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Luis L. T. Gama

University of Nebraska-Lincoln

R. K. Johnson

University of Nebraska-Lincoln, rjohnson5@unl.edu

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Changes in Ovulation Rate, Uterine Capacity, Uterine Dimensions, and Parity Effects with Selection for Litter Size in Swine¹

Luis L. T. Gama and R. K. Johnson

Department of Animal Science, University of Nebraska, Lincoln 68583-0908

ABSTRACT: This study was conducted with random samples of pigs of a line (LS) selected for eight generations for litter size and a randomly selected control line (RS) in the Nebraska Gene Pool population and of crosses of these lines with a Large White-Landrace composite line (I) that was selected for an index of ovulation rate and embryonic survival to 50 d of gestation. Two experiments were done to obtain information on ovulation rate, uterine dimensions, and uterine capacity. In Exp. 1, 103 gilts were slaughtered 9 to 16 d after their second estrus to obtain reproductive tracts for evaluation of ovulation rate and uterine dimensions. In Exp. 2, unilateral hysterectomy-ovariectomy was performed 3 to 10 d after puberty in 109 gilts that were then mated at their next estrus and slaughtered at 93 to 100 d of gestation to recover reproductive tracts for evaluation. Litter size at birth was recorded at first ($n = 414$), second ($n = 159$), and third ($n = 143$) parity of pureline and crossline gilts. The cumulative response

to eight generations of selection for litter size pooled over type of cross and parity was $1.21 \pm .38$ pigs, in good agreement with the realized response of 1.06 pigs previously estimated from the period of selection. This response was due to an increase of $1.30 \pm .54$ eggs in ovulation rate (measured by the number of corpora lutea in cyclic and pregnant gilts) and $.66 \pm 1.28$ pigs in uterine capacity (measured after unilateral hysterectomy-ovariectomy). No significant changes were found in uterine dimensions in cyclic gilts. Approximately 25% of the increase in litter size could be explained by a reduction in number of mummified pigs at birth, an indication that uterine capacity in late gestation was increased. Estimated differences between lines ($g_{LS} - g_{RS}$) were not significantly different for pureline and crossline gilts and sows, and no interactions of these estimates with parity were detected. Estimates of heterosis for $LS \times I$ and $RS \times I$ did not differ significantly, nor were interactions of heterosis with parity significant.

Key Words: Pigs, Litter Size, Selection, Ovulation, Parity, Heterosis

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Introduction

Direct selection for litter size has been effective in mice (Bradford, 1968; Falconer, 1971; Gion et al., 1990) but was not successful in one experiment with swine when selection was practiced for 11 generations (Ollivier, 1982; Bolet et al., 1989). Lamberson et al. (1991) reported that after eight generations of selection for litter size in a line of pigs previously selected for ovulation rate, response was approximately one additional pig at birth, with a realized heritability of .15.

Johnson et al. (1984) proposed a model in which litter size is considered as the product of two components, ovulation rate and embryonic survival.

Bennett and Leymaster (1989) proposed an alternative model in which litter size equals the minimum number of viable embryos (a function of ovulation rate) or uterine capacity. In this model, mean litter size is then a function of the means for ovulation rate and for uterine capacity, plus their interaction, and selection for litter size would correspond to selection for the most limiting component.

The objectives of this study were 1) to determine responses in ovulation rate, uterine dimensions, and uterine capacity in a line of pigs successfully selected for litter size for eight generations; 2) to investigate how much of the response in litter size could be explained by an increase in uterine capacity in late gestation, as expressed by a decrease in the number of mummified pigs at birth; and 3) to examine whether the increase in litter size obtained by selection practiced in first-parity gilts was maintained in later parities.

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Table 1. Number of litters produced in the evaluation phase of gene pool lines, by parity and generation of evaluation

Line of dam	Line of sire	Parity								
		1			2 ^a			3 ^a		
		9 ^b	10	11	9	10	11	9	10	11
RS	RS	19	23	18	10	13	10	9	10	12
RS	I	18	18	20	—	—	—	—	—	—
LS	LS	18	20	16	10	10	10	10	8	9
LS	I	18	20	19	—	—	—	—	—	—
I	I	20	19	19	8	8	11	6	7	10
I × RS	RS	23	20	24	12	12	12	11	11	10
I × LS	LS	19	19	24	11	10	12	10	10	10

^aSires of litters from Parity-2 and 3 sows were the same for all sows and were crossbred boars from another population.

^bGenerations 9, 10, and 11 were the first, second, and third generations of evaluation and correspond to generation of the dam for lines RS and LS following eight generations of selection for litter size. Line I was a common tester line mated with lines LS and RS that was undergoing random selection.

Materials and Methods

Population

This study was conducted with pigs of a line selected for litter size and a randomly selected line in the Nebraska Gene Pool population. The management, selection procedures, and direct responses in this population were reported in detail by Lamberson et al. (1991). Briefly, the Nebraska Gene Pool is a 14-breed composite line (Zimmerman and Cunningham, 1975) in which two lines were established in 1967, one line selected for high ovulation rate (**OR**) for nine generations and a randomly selected contemporary control line (**C**, Cunningham et al., 1979). After this first phase of the selection experiment and two additional generations of random selection for both the OR and C lines, three lines were derived from the OR line. One line was selected for increased litter size (**LS**), one line was selected for decreased age at puberty, and one line was randomly selected (**RS**). The initial control line was also maintained during this second phase of the experiment, which consisted of eight generations of selection and three additional generations of evaluation during which all lines were randomly selected.

In 1981, another experiment was initiated, in which a Large White-Landrace composite line was selected on an index combining ovulation rate and embryonic survival to 50 d of gestation (line **I**, Neal et al., 1989). A sample of gilts and boars born in the fifth generation of this experiment was maintained contemporaneously with the Gene Pool population, with random selection. Random samples of LS and RS gilts in Generations 8, 9, and 10 of the second phase of the experiment were mated to produce pureline (RS × RS and LS × LS) and crossline (I × RS and I × LS) litters (Table 1). In Generations 9, 10, and 11, I × RS and I × LS gilts were back-crossed to produce RS(I × RS) and LS(I × LS) progeny. Approximately 20 litters by 15

sires were produced per generation in the LS and RS lines, with approximately one replacement gilt selected per litter to be mated by a boar of the same line, and another littermate selected to be mated by a boar of line I. In line I and in I × RS and I × LS crosses there were approximately 20 litters by 15 sires per generation. As a result, there were very few half-sib gilts and almost no full-sib gilts in the same population with data recorded.

Of the RS, LS, I × RS, I × LS, and I gilts farrowing in 1988, 1989, and 1990, a random sample of approximately 12 gilts per line and year was kept to produce second- and third-parity litters. Second- and third-parity sows of all lines were mated to boars of an unrelated line.

Data Collected

Ovulation Rate, Uterine Dimensions, and Uterine Capacity. Two experiments were conducted to obtain information on ovulation rate, uterine dimensions, and uterine capacity in gilts of LS and RS crosses. In Exp. 1, cyclic gilts (n = 103) of I × RS, I × LS, RS(I × RS), and LS(I × LS) breeding were slaughtered at approximately the same physiological stage (i.e., 9 to 16 d after their second estrus). Reproductive tracts were collected in a commercial slaughter plant and immediately placed in an isothermic container at a temperature of approximately 39°C, and data were obtained 2 to 5 h after collection of the tracts. Ovulation rate (**ORC**) was determined by counting the number of corpora lutea, without ovarian dissection, in both ovaries. The length of each uterine horn was measured with a flexible tape, from the uterotubal junction to the junction of the uterine body and cervix, along the mesometrial border. The length of both horns was added together to determine total uterine length (**UL**). After uterine weight (**UW**) was obtained, warm physiological saline solution was injected at constant pressure into the uterus, after a

clamp had been placed on the cervix. When no more solution could be injected, the uterus was weighed again, and the difference from UW was uterine volume (UV), assuming that 1 g = 1 mL of physiological saline. Under the assumption that the uterus is essentially cylindrical, uterine diameter (UD) was calculated for each gilt from the information on UV and UL.

In Exp. 2, unilateral hysterectomy-ovariectomy (UHO) was performed 3 to 10 d after puberty in gilts ($n = 109$) of the same line crosses described in Exp. 1. Ovulation rate at puberty (ORP) was estimated by counting the number of corpora lutea, and each gilt was randomly assigned to removal of either the left or right ovary and ipsilateral uterine horn by a surgical procedure similar to that described by Huang et al. (1987). Gilts were mated by a fertile boar of an unrelated line as soon as they showed signs of estrus after the surgery and were given three additional opportunities to be bred. Pregnant gilts ($n = 91$) were slaughtered at 93 to 100 d of gestation and, immediately after slaughter, information was collected on ovulation rate (ORM) by counting the number of corpora lutea after ovarian dissection, number of fully formed pigs (FFP), and number of fully formed plus mummified pigs (FFM). Uterine capacity was calculated as $2 \times \text{FFP}$.

All data in Exp. 1 were collected during one season by the same person. Experiment 2 was done in a different season, but again all data were collected by one individual.

Number of Mummified Pigs. Information was collected on the number of mummified pigs per litter in lines RS, LS, and C during the selection phase of the experiment, and in three additional generations of evaluation (random selection).

Parity Effects. Information on number of fully formed pigs produced by first-, second-, and third-parity dams of the different lines and crosses was used in this analysis, with data pooled by line of the gilt or sow, regardless of breeding of the litter.

Statistical Analyses

Ovulation Rate, Uterine Dimensions, and Uterine Capacity. The analysis was conducted in two steps to obtain estimates of line differences for the different traits. First, least squares means were obtained for the different crosses using the GLM procedure (SAS, 1985). The statistical model for uterine dimensions in Exp. 1 included the effects of line cross and day of the cycle as a linear and quadratic covariate. The effects of ovulation rate on uterine dimensions were not statistically significant ($P > .05$), so ovulation rate was not included in the model for those traits. The linear model for ORC included only the effect of line cross. In Exp. 2, a preliminary analysis was conducted for ORM, FFP, and FFM including the effects of line cross, side removed (left or right), and day of surgery

($n = 26$) as a linear and quadratic covariate. After sequentially excluding from the model the effects that had no statistical significance ($P > .2$), but keeping line cross in all cases, the linear model for FFP included only line cross, the model for FFM included line cross and day of surgery linear, and the model for ORM included line cross, day of surgery linear, and side removed. The model for ORP included only line cross.

The second step in the analysis was to estimate the difference between the direct effects of line LS and RS by weighted least squares. The expectations of the different crosses in terms of crossbreeding parameters (Dickerson, 1969), ignoring recombination effects, maternal heterosis, and maternal effects and assuming that individual heterosis was the same in $I \times RS$ and $I \times LS$ crosses, are shown in Table 2.

The genetic model for each trait was as follows: $y = Xb + e$ with $E(y) = Xb$ and $V(y) = V$, where y is a 4×1 vector of least squares means for the $I \times RS$, $I \times LS$, $RS(I \times RS)$, and $LS(I \times LS)$ crosses and V is a diagonal matrix of variances of means.

Because only four means were used to estimate the crossbreeding parameters, and heterosis and the direct effects of line I were completely confounded, the incidence matrix shown in Table 2 for lines $I \times RS$, $I \times LS$, $RS(I \times RS)$, and $LS(I \times LS)$ was reparameterized to yield X as follows:

$$X = \begin{bmatrix} \frac{1}{2} & 0 & \frac{1}{2} \\ 0 & \frac{1}{2} & \frac{1}{2} \\ \frac{3}{4} & 0 & \frac{1}{4} \\ 0 & \frac{3}{4} & \frac{1}{4} \end{bmatrix}$$

The solution vector was then obtained as $\hat{b} = (X'V^{-1}X)^{-1}X'V^{-1}y$, where

$$\hat{b} = \begin{bmatrix} u & + g_{RS} \\ u & + g_{LS} \\ u & + g_I + 2h \end{bmatrix}$$

Given the restrictions used, \hat{b} is not unique, but functions of the form $k'\hat{b}$ can be if they are estimable (Searle, 1971). The function we wished to estimate is $k' = [-1 \ 1 \ 0]$, which estimates the difference between the direct effects of lines LS and RS ($g_{LS} - g_{RS}$) as follows: $g_{LS} - g_{RS} = k'\hat{b}$, with variance $V(k'\hat{b}) = k'(X'V^{-1}X)^{-1}k$.

Number of Mummified Pigs. For analysis of number of mummified pigs during the selection phase, the procedure described by Richardson et al. (1968) was used, with the following model: $Y_{ij} = A_i + G_j + Z_{ij}B + E_{ij}$, where Y_{ij} = mean number of mummified pigs in the j^{th} generation of the i^{th} line, A_i = expected performance in the base generation, G_j = environmental effect common to each line in the j^{th} generation, B = linear regression coefficient for number of mummified pigs on cumulative selection differential (Z_{ij}) for

Table 2. Expectations for the different lines and crosslines in terms of crossbreeding parameters (from Dickerson, 1969)

Genotype	Parameters ^a				
	μ	g_{RS}	g_{LS}	g_I	h
RS	1	1	0	0	0
LS	1	0	1	0	0
I	1	0	0	1	0
I × RS	1	.5	0	.5	1
I × LS	1	0	.5	.5	1
RS(I × RS)	1	.75	0	.25	.5
LS(I × LS)	1	0	.75	.25	.5

^a μ = overall mean; g_{RS} , g_{LS} , g_I = genetic effects of lines RS, LS, and I, respectively; h = heterosis. RS = randomly selected control line; LS = line selected for litter size; I = Large White-Landrace composite line.

litter size in the j^{th} generation of the i^{th} line, and E_{ij} = random error.

Estimates of fixed effects were obtained by weighted least squares, with each line-generation mean weighted by the corresponding number of observations.

Parity Effects. A preliminary least squares analysis was conducted for litter size, including the effects of group (year of birth of the gilt), genotype, parity, group × genotype, group × parity, genotype × parity, and group × genotype × parity. Because none of the interactions was significant ($P > .1$), a reduced model was used in a second analysis, including the same main effects as before, plus the interaction of genotype and parity. A set of nonorthogonal contrasts was used to investigate the nature and magnitude of line differences and heterosis for litter size at different parities.

Results

Ovulation Rate, Uterine Dimensions, and Uterine Capacity. Least squares means for the different line crosses and traits in Exp. 1 (Table 3) consistently

indicated a higher ORC in LS than in RS crosses, but the only clear pattern for uterine dimensions was that I × LS gilts always had the smallest measurements. Least squares means for Exp. 2 (Table 4) indicated some advantage of LS(I × LS) gilts in ORM, even though they had the lowest ORP. Uterine capacity, estimated as twice FFP, was greatest in I × LS gilts, but differences between crosses in FFM were minor.

Correlations between ORC and uterine dimensions in Exp. 1 ranged from .06 to .15 ($P > .1$) and correlations among uterine dimensions ranged from .57 to .82 ($P < .05$). In Exp. 2, correlations were .19 ($P < .1$) between ORP and ORM (range of .09 to .42 within line cross) and .10 ($P > .1$) between ORM and FFP. This low correlation indicates that FFP was nearly independent of ovulation rate, as intended in the UHO model.

Estimates of line direct effects for the different traits are shown in Table 5. Line LS had an advantage over RS of approximately 1.4 eggs in cyclic gilts ($P < .05$) and approximately 1.2 eggs in UHO-mated gilts ($P < .1$) but lower ovulation rate at puberty. Uterine length, weight, volume, and diameter were all smaller in LS than in RS gilts, but the differences were not statistically significant. Uterine capacity, estimated by twice the number of fully formed pigs in one uterine horn, was $.66 \pm 1.28$ pigs higher in LS gilts. A relatively higher number of mummified pigs was observed in RS than in LS gilts, as indicated by line differences in FFM. Nevertheless, line differences in either FFP or FFM did not differ from zero ($P > .1$).

Line differences ($g_{LS} - g_{RS}$) by side of the reproductive tract remaining intact were $1.0 \pm .9$ FFP and $.9 \pm 1.1$ eggs in ORM for the left side and $-.6 \pm .9$ FFP and 1.4 ± 1.1 eggs in ORM for the right side.

Number of Mummified Pigs. The mean number of mummified pigs per litter for lines C, RS, and LS over the selection phase and three generations of evaluation is presented in Figure 1. The cumulative selection differentials after eight generations of selection for litter size were, respectively, 3.6, 2.0, and 17.1 pigs/litter for lines C, RS, and LS (Lamberson et al., 1991). The regression coefficient of number of mum-

Table 3. Least squares means ± SE and number of gilts measured for the different traits and crosses in Experiment 1

Trait ^a	I × RS ^b	I × LS ^b	RS(I × RS)	LS(I × LS)
ORC	14.5 ± .5	15.3 ± .4	14.6 ± .5	15.7 ± .5
UL, cm	312 ± 13	300 ± 11	305 ± 12	314 ± 14
UW, g	626 ± 27	538 ± 23	590 ± 26	595 ± 29
UV, mL	1,169 ± 85	1,009 ± 72	1,203 ± 83	1,260 ± 91
UD, mm	21.8 ± .6	20.5 ± .5	21.9 ± .6	22.0 ± .6
n	24	33	25	21

^aORC = ovulation rate in cyclic gilts; UL = uterine length; UW = uterine weight; UV = uterine volume; UD = uterine diameter.

^bI = Large White-Landrace composite line; RS = randomly selected control line; LS = line selected for litter size.

Table 4. Least squares means \pm SE and number of gilts measured for the different traits and crosses in Experiment 2

Trait ^a	I \times RS ^b	I \times LS ^b	RS(I \times RS)	LS(I \times LS)
ORP	13.3 \pm .5	13.4 \pm .5	13.2 \pm .4	12.4 \pm .5
n	24	24	37	24
ORM	14.8 \pm .6	14.5 \pm .5	14.1 \pm .4	15.3 \pm .5
FFP	4.8 \pm .5	5.7 \pm .4	5.0 \pm .4	4.8 \pm .4
FFM	5.7 \pm .5	5.9 \pm .5	6.0 \pm .4	5.5 \pm .5
n	17	22	31	21

^aORP = ovulation rate at puberty; ORM = ovulation rate at mating in unilateral hysterectomy-ovariectomy gilts; FFP = number of fully formed pigs; FFM = number of fully formed plus mummified pigs.

^bI = Large White-Landrace composite line; RS = randomly selected control line; LS = line selected for litter size.

mified pigs per litter on cumulative selection differential for litter size was $-.017 \pm .009$. Given the differences between lines LS and RS in cumulative selection differentials for litter size, the predicted reduction in number of mummified pigs per litter in LS gilts compared with RS gilts after eight generations of selection is .26. During the three generations of evaluation (random selection) following selection for litter size, LS gilts had on the average .22 fewer mummified pigs per litter than RS gilts.

Parity Effects. In an analysis of variance the interaction between genotype and parity was not significant ($P > .2$), suggesting that litter size increased similarly with parity in all lines and crosses or that there were insufficient data to detect an interaction. In all parities, litter size was higher in LS than in RS and in I \times LS than in I \times RS dams, even though the difference was small in second-parity crossline sows and third-parity pureline sows (Table 6).

Least squares means by line and parity were equated to their expectations (Table 2) to obtain estimates of heterosis and line differences for litter

size (Table 7). The pooled estimates of heterosis were $1.22 \pm .30$ and $.67 \pm .29$ pigs per litter for I \times LS and I \times RS crosses, respectively. Line differences ($g_{LS} - g_{RS}$) estimated from data on pureline dams were approximately .8, 1, and .1 pigs per litter at first, second, and third parity, respectively.

The difference between heterosis in I \times LS and in I \times RS crosses did not interact with parity (Table 8, Contrast 1). Furthermore, the estimated heterosis from I \times LS and I \times RS crosses did not differ significantly from each other (Contrast 2), but average heterosis differed significantly from zero (Contrast 3).

Given the nonsignificance of Contrasts 1 and 2 (Table 8), line differences could be estimated from data on crossline dams, using a common heterosis estimate. Except for parity two, line differences were substantially higher when estimated from crossline

Table 5. Estimated differences between lines LS^a and RS^a ($g_{LS} - g_{RS}$) \pm SE for the different traits

Trait ^b	$g_{LS} - g_{RS}$
ORC	1.44 \pm .73
UL, cm	-.5 \pm 19.7
UW, g	-57 \pm 42
UV, mL	-63 \pm 132
UD, mm	-.8 \pm .9
ORP	-.63 \pm .79
ORM	1.15 \pm .79
FFP	.33 \pm .64
FFM	-.38 \pm .71

^aLS = line selected for litter size; RS = randomly selected control line.

^bORC = ovulation rate in cyclic gilts; UL = uterine length; UW = uterine weight; UV = uterine volume; UD = uterine diameter; ORP = ovulation rate at puberty; ORM = ovulation rate at mating in unilateral hysterectomy-ovariectomy gilts; FFP = number of fully formed pigs; FFM = number of fully formed plus mummified pigs.

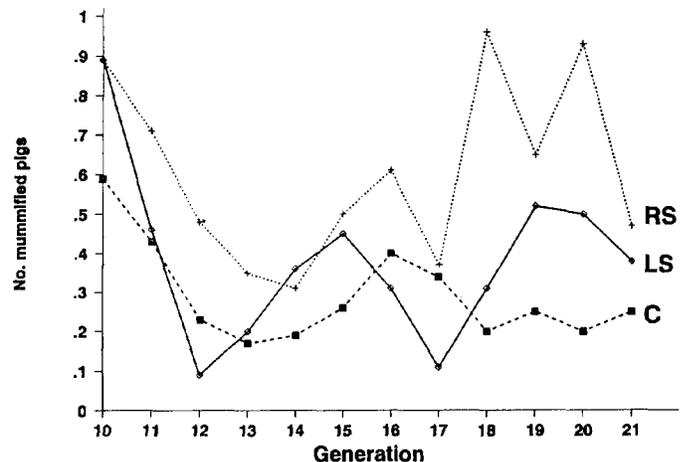


Figure 1. Average number of mummified pigs per litter, by line and generation. RS = relaxed selection following nine generations of selection for high ovulation rate (Generations 0 to 9), LS = selection for litter size in Generations 11 to 18, after two generations of relaxed selection (Generations 9 and 10), and followed by relaxed selection in Generations 18 to 21, and C = control line.

Table 6. Least squares means \pm SE for litter size, by parity and line. Numbers in parentheses are number of litters

Line of gilt or sow ^a	Parity		
	1	2	3
RS	10.04 \pm .24 (116)	10.92 \pm .45 (33)	11.78 \pm .46 (31)
LS	10.87 \pm .25 (111)	11.93 \pm .47 (30)	11.91 \pm .50 (27)
I \times RS	10.62 \pm .32 (67)	12.25 \pm .43 (36)	13.06 \pm .46 (32)
I \times LS	12.30 \pm .33 (62)	12.54 \pm .45 (33)	13.73 \pm .47 (30)
I	10.39 \pm .34 (58)	12.52 \pm .50 (27)	12.19 \pm .54 (23)

^aRS = randomly selected control line; LS = line selected for litter size; I = Large White-Landrace composite line.

than from pureline sows (Table 7). When data from pureline and crossline dams were pooled, the resulting estimates of line differences ($g_{LS}-g_{RS}$) were approximately 2.1, .8, and .7 pigs per litter at first, second, and third parity, respectively. Nevertheless, there was no indication of significance for the interaction between parity and line differences for litter size, estimated either from data on pureline gilts, crossline gilts, or pooled from both (Contrasts 4, 5, and 6, respectively). Estimates of line differences ($g_{LS}-g_{RS}$) for litter size, pooled over parity, and obtained from pureline or crossline gilts were, respectively, $.66 \pm .33$ and $1.76 \pm .67$ pigs per litter (Contrasts 7 and 8). Nevertheless, the two estimates did not differ significantly from each other (Contrast 9), and the estimate for line difference between g_{LS} and g_{RS} , pooled over genotypes and parities, was $1.21 \pm .38$ pigs per litter, which differed significantly from zero (Contrast 10).

Discussion

After nine generations of selection for ovulation rate in the first phase of the experiment, cumulative responses were 3.7 eggs (Cunningham et al., 1979) and .8 pigs per litter (Lamberson et al., 1991), indicating that only approximately 20% of the response in ovulation rate was realized as increased litter size. Geisert et al. (1978) reported that embryonic survival at 30 and 70 d of gestation was, respectively, 5.2 and 10.6 percentage points lower in

the OR than in the C line. These results were interpreted as indicating that either embryonic survival or uterine capacity, or both, were limiting response in litter size, and that direct selection for litter size practiced in the line previously selected for ovulation rate should place most pressure on embryonic survival or on uterine capacity (Johnson and Neal, 1988). After eight generations of selection for litter size in the second phase of the experiment, realized cumulative response was 1.06 pigs per litter when estimated from pureline gilts during the period of selection (Lamberson et al., 1991) or .83 pigs per litter in first-parity gilts when estimated from the evaluation phase (Table 8).

Our results suggest that selection for litter size after selection for ovulation rate resulted in further increases in ovulation rate and possibly some increase in uterine capacity. Even though ovulation rate at puberty declined by approximately .6 eggs after selection for litter size, ovulation rate at the second estrus was approximately 1.4 eggs higher in cyclic gilts of the LS line. A similar trend in ovulation rate was observed in UHO gilts mated at the second to fifth estrus, with an advantage of approximately 1.2 eggs in gilts selected for litter size. Because complete compensation in ovulation rate is expected to occur after UHO (Fenton et al., 1968; Monk and Erb, 1974; Webel and Dziuk, 1974; Knight et al., 1977; Christenson et al., 1987; Huang et al., 1987), the combined results of Exp. 1 and 2 indicate that the average increase in ovulation rate after selection for litter size was 1.3

Table 7. Estimated heterosis and line differences ($g_{LS}-g_{RS}$) for litter size at different parities

Parity	h_{ILS}	h_{IRS}	$g_{LS}-g_{RS}^a$		
			Pure	Cross	All
1	1.66 \pm .39	.40 \pm .38	.83 \pm .34	3.35 \pm .91	2.10 \pm .49
2	.31 \pm .56	.53 \pm .54	1.01 \pm .65	.58 \pm 1.24	.80 \pm .70
3	1.68 \pm .60	1.07 \pm .58	.13 \pm .68	1.35 \pm 1.31	.74 \pm .74
All	1.22 \pm .30	.67 \pm .29	.66 \pm .33	1.76 \pm .67	1.21 \pm .38

^aLine differences estimated from pureline, crosslines, or all dams.

Table 8. Contrasts among least squares means for litter size, hypotheses tested, and tests of significance

Contrasts	Parity												df	H ₀	Estimate ^a	P ^b	P						
	1						2											3					
	LS	RS	LSI	RSI	I		LS	RS	LSI	RSI	I							LS	RS	LSI	RSI	I	
1	-1/2	1/2	1	-1	0	0	1/2	-1/2	-1	1	0	0	0	0	0	0	0	0	2	$h_{LS1} - h_{RS1} = h_{LS2} - h_{RS2}$ $= h_{LS3} - h_{RS3}$	—	1.51	.22
2	-1/2	1/2	1	-1	0	0	0	0	0	0	0	0	1/2	-1/2	-1	1	0	0	1	$h_{LS} - h_{RS} = 0$.55 ± .38	—	.14
3	-1/6	1/6	1/3	-1/3	0	0	-1/6	1/6	1/3	-1/3	0	0	-1/6	1/6	1/3	-1/3	0	0	1	$h = 0$.94 ± .23	—	< .01
4	-1/12	-1/12	1/6	1/6	-1/6	-1/6	-1/12	-1/12	1/6	1/6	-1/6	-1/6	-1/12	-1/12	1/6	1/6	-1/6	-1/6	2	$g_{LS1}^P - g_{RS1}^P = g_{LS2}^P - g_{RS2}^P$ $= g_{LS3}^P - g_{RS3}^P$	—	.53	.59
5	0	0	0	0	0	0	1	-1	0	0	0	0	-1	1	0	0	0	0	2	$g_{LS1}^C - g_{RS1}^C = g_{LS2}^C - g_{RS2}^C$ $= g_{LS3}^C - g_{RS3}^C$	—	1.85	.16
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	$g_{LS1} - g_{RS1} = g_{LS2} - g_{RS2}$ $= g_{LS3} - g_{RS3}$	—	1.77	.17
7	0	0	0	0	0	0	1/2	-1/2	1	-1	0	0	-1/2	1/2	-1	1	0	0	1	$g_{LS}^P - g_{RS}^P = 0$.66 ± .33	—	.05
8	1/3	-1/3	0	0	0	0	1/3	-1/3	0	0	0	0	1/3	-1/3	0	0	0	0	1	$g_{LS}^C - g_{RS}^C = 0$	1.76 ± .67	—	< .01
9	0	0	2/3	-2/3	0	0	0	0	2/3	-2/3	0	0	0	0	2/3	-2/3	0	0	1	$g_{LS}^P - g_{RS}^P = 0$	—	—	.14
10	1/3	-1/3	-2/3	2/3	0	0	1/3	-1/3	-2/3	2/3	0	0	1/3	-1/3	-2/3	2/3	0	0	1	$g_{LS}^C - g_{RS}^C = g_{LS}^P - g_{RS}^P$	-1.10 ± .75	—	< .01
	1/6	-1/6	1/3	-1/3	0	0	1/6	-1/6	1/3	-1/3	0	0	1/6	-1/6	1/3	-1/3	0	0	1	$g_{LS} - g_{RS} = 0$	1.21 ± .38	—	< .01

^aValues of linear contrasts and their SE are shown only for those contrasts with 1 df.
^bF-statistic is shown only for those contrasts with 2 df, and these test the H₀ hypothesis.

eggs. Selection for litter size in mice has consistently resulted in increased ovulation rate (Falconer, 1971; Bakker et al., 1978; Bradford, 1979; Gion et al., 1990), but no reports were found in the literature in which selection for litter size was practiced in dams with naturally occurring high ovulation rates. Bradford (1968) practiced selection for litter size in superovulated mice, but no response in litter size was observed after eight generations of selection.

In our experiment, no significant changes were found in uterine dimensions after selection for litter size. Nevertheless, there was some indication of a reduction in uterine length, weight, volume, and diameter in the line selected for litter size. There was also an indication of an increase in uterine capacity after litter size selection. This suggests that uterine dimensions in cyclic gilts may not be a good indicator of uterine capacity. The fact that the I × LS cross had the smallest uterine dimensions and the largest uterine capacity supports this idea. These results are in disagreement with those reported by Spruill and Eisen (1985), who found that selection for litter size resulted in longer uteri in cyclic and pregnant mice. However, Christenson et al. (1989) found that the correlation between uterine length before puberty and uterine capacity in gilts was only .08. Bazer et al. (1988) reported that uterine dimensions in cyclic and pregnant Meishan gilts, known for their high embryonic survival (Bolet et al., 1986), were smaller than those of Large White gilts at the same physiological stage.

Line differences in uterine capacity can be estimated by twice the number of pigs (fetuses) after UHO (Christenson et al., 1987). The estimated difference between lines LS and RS is then $.66 \pm 1.28$ pigs. Even though this difference was not statistically significant, it is of biological importance. The additional variation introduced by the UHO surgery reduced the power of statistical tests. The CV for number of fetuses after UHO was 38% in our experiment, compared with a CV of approximately 26% for litter size in intact gilts (Hill, 1982). These results indicate that additive genetic variance for uterine capacity does exist in swine, as shown in mice in an experiment in which selection was directly for uterine capacity (Gion et al., 1990).

Selection for litter size took place in a line previously selected for ovulation rate. Little change in ovulation rate was expected in this trait with selection for litter size, because it was anticipated that most pressure would be applied on uterine capacity and embryonic survival. No direct estimates of either ovulation rate or uterine capacity were obtained for each of the LS and RS lines, but it can be speculated that ovulation rate and uterine capacity reached an equilibrium in the LS line, such that changes in litter size would require joint changes in both components (Bennett and Leymaster, 1989). Koenig et al. (1986)

reported that the incidence of immature ova was six percentage points higher in the line selected for ovulation rate than in the C line. To be effective, selection for litter size in this high ovulating line would require an increase in ovulation rate to compensate for the increased ova loss.

Mean ovulation rate in the RS line during the second phase of the selection experiment was approximately 16.5 eggs (Lamberson et al., 1991) and the mean litter size in first-parity gilts during the three generations of evaluation was 10.87 and 10.04 pigs for the LS and RS lines, respectively (Table 7). Using the estimated line differences in ovulation rate and litter size, the model and regression coefficients reported by Bennett and Leymaster (1989) were used to predict line differences in uterine capacity. Under the assumptions of this model, uterine capacity is predicted to be one pig larger in the LS than in the RS line. The difference estimated from the UHO model was approximately .7 pigs (Table 5, $2 \times .33$).

The reduction in number of mummified pigs observed with selection for litter size ($-.26$ after eight generations of selection, $-.22$ in three generations of evaluation) indicates an increase in uterine capacity in late gestation (Wu et al., 1988), and it explains approximately 25% of the increase in number of fully formed pigs in the LS line.

Litter size in swine tends to increase with parity up to the fourth or fifth parity (Kernkamp, 1965; Strang, 1970; Ahlschwede, 1978; Alsing et al., 1980), and this is due to an increase in both ovulation rate and embryonic survival with parity (Wrathall, 1971). Some authors (e.g., Legault, 1983) have suggested that uterine capacity may be more of a limiting factor in first than in later parities, resulting in a genetic correlation between litter size in the first and in later parities that would be less than unity. Therefore, selection practiced in first-parity gilts might be poorly expressed in later parities. Our results indicate that when selection for litter size was practiced in first-parity gilts, the response was at least partially maintained in second- and third-parity sows. Actually, if only results in pureline dams are considered, line differences were increased in the second parity but reduced in the third parity. When information on both pureline and crossline dams is used, the response maintained in second- and third-parity sows is approximately 40% of that observed in first-parity gilts. These results are in disagreement with those published for mice, in which lines selected for litter size do not show the increase in number of pups born with parity that is usually observed in control lines (Wallinga and Bakker, 1978; Eisen and Durrant, 1980). However, gilts selected for litter size using the hyperprolific scheme (Legault, 1983) maintain their advantage over control-line gilts in later parities (Legault, 1985).

There was some indication that heterosis for litter size was somewhat higher in I × LS than in I × RS

crosses, even though the difference was not statistically significant ($P = .14$). Results summarized by Johnson (1981) indicate that heterosis is near zero for ovulation rate but is approximately 10% for embryonic survival (which can be considered as an indicator of uterine capacity). In our experiment, selection for litter size resulted in increases in ovulation rate and, to a lesser extent, in uterine capacity. Thus, it is possible that, in $I \times LS$ gilts, the increase in ovulation rate obtained by selection for litter size could be expressed as increased number of pigs born, because of the increase in uterine capacity resulting from heterosis. For the same reason, when a pooled estimate of heterosis was used for both cross types, the estimated difference between line direct effects was higher when obtained from crossline than from pureline gilts. These results suggest that response to selection can be further enhanced if selection is followed by crossbreeding.

Implications

Selection for litter size in pigs is feasible, and the response obtained in first-parity gilts is maintained in second- and third-parity sows. Commercial producers also should realize high levels of heterosis for litter size in crosses of lines selected for increased litter size. Further work is needed to determine whether more rapid progress could be made from selection for ovulation rate and uterine capacity than from direct selection for litter size.

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