.05	—	0.38
BA, pig	5,403	9.39	0.20	—	—	0.02	—	0.78
FF, pig	5,403	10.22	0.20	—	—	0.02	—	0.78
MUM, pig	5,403	0.88	0.17	—	—	0.00	—	0.83
SB, pig	5,403	3.17	0.14	—	—	0.07	—	0.79
LBW, kg	5,397	11.42	0.34	—	—	0.00	—	0.65
LWW28, kg	1,594	97.02	0.21	—	—	0.00	—	0.79
LWW12, kg	2,661	39.91	0.21	—	—	0.00	—	0.79
LWW18, kg	876	85.78	0.27	—	—	0.00	—	0.73
NW28, pig	1,627	1.70	0.11	—	—	0.01	—	0.88
NW12, pig	2,753	3.03	0.13	—	—	0.06	—	0.81
NW18, pig	892	3.10	0.23	—	—	0.00	—	0.77
PBW, kg	54,174	0.08	0.06	0.16	0.13	0.17	—	0.60
WW28, kg	14,532	1.60	0.05	0.12	-0.06	0.22	—	0.62
WW12, kg	21,169	0.47	0.01	0.11	0.98	0.23	—	0.63
WW18, kg	7,376	0.99	0.06	0.07	0.00	0.24	—	0.63
WT180, kg	13,714	131.77	0.36	0.05	0.14	0.06	0.01	0.51
ABF(age), cm	7,683	0.17	0.39	—	—	0.10	0.08	0.42
ABF(wt), cm	7,683	0.12	0.35	—	—	0.11	0.13	0.41
BF10(age), cm	5,796	0.23	0.51	—	—	0.04	0.01	0.44
BF10(wt), cm	5,796	0.16	0.47	—	—	0.04	0.01	0.48
LMA(age), cm ²	5,797	15.25	0.28	—	—	0.06	0.03	0.63
LMA(wt), cm ²	5,797	10.85	0.44	0.02	-0.74	0.04	0.05	0.51

¹OR = ovulation rate; E = number of embryos at 50 d of gestation; ES = embryo survival rate; AP = age of puberty; BA, FF, MUM, and SB = number of live, fully formed, mummified, and stillborn pigs per litter, respectively; LBW and PBW = litter and pig birth weights, respectively; LWW28, LWW12, LWW18, NW28, NW12, NW18, WW28, WW12, WW18 = litter weaning weight, number of pigs weaned per litter, and pig weaning weight, respectively, at 28, 12, and 28 d; WT180 = weight at 180 d of age with age fitted as a covariate; ABF(age) and ABF(wt) = average of back fat thickness recorded at 3 locations with age and weight, respectively, as covariates; BF10(age) and BF10(wt) = back fat thickness recorded at the 10th rib with age and weight, respectively, fitted as covariates; and LMA(age) and LMA(wt) = longissimus muscle area recorded at the 10th rib with age and weight, respectively, fitted as covariates.

not differ significantly between the 2 periods of index selection (G0 to G5, $I = 10.6 \text{ OR} + 72.6 \text{ ES}$ and G6 to G11, $I = 9.9 \text{ OR} + 148.6 \text{ ES}$). Phenotypic changes per generation in BA (0.005 ± 0.05 pigs) and FF (0.126 ± 0.06 pigs) were also small relative to changes in OR. These changes reflect the relatively low genetic correlations of BA with OR (-0.05) and ES at 50 d of gestation (0.30). The number of embryos at 50 d of gestation increased more than twice the rate of increase in FF, and almost no change in BA occurred.

Genetic response to 2-stage selection for OR and FF in L4, which was derived from L2, which had increased OR, resulted in an increase of 0.05 ± 0.09 ova per generation (Table 10). Two-stage selection in L5, which was derived from LC1 with lower OR than L2, was selected more for OR than uterine capacity (UC) and resulted in an increase of 0.21 ± 0.07 ova per generation. This selection resulted in genetic changes of 0.27 ± 0.05 fully formed pigs and 0.19 ± 0.05 live pigs (L4) and 0.29 ± 0.04 fully formed pigs and 0.28 ± 0.05 live pigs (L5)

per generation, substantially greater than what occurred from index selection in L2.

When index selection in L2 was terminated and selection was for FF or BA, responses in these traits were similar from G12 to G28 (Table 9). Genetic changes in FF and BA were 0.20 ± 0.08 and 0.22 ± 0.08 (G12 to G14), 0.12 ± 0.06 and 0.12 ± 0.06 (G15 to G19), and 0.17 ± 0.05 and 0.18 ± 0.03 (G20 to G28), respectively. Because of the relatively great increase in OR from the previous index selection in L2, presumably selection during G12 to G28 was mostly for UC, and the increases in litter size were due more to increased genetic merit for UC than for OR, as proposed by the work of Bennett and Leymaster (1990 a,b).

Changes in numbers of mummified and stillborn pigs provide additional insight into the nature of genetic changes in litter size in these lines. There was an increase of 0.068 ± 0.02 stillborn and 0.021 ± 0.01 mummified pigs per generation in L2 during G0 to G11 (Table 9). Thus, UC, particularly after 50 d of gestation, was insufficient to accommodate the large number of embryos that

Table 6. Genetic (upper diagonal) and phenotypic (lower diagonal) correlations among traits recorded at 50 d of gestation through weaning of litters¹

Trait ²	OR	E	ES	AP	BA	FF	MUM	SB	LBW	LW28	LW12	LW18	NW28	NW12	NW18	PBW	WW28	WW12	WW18
OR	—	0.32	-0.81	-0.18	-0.05	0.09	0.09	0.53	-0.10	-0.23	-0.18	—	-0.41	-0.41	—	0.02	0.00	-0.16	—
E	0.13	—	0.02	-0.11	0.49	0.74	0.17	0.69	0.45	0.08	—	—	0.00	—	—	-0.23	0.14	—	—
ES	-0.40	0.65	—	0.17	0.30	0.13	-0.07	-0.41	0.39	0.36	—	—	0.93	—	—	-0.31	0.16	—	—
AP	-0.07	0.00	0.10	—	0.03	0.09	-0.03	-0.17	0.10	0.05	-0.38	—	-0.11	-0.18	—	0.14	0.30	-0.95	—
BA	-0.08	0.51	0.36	0.02	—	0.89	-0.10	-0.07	0.68	0.15	-0.40	-0.15	0.27	-0.46	-0.06	-0.01	0.32	0.46	0.09
FF	-0.06	0.67	0.31	-0.02	0.84	—	-0.06	0.39	0.82	0.15	-0.42	-0.06	0.04	-0.53	-0.17	-0.03	0.41	0.59	0.09
MUM	0.05	0.15	0.04	-0.05	-0.13	-0.09	—	0.11	-0.14	0.00	-0.23	0.05	-0.24	-0.23	-0.20	-0.06	0.16	0.28	0.15
SB	0.04	0.24	0.13	-0.04	-0.21	0.35	0.05	—	0.41	0.01	-0.25	0.17	-0.20	-0.34	-0.04	-0.05	0.20	0.43	0.25
LBW	-0.14	0.45	0.39	-0.03	0.76	0.83	-0.15	0.21	—	0.55	0.32	0.49	0.34	-0.15	0.19	0.45	0.53	0.62	0.63
LW28	-0.08	-0.09	0.00	0.07	-0.13	-0.18	0.01	-0.12	0.17	—	—	—	0.57	—	—	0.37	-0.26	—	—
LW12	-0.14	—	—	-0.06	-0.28	-0.36	-0.07	-0.22	0.16	—	—	—	—	0.80	—	0.04	—	0.01	—
LW18	—	—	—	—	-0.05	-0.28	0.00	-0.20	0.22	—	—	—	—	—	0.87	0.04	—	—	0.00
NW28	-0.13	0.00	0.10	0.03	0.03	-0.03	-0.01	-0.11	0.14	0.74	—	—	—	—	—	0.54	0.80	—	—
NW12	-0.24	—	—	-0.04	-0.20	-0.27	-0.04	-0.19	-0.01	—	0.83	—	—	—	—	0.01	—	0.11	—
NW18	—	—	—	—	-0.01	-0.17	-0.03	-0.17	0.12	—	—	0.84	—	—	—	0.01	—	—	0.45
PBW	0.06	-0.01	-0.06	-0.01	-0.07	-0.13	-0.02	-0.04	0.11	0.08	0.08	0.09	-0.01	0.04	0.03	—	0.34	0.97	0.91
WW28	0.07	0.03	-0.06	-0.07	-0.01	-0.02	0.02	-0.02	0.07	0.05	—	—	-0.02	—	—	0.51	—	—	—
WW12	0.12	—	—	-0.15	-0.05	-0.08	0.02	-0.01	-0.01	—	0.18	—	—	0.02	—	0.68	—	—	—
WW18	—	—	—	—	-0.06	-0.09	0.02	-0.04	0.04	—	—	0.12	—	—	0.05	0.61	—	—	—

¹Cells with dashes are for traits for which records were not recorded in the same generation.

²OR = ovulation rate; E = number of embryos at 50 d of gestation; ES = embryo survival rate; AP = age of puberty; BA, FF, MUM, and SB = number of live, fully formed, mummified, and stillborn pigs per litter, respectively; LBW and PBW = litter and pig birth weights, respectively; LW28, LW12, LW18, NW28, NW12, NW18, WW28, WW12, and WW18 = litter weaning weight, number of pigs weaned per litter, and pig weaning weight, respectively, at 28, 12, and 28 d.

existed at 50 d of gestation. Selection on an index of OR and ES at 50 d of gestation was not an effective strategy to increase litter size at birth. Direct selection for litter size after G11 in L2 resulted in a decline in the number of mummified pigs from G12 to G19, suggesting genetic improvement in UC during late gestation. Changes in the number of stillborn pigs also tended to decrease.

Changes in MUM and SB in L4, L5, and L45 were less consistent (Table 10). During 2-stage selection (G8 to G16), MUM decreased (-0.019 ± 0.015) and SB increased (0.059 ± 0.029) in L4 ($P < 0.10$). Changes in L5 were substantially less; however, both MUM and SB increased (0.017 ± 0.015 and 0.011 ± 0.021 , respectively). Thereafter, when selection was directly for litter size, changes in SB and MUM in L4, L5, and L45 were inconsistent but relatively small compared with the changes in FF and BA.

From G8 to G19, BA increased faster in L5 than in L4 (Fig. 2). Prior selection increased OR in L2 without a concomitant increase in UC. Litter size selection during this period in L4 and L5 was direct selection on UC. Therefore, 2-stage selection for OR and FF in L4 was unbalanced, placing too much emphasis on OR and too little on UC as measured by litter size in females with a high ovulation rate. However, in L5, which began with lower OR than L4, 2-stage selection appeared to be more balanced, placing approximately optimum se-

lection pressure on both OR and UC, resulting in rapid increases in both BA and FF pigs per litter.

As in LC, selection for decreased AP in L2, L4, and L5 as a result of the management regimen occurred. Regressions of CSD on generation number were -1.45 , -1.67 , and -1.67 d in L2, L4, and L5, respectively. Genetic change per generation in L2 from G0 to G11 was -0.71 ± 0.62 d (Table 9), whereas changes per generation in L4 and L5 from G8 to G16 were -1.72 ± 0.79 and -1.62 ± 0.64 d (Table 10), respectively. As in LC, the change in L2 is consistent with the heritability of AP (0.57; Table 5); however, greater change than predicted from the CSD occurred in L4 and L5. Phenotypic change in L2 (-0.41 ± 0.74 d/G, G0 to G11) was less than the genetic change; however, in L4 and L5, phenotypic changes per generation were -3.65 ± 1.15 and -3.55 ± 0.84 d, respectively, substantially greater than the genetic changes. The explanation for these relatively great decreases in AP is not apparent as a similar environmental change did not occur in the control line (Table 8).

Genetic trends in both direct and maternal genetic effects on PBW were small (0.03 kg/G) in all selection lines during all periods of selection (Tables 9 and 10). Phenotypic trends were either slightly negative or zero. Therefore, none of the selection criteria aimed at increasing litter size had an adverse effect on PBW genetic values. Thus, the small, negative phenotypic trends were environmental, associated with larger litters. Genetic

Table 7. Genetic and phenotypic correlations among traits recorded at 180 d and between these traits and those recorded for females and litters through weaning¹

Trait ²	Genetic correlations				Phenotypic correlations			
	WT180	BF10	ABF	LMA	WT180	BF10	ABF	LMA
BF10	0.60	—	—	0.08	0.55	—	—	0.24
ABF	0.83	—	—	—	0.53	—	—	—
LMA	0.53	0.08	—	—	0.56	0.24	—	—
BA	0.08	0.10	0.09	0.11	0.04	-0.01	-0.02	0.04
OR	-0.01	—	-0.04	—	0.11	—	-0.02	—
E	0.12	—	-0.16	—	0.08	—	-0.02	—
ES	0.15	—	-0.03	—	-0.06	—	0.02	—
AP	-0.12	—	-0.19	—	-0.27	—	-0.15	—
FF	0.13	-0.04	0.01	0.15	0.07	-0.04	-0.02	0.03
MUM	0.08	-0.41	-0.23	0.21	0.05	-0.04	-0.03	0.02
SB	0.11	-0.43	-0.14	-0.04	0.06	-0.06	0.00	-0.05
LBW	0.24	-0.15	-0.22	-0.02	0.12	-0.08	-0.09	-0.05
LWW28	0.19	—	-0.23	—	0.08	—	-0.10	—
LWW12	0.28	0.04	0.07	0.10	0.01	-0.02	0.00	0.02
LWW18	0.33	0.04	—	-0.26	0.07	0.03	—	0.05
NW28	0.10	—	0.03	—	0.01	—	-0.05	—
NW12	-0.01	0.04	0.25	0.17	-0.02	0.02	0.01	0.01
NW18	0.13	0.19	—	-0.27	0.01	0.03	—	0.05
PBW	0.27	0.08	-0.18	-0.25	0.33	-0.10	-0.12	0.00
WW28	0.46	—	-0.15	—	0.41	—	0.13	—
WW12	0.24	-0.12	0.26	-0.58	0.35	-0.11	0.09	-0.05
WW18	0.42	-0.11	—	0.15	0.39	-0.12	—	0.00

¹Cells with dashes are for traits for which records were not recorded in the same generation.

²BA = number of pigs born alive; OR = ovulation rate; E = number of embryos at 50 d of gestation; EV = embryo survival rate; AP = age of puberty; FF = number of fully formed pigs; MUM = number of mummified pigs; SB = number of stillborn pigs; LBW = litter birth weight; LWW28, LWW12, LWW18, NW28, NW12, NW18, WW28, WW12, and WW18 = litter weaning weight, number weaned, and pig weaning weight at 28 d (G0–11), 12 d (G12–21), and 18 d (G 22–27), respectively; PBW = birth weight; WT180 = weight at 180 d; BF10, ABF, and LMA = back fat depth of the 10th rib, average back fat, and longissimus muscle area with weight as a covariate.

trends for LBW closely followed those of FF because of the high genetic correlation ($r_g = 0.82$) between them.

Although some phenotypic and genetic trends in NW and WW were significant, these were inconsistent across lines and selection periods. Averaged across periods, these trends were very close to zero. Thus, after adjustment to a standard weaning age and number nursed by dams, direct genetic effects on NW, WW, and LWW were not affected by any set of selection traits.

Genetic changes in WT180 were negative in L2 (Table 9) through G14 (Fig. 2), averaging approximately -0.55 kg/G, consistent with the negative CSD (-20.0 kg at G14; Table 4) and a heritability of 0.36 (Table 5). Thereafter, CSD for WT180 increased to 33.7 kg at G27 and resulted in substantial genetic change, especially during G20 to G28 (1.81 kg/G in L2; 1.55 kg/G in L45) when selection for WT180 occurred and the greatest increase in CSD occurred. Phenotypic changes in WT180

Table 8. Average genetic and phenotypic changes per generation (G) in control lines (LC) estimated as regression coefficients of mean phenotypes (P) and direct (A^d) and maternal (A^m) breeding values on generation

Trait ¹	G	P	A^d	A^m
OR	0–16	-0.03	-0.02	—
E	0–11	0.06	-0.00	—
ES, E/OR	0–11	-0.00	0.00	—
AP, d	0–16	-0.71*	-0.57**	—
BA	0–28	-0.03	0.01	—
FF	0–28	-0.02	-0.01	—
MUM	0–28	-0.02	0.00	—
SB	0–28	0.01	-0.02	—
LBW, kg	0–28	-0.07	0.04	—
LWW28	0–11	-0.10	0.15*	—
LWW12	12–21	-0.05	-0.03	—
LWW18	22–27	0.21	0.02	—
NW28	0–11	0.04	0.02	—
NW12	12–21	-0.03	0.02	—
NW18	22–27	0.02	0.03	—
PBW, kg	0–28	-0.01	0.00	0.00
WW28	0–12	-0.05	0.00	0.01*
WW12	13–22	0.00	-0.00	-0.00
WW18	23–28	0.01	0.01	0.03
WT180, kg	0–28	0.27**	0.03	-0.01
WT180, kg	0–19	0.33*	-0.20**	-0.02**
WT180, kg	20–28	-0.04	0.27**	0.07*
ABF, cm	0–17	0.03	0.01	—
BF10, cm	18–28	0.03	0.01	—
LMA, cm ²	18–28	-0.62†	0.11†	-0.00†

† $P < 0.10$; * $P < 0.05$; ** $P < 0.01$.

¹OR = ovulation rate; E = number of embryos; ES = embryo survival rate; AP = age at puberty; BA, FF, MUM, and SB = number of live, fully formed, mummified, and stillborn pigs per litter, respectively; LBW = litter birth weight; LWW = litter weaning weight; NW = number of pigs weaned per litter; PBW = pig birth weight; WW = pig weaning weight; WT180 = weight at 180 d of age; ABF, BF10, and LMA = average of back fat at first rib, last rib, and last lumbar vertebrae, back fat at 10th rib, and longissimus muscle area at 10th rib, respectively, adjusted for weight.

were inconsistent with genetic changes through G19 in L2. Apparently, positive environmental changes were occurring, especially from G0 to G19 as positive phenotypic change also occurred in LC during this period, offsetting the negative genetic trend in LC (Table 8). Genetic changes in L4 and L5 during the period of 2-stage selection (G9 to G16) were positive, but phenotypic changes were inconsistent because they were positive in L4 but negative in L5 (Table 10). As in L2, a substantial increase in WT180 occurred in L45 during G20 to G28 when direct selection for it occurred (Fig. 2).

Almost no change in ABF or BF10 occurred in L2 during the experiment (Table 9). A significant increase in LMA occurred during G20 to G28 (0.46 cm²/G), but it was relatively small and offset by negative phenotypic change (-0.69 cm²/G). These changes are consistent with trends in LC (Table 8), and the negative phenotypic

Table 9. Genetic and phenotypic changes per generation (G) in line 2 estimated as regression coefficients of generation mean phenotypes (P) and direct (A^d) and maternal (A^m) breeding values on generation number, selection for OR and ES during G0 to G11, selection for FF during G12 to G14, selection for BA and PBW during G15 to G19, selection for BA, and weight, back fat, and longissimus muscle area at 180 d of age during G20 to G28

Trait ¹	G0–G11			G12–G14			G15–G19			G20–G28		
	P	A^d	A^m	P	A^d	A^m	P	A^d	A^m	P	A^d	A^m
OR	0.77**	0.53**	—	—	—	—	—	—	—	—	—	—
E	0.29**	0.26**	—	—	—	—	—	—	—	—	—	—
ES, E/OR	-0.01**	-0.002	—	—	—	—	—	—	—	—	—	—
AP, d	-0.41	-0.71	—	-2.25	0.01	—	—	—	—	—	—	—
BA	0.01	0.05	—	-0.06	0.22	—	0.11	0.12	—	0.22	0.18**	—
FF	0.13*	0.12*	—	-0.18	0.20	—	0.10	0.12	—	0.18	0.17**	—
MUM	0.06	0.02	—	-0.06	-0.03	—	0.03	-0.02	—	0.01	0.00	—
SB	0.12**	0.07**	—	-0.12	-0.03	—	-0.01	-0.00	—	-0.04	-0.01	—
LBW, kg	-0.15†	0.03	—	-0.43	0.17	—	-0.03	0.10	—	0.20*	0.31**	—
LWW, kg	-0.81**	-0.21*	—	1.52	-0.36	—	0.34	-0.09	—	0.43	0.09	—
NW	-0.04	-0.03*	—	-0.04	-0.08	—	0.07	-0.03	—	-0.06	0.02	—
PBW, kg	-0.03**	-0.00	-0.01	-0.01	-0.00	-0.01	-0.01	0.00	-0.01	0.00	0.001*	-0.00
WW, kg	-0.08**	0.00	-0.01	-0.28	-0.02	0.00	-0.02	-0.00	-0.01	0.08**	0.00	0.01**
WT180, kg	0.38	-0.61**	0.04	-1.30	-0.23	-0.02	-2.75	0.54	0.13	1.28†	1.81**	0.11
ABF, cm	-0.00	-0.00	—	0.02	-0.01	—	0.02	-0.01	—	—	—	—
BF10, cm	—	—	—	—	—	—	—	—	—	0.01	-0.01	—
LMA, cm ²	—	—	—	—	—	—	—	—	—	-0.69	0.46**	-0.02†

† $P < 0.10$; * $P < 0.05$; ** $P < 0.01$.

¹OR = ovulation rate; E = number of embryos; ES = embryo survival rate; AP = age at puberty; BA, FF, MUM, and SB = number of live, fully formed, mummified, and stillborn pigs per litter, respectively; LBW and PBW = litter and pig birth weights, respectively; LWW, NW, and WW = litter weaning weight, number of pigs weaned per litter, and pig weaning weight, respectively; WT180, ABF, BF10, and LMA = weight, average of first rib, last rib, and last lumbar back fat, 10th rib back fat, and longissimus muscle area at 180 d, respectively.

ic change is likely an environmental effect associated with scanning technicians. The same individual scanned all pigs within a generation, but 2 different technicians scanned pigs during this period. Although changes were relatively small, significant genetic (0.02 cm/G) and phenotypic increases (0.09 cm/G) in ABF accompanied 2-stage selection in both L4 and L5 during G9 to G16 (Table 10). Selection for BF10 and LMA in L45 during G20 to G28 resulted in a genetic decrease of -0.04 cm/G in BF10 and an increase in LMA of 0.54 cm²/G ($P < 0.01$). Phenotypic changes per generation, however, were close to zero for BF10 and negative (-0.97 cm²) for LMA.

Investigation of a Plateau in BA

The heritability of BA estimated in L2 and L45 using a complete pedigree file and phenotypic data for G20 to G27 was 0.17 ± 0.02 , compared with the estimate of 0.20 ± 0.03 using all data over all generations. Phenotypic variance in these lines during these generations was 9.86, similar to the overall estimate of 9.39 pigs². In addition, linear regression coefficients for CSD (1.47 pigs/G in L2; 1.36 pigs/G in L45) and mean EBV (0.18 pigs/G in L2; 0.17 pigs/G in L45) on generation during these generations were significant ($P < 0.01$), but

the quadratic coefficients were not, indicating that both the opportunity for selection and responses were similar to those of earlier generations. Thus, no evidence for a decline in genetic variance or selection response in later generations in L2 and L45 existed.

DISCUSSION

Considerable phenotypic and genetic variation existed for all reproductive traits. The h_a^2 ranged from 0.11 (ES) to 0.57 (AP). The h_a^2 of other studies in swine are similar to the h_a^2 of most traits in this study. The estimates of h_a^2 are in agreement with those of Holl and Robison (2003), Holm et al. (2004), Arango et al. (2005), and Rosendo et al. (2007b) for BA (0.20), with those of Mesa et al. (2005) for FF (0.20), with those of Neal et al. (1989) for E (0.17), and with those of Neal et al. (1989), Blasco et al. (1998, 2005), Holm et al. (2004), and Rosendo et al. (2007c) for ES (0.11). The h_a^2 for OR (0.27) is similar to those reported by Blasco et al. (1998, 2005) and Rosendo et al. (2007a) on the left, right, and both ovaries at puberty but is smaller than estimates of moderate realized heritability reported by Zimmerman and Cunningham (1975) and Cunningham et al. (1979), which were based on the response of selection for increased OR in the Nebraska Gene Pool population. Low

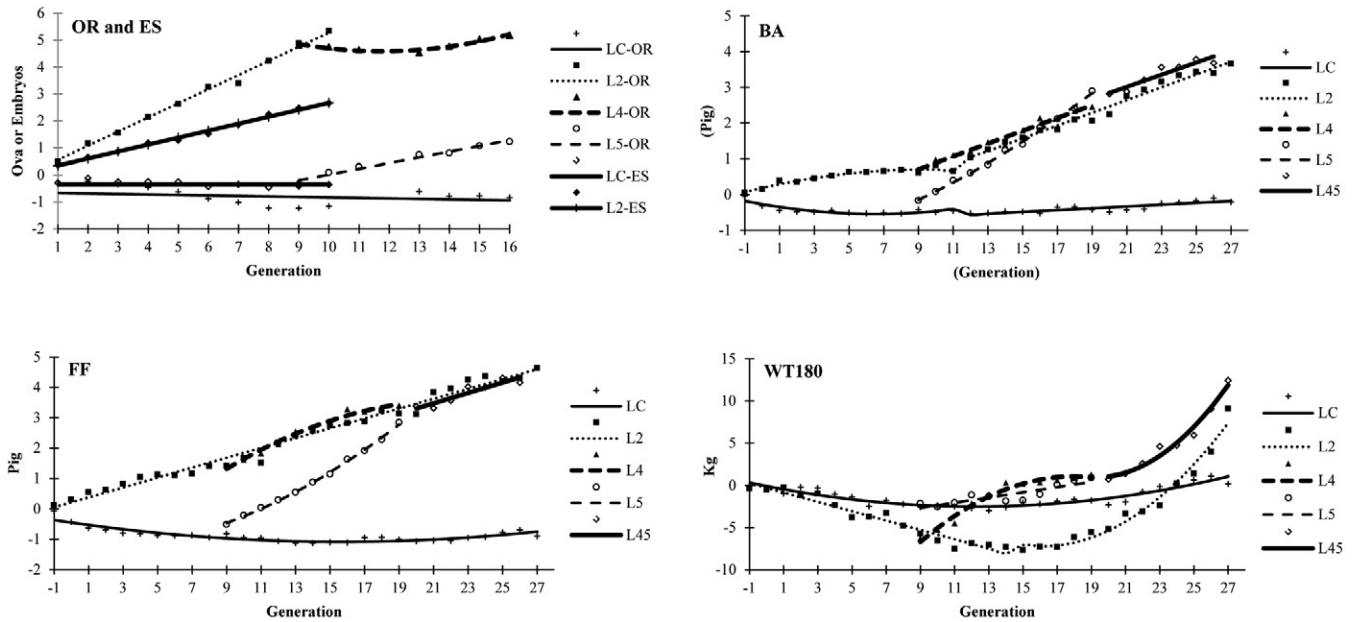


Figure 2. Estimated genetic trends for ovulation rate (OR), number of surviving embryos (E), number of fully formed pigs (FF) and number of pigs born alive (BA) per litter, and 180-d weight with a covariate of age (WT180) by line. Symbols show the actual mean EBV on generation; curved lines show the linear or quadratic line estimated from linear and quadratic regression coefficients. LC = control line LC1 for G0 to G8, average of controls LC1 and LC6 for G9 to G21, and average of control lines LC16 and LC61 for G21 to G27; L2, L4, L5, and L45 = selection lines.

h_a^2 for PBW and WW are in agreement with those of Fredeen and Mikami (1986b), Chen et al. (2003), Mesa et al. (2005), and Rosendo et al. (2007c). Moderate h_a^2 for WT180 are in agreement with those of Holm et al. (2004), h_a^2 for BF10 is similar to those in Chen et al. (2003) and Arango et al. (2005), and h_a^2 of LMA agrees with the ones in Chen et al. (2003) and Holm et al. (2004).

Selection for OR caused a decrease in E and fetus survival, which is in agreement with Cunningham et al. (1979), Johnson et al. (1999), Ruiz-Flores and Johnson (2001), and Petry and Johnson (2004) and the models of Bennett and Leymaster (1989). However, the negative estimate of r_g of OR and ES is greater than the estimates of Rosendo et al. (2007a) in OR at puberty and at fertilization. Moderate to high positive r_g and r_p of OR with ES in rabbit were reported by Blasco et al. (2005), but estimates herein were opposite in sign. A plausible explanation for these quite different results is that the limit of UC may not have occurred in the experiment of Blasco et al. (2005). In our study, uterine overcrowding from high OR may have caused the high negative correlation between OR and ES. Estimates of r_g of OR and FF are small and positive and similar to the estimates in Cunningham et al. (1979) and Rosendo et al. (2007a). The estimate of r_g of OR and BA in our study was small and negative, the estimate of Rosendo et al. (2007b) was moderate and positive, and the estimate of Cunningham et al. (1979) was small and positive. Again, this may be because of different relationships of OR and UC in the populations used in these studies. When OR exceeds UC,

then negative correlations are expected. However, if OR is less than UC, then positive associations between the traits is expected (Bennett and Leymaster, 1989).

Cunningham et al. (1979) obtained r_g of OR with NW, LBW, and LWW that are opposite in sign to the estimates of this study. Rosendo et al. (2007b) obtained very high r_g and r_p between BA and NW that are very different from estimates herein. This result can be expected because in our study the relationship between OR and BA was small and negative, whereas the estimates of Cunningham et al. (1979) and Rosendo et al. (2007b) were positive. Again, these relationships are dependent on the balance between OR and UC, which determine LS at birth, in the populations studied.

The estimates of (0.89) r_g and r_p (0.84) of BA with FF are high and similar to the estimates of Young et al. (1978) and explain why BA and FF had similar genetic trends. Selection on either FF or BA increased the other (L2, G12 to G19). However, selection for OR and ES improved FF linearly but produced a quadratic response in BA (G0 to G11). The limit of UC would result in increased SB and a different response in FF and BA (Bennett and Leymaster, 1990b).

Almost zero r_g of PBW with OR, FF, and BA were found herein and are different from correlations obtained by Mesa et al. (2005) and Rosendo et al. (2007b). The results indicate that genes affecting PBW in the populations used herein had very small effects on reproductive traits.

We found very low genetic correlations of reproductive traits with both growth and carcass traits, similar to results of many other studies (e.g., Young et al.,

Table 10. Genetic and phenotypic changes per generation (G) in lines 4, 5, and 45 estimated as regression coefficients of generation mean phenotypes (P) and direct (A^d) and maternal (A^m) breeding values on generation number, selection for OR and FF during G9 to G16, selection for BA and PBW during G17 to G19, selection for BA, and weight, back fat, and longissimus muscle area at 180 d of age during G20 to G28

Trait ¹	G9–G16						G17–G19						G20–G28		
	Line 4			Line 5			Line 4			Line 5			Line 45		
	P	A^d	A^m	P	A^d	A^m	P	A^d	A^m	P	A^d	A^m	P	A^d	A^m
OR	0.26*	0.05	—	0.34**	0.21*	—	—	—	—	—	—	—	—	—	—
AP, d	-3.65*	-1.72*	—	-3.55**	-1.62*	—	—	—	—	—	—	—	—	—	—
BA	0.10	0.19**	—	0.11	0.28**	—	-0.52	0.17	—	0.35	0.39*	—	0.14	0.17**	—
FF	0.27*	0.27**	—	0.15	0.29**	—	-0.88	0.11	—	0.52	0.46*	—	0.03	0.17**	—
MUM	0.09*	-0.02	—	0.10*	0.02	—	0.01	-0.01	—	-0.05	-0.04	—	0.05*	0.02*	—
SB	0.17	0.06†	—	0.05	0.01	—	-0.37*	-0.04	—	0.17	0.05	—	-0.11*	-0.00	—
LBW, kg	0.24	0.39**	—	-0.01	0.22**	—	-0.67	0.20	—	1.04	0.78*	—	0.06	0.31**	—
LWW, kg	-1.23**	0.05	—	-1.52*	-0.50*	—	-0.69†	0.44†	—	-2.92†	-0.20	—	0.13	0.98**	—
NW	-0.17*	-0.07**	—	-0.06	0.01	—	-0.16*	0.03	—	-0.78†	-0.04	—	-0.07	0.08**	—
PBW, kg	-0.01	0.01*	0.00	-0.02**	-0.00	-0.01*	0.01	0.01	-0.01	-0.01	0.01	-0.01	0.00	0.01**	-0.00
WW, kg	-0.11**	-0.00	0.03*	-0.17**	-0.02**	-0.03†	0.00	0.00	0.00	-0.07†	-0.00	-0.01	0.06*	0.03**	0.04**
WT180	0.12	1.07**	0.10	-1.02*	0.14	-0.03	2.22	0.33	-0.05	3.16*	0.42	0.15	1.25	1.55**	0.12*
ABF	0.09**	0.02*	—	0.09**	0.03**	—	—	—	—	—	—	—	—	—	—
BF10	—	—	—	—	—	—	—	—	—	—	—	—	-0.01	-0.04**	—
LMA	—	—	—	—	—	—	—	—	—	—	—	—	-0.97*	0.54**	-0.02*

† $P < 0.10$; * $P < 0.05$; ** $P < 0.01$.

¹OR = ovulation rate; AP = age at puberty; BA, FF, MUM, and SB = number of live, fully formed, mummified, and stillborn pigs per litter, respectively; LBW and PBW = litter and pig birth weights, respectively; LWW, NW, and WW = litter weaning weight, number of pigs weaned per litter, and pig weaning weight, respectively; WT180, ABF, BF10, and LMA = weight, average of first rib, last rib, and last lumbar back fat, 10th rib back fat, and longissimus muscle area at 180 d, respectively.

1977, 1978; Fredeen and Mikami, 1986a; Estany et al., 2002; Holl and Robison, 2003; Rosendo et al., 2007c). Selection for reproduction is expected to produce very little response in growth and carcass traits, and selection for growth and carcass traits is expected to cause little if any change in reproduction traits.

The results of our study showed that direct and indirect selection on components of LS can improve LS, and the results are in agreement with the work of Bennett and Leymaster (1989, 1990a,b) and Rosendo et al. (2007a). Genetic merit for BA (0.10 to 0.29 pigs/G; $P < 0.05$), FF (0.10 to 0.33 pigs/G; $P < 0.05$), and LBW (0.14 to 0.28 kg/G; $P < 0.10$) increased in all selection lines over 28 generations. Indirect selection for decreased AP occurred in both selection and control lines, and responses were consistent with the relatively high heritability (0.57) and the realized selection differentials that occurred because of the management protocol. After adjustment to a standard weaning age and number nursed by dams, direct genetic effects on NW, WW, and LWW were not affected by any set of selection criteria.

Index selection for OR and ES to 50 d of gestation increased both FF and BA, but SB also increased because of insufficient UC during the last half of the gestation period, as proposed by the modeling work of Bennett and Leymaster (1990b). Thus, the change in BA was less than that in FF.

In other studies, direct selection for increased LS in pigs produced only small responses (Ollivier, 1982; Haley et al., 1988; Bolet et al., 1989; Pérea-Enciso and Bidanel, 1997; Estany et al., 2002; Holl and Robison, 2003). Response to litter size selection in mice was similar (Bakker et al., 1978). Selection for OR and ES, direct selection for FF, or 2-stage selection for OR and FF can improve LS. Selection for FF or an index of OR and FF in populations in which UC is restricting litter size UC can improve BA because such selection also places selection pressure on UC in late gestation. Two-stage selection for OR and FF increased genetic responses in BA, FF, SB, and LBW in both L4 and L5 but produced a greater response in L5, which was derived from the control line (LC1) and thus started with a lower ovulation rate.

Kerr and Cameron (1995), Arango et al. (2005), Canario et al. (2006), and Rosendo et al. (2007b) reported that selection for LS is expected to decrease PBW and decrease piglet survival. We also observed a small decrease in PBW in the first 14 generations in L2 and in the first 16 generations in L5. However, when the selection protocol included PBW or WT180 without any loss in selection pressure on BA, PBW increased slightly.

Chen et al. (2003), Holm et al. (2004), and Arango et al. (2005) concluded that long-term selection for production traits may have negative effects on reproductive traits. Similarly, Estany et al. (2002) concluded

that long-term selection for LS may result in significant negative effects on lean growth. However, we found very weak genetic associations of reproduction traits with weight, back fat thickness, and LMA at 180 d of age. Furthermore, during the last 8 generations of the 28-generation experiment when secondary selection was applied to these traits after selection of BA, favorable responses in these traits occurred, and they were consistent with the selection differentials and heritabilities of the traits. Thus, selection for BA had very little effect on WT180, BF10, and LMA.

During the last 8 generations, linear increases ($P < 0.01$) in both CSD and mean EBV occurred in both L2 and L45; quadratic effects were not significant. Phenotypic variance in these lines in these generations was (9.86), similar to that of earlier generations, and heritability of BA was 0.17. Thus, there was no evidence for a plateau in response for BA after 28 generations of selection.

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