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Responses to 14 Generations of Selection for Components of Litter Size

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Summary and Implications

Eleven generations of selection for increased index of ovulation rate and embryonal survival rate, followed by three generations of selection for litter size, were practiced. Laparotomy was used to count corpora lutea and fetuses at 50 days of gestation. High indexing gilts, approximately 30 percent, were farrowed each generation. All gilts in these litters were mated to boars selected from litters of gilts in the upper 15 percent of the distribution for index. Selection from generation 12 to 14 was for increased number of fully formed pigs. Replacement boars and gilts were selected from the largest 25 percent of the litters. Total response in the selected line compared to the control was approximately 6.7 ova, 3.9 fetuses, 3 fully formed pigs, and 1.4 live pigs (P < .01) at birth. Ovulation rate and number of fetuses had positive genetic correlations with number of stillborn and mummified pigs, which increased with selection for the index. Approximately 77 percent of the increase in fetuses was represented by a pig at birth, and 36 percent of the increase was a live pig. Average pig birth weight declined as litter size increased. Smaller pigs, and the higher rate of inbreeding in the select line, may have contributed to greater fetal losses in late gestation, greater number of stillborn pigs and lower preweaning viability in the select line. Phenotypic variation in litter size and its component traits is high. Heritabilities were between 10 and 25 percent; sufficient genetic variation exists to increase litter size with selection. Response in total born per litter was approximately 15 percent greater than response predicted from direct litter size selection. This is probably not enough to justify implementation of this procedure in industry breeding programs. Because of undesirable genetic relationships between ovulation rate and the number of stillborn and mummified pigs and decreased birth weight with increased litter size, genetic improvement programs should emphasize live born pigs and perhaps weight of liveborn pigs in selection programs.

Introduction

Reproductive efficiency is one of the most important variables in economic efficiency of swine enterprises. Litter size, the most important reproductive trait, is weighted heavily in development of maternal lines.

Economic value of litter size relative to other traits will likely increase in the future due to decreasing emphasis on leanness as a result of successful genetic selection for decreased backfat. Swine breeders must have reliable information on genetic parameters for litter size and its components to develop optimum breeding strategies. Correlated responses expected in pig weights, survival and litter weaning weights from continued selection for increased litter size and its components must be known.

In 1981, an experiment began to select for increased index of ovulation rate and embryonal survival at 50 days of gestation. After 10 generations, index selection was discontinued and selection for increased litter size was practiced. This report presents results of 14 generations of selection. Responses in litter size and its component traits litter birth weights, and litter weaning traits are presented.

Methods

The population was a composite of the Large White and Landrace breeds. Boars and gilts of each breed were reciprocally crossed in 1979 to make a population with 50 percent of genes from each breed. Random mating was practiced for two generations to reduce linkage relationships created in the F_1 cross. Then select (Line I) and control (Line C) lines were formed by randomly assigning littermates to lines. Lines were maintained as closed populations with generation interval of one year.

Line I was selected 10 generations for increased index followed by one generation of random selection (generation 11) and three generations of selection for increased number of fully formed pigs at birth (generations 12-14). The index included number of corpora lutea as a measure of ovulation rate (OR) and the ratio of fetuses (F) to OR (F/OR) at 50 days of gestation. The index was constructed to make maximum expected change in litter size. The index used from generations 0 to 5 was I_1 = 10.6 x OR + 72.6 x F/OR. Because of the increase in OR during the first five generations, the index was changed to place more emphasis on embryonal survival rate. The index used from generations 6 to 10 was I_2 = 9.9 x OR + 148.6 x F/OR.

Laparotomy was performed at 50 days of gestation in all pregnant Line I gilts (n = 1,618) and a random sample of one-half of Line C gilts(n = 269). Uteri and ovaries were exposed and number of corpora lutea and fetuses were counted. The index was calculated and the highest ranking Line I gilts (45 to 55 per generation) were selected. The remainder were culled before parturition. The number of litters during generations 0 to 10 was 43 to 53 in Line I, and 36 to 44 in Line C.

Two sons of each of the 15 Line I dams with greatest index values were selected. One boar from each litter and two from the five highest indexing dams were used as breeders; the remaining boars were alternates and used only if primary boars died or failed to breed.

Approximately 30 boars and 55 gilts in Line C were selected. Of the 55 gilts, one gilt was selected randomly from every litter and one additional gilt was selected from randomly chosen litters. Two boars were selected from each paternal half-sib family (15 families per generation); one was designated as a breeder, the other an alternate.

Index selection was terminated after 10 generations, but generation 10 Line I gilts that farrowed were a selected sample. A random sample of their progeny, the generation 11 gilts, was selected, mated and farrowed to estimate selection response in litter size in unselected gilts in which laparotomy had not been performed. However, because their sires were selected on the index, the total index selection applied was calculated through generation 11. There were 60 Line I litters in generation 11.

Selection during generations 12-14 in Line I was based on number of fully formed pigs in the litter in which pigs were born. Two boars, a primary breeder and an alternate, were selected from each of the 15 largest litters. All gilts from the largest litters were selected until the desired number was attained. Number of litters in Line I was increased at generation 13. There were 47, 79 and 97 Line I litters by generations 12, 13, and 14 dams, respectively. These dams were selected from 15, 22 and 28 litters, respectively.

Management of pigs

Pigs were transferred among litters both within and across lines within two days of birth. The objective was to give each sow between eight and 11 pigs to nurse, which was accomplished for 73 percent of litters; 12 percent of the sows had fewer than eight pigs after transfer, 15 percent had more than 11.

Pigs were weaned at 28 days of age through generation 12 and approximately 12 days of age for generations 13 and 14. Pigs were moved to nursery rooms at weaning where they stayed to approximately 56 days of age when selections were made. Selected pigs were moved to naturally ventilated buildings with 10 pigs per pen. Boars and gilts were in separate buildings.

Estrus detection in gilts began on the day the oldest pig in each pen reached 130 days of age. After expressing their pubertal estrus and the subsequent estrus, they were moved to a breeding building. The objective was to mate gilts at their third or later estrus. Gilts averaged approximately 250 days of age when mated. Some gilts were mated at their second estrus and, in a few cases, at their pubertal estrus. A total of 2,510 gilts were mated and became pregnant during the experiment, 33 were mated at their pubertal estrus and 58 at their second estrus. Gilts were mated each day they were in estrus. They were in stalls during gestation.

Standard corn- or milo-soybean meal diets, balanced to meet nutrient requirements for age and production status of pig, were used. Pigs were provided ad libitum access to feed until they were approximately 180 days of age (gilts) or 160 days of age (boars), after which they were given approximately 5 lb feed per day until mating. Gilts were given 4.6 lb of feed per day during the gestation period, except during the last 14 days when the amount was increased to 5.5 lb. Sows had ad libitum access to feed during lactation.

Table 1. Difference in realized cumulative selection differentials between Lines I and C [a]

Gen	I	OR	F	ES
1	12.7	1.1	1.13	0.01
2	33.7	3.15	2.47	0.00
3	50.8	4.97	3.37	-0.02
4	71.4	6.67	5.20	0.01
5	95.9	9.04	6.69	0.00
6	115.5	10.52	7.72	0.01
7	130.0	12.29	9.36	0.00
8	150.5	14.05	11.07	0.02
9	182.3	17.15	12.43	0.02
10	217.1	21.75	13.44	0.00
11	257.9	25.51	14.73	-0.02

[a]Gen = generation, I = Index, OR = number of corpora lutea, F = number of fetuses, and ES = embryonal survival rate.

Traits measured

The traits measured at 50 days of gestation were number of corpora lutea and number of fetuses. Embryonal survival and index were calculated from these values. Number of fully formed pigs, number of live pigs, number of stillborn pigs, number of mummified pigs and weight of all fully formed pigs were recorded at birth. Nurse dam was recorded for all pigs transferred to another litter. Each pig was weighed when weaned.

Traits included in the analyses were OR, F, F/OR, total born per litter (TB), number born alive per litter (NBA), number of stillborn pigs (SB), number of mummified pigs (MUM), total weight of fully formed pigs at birth (LBW), number of pigs weaned (NW) and total weight of pigs weaned by each sow (LWW). All records were considered a trait of the gilt.

Data analyses

Appropriate statistical procedures were used to estimate genetic parameters and responses in each trait. The analyses performed produced estimated breeding values for each animal, using all pedigree information. Mean breeding values were calculated for each line and plotted to illustrate selection responses. Responses in both Line I and C were estimated with regressions of breeding values on generation and by contrasts among breeding values for specific generations.

Results

Cumulative selection differentials for Index and for component traits are in Table 1. Relative to Line C, total selection applied in Line I accumu-

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Table 2. Means for traits[a] at 50 days gestation[b]

	N		OR		F		ES	
Gen	I	C	I	C	I	C	I	C
0	128		13.98		10.81		0.79	
1	127	23	14.31	13.04	11.15	9.57	0.79	0.74
2	132	24	15.11	14.32	10.85	10.96	0.73	0.78
3	148	23	15.76	14.35	11.56	10.48	0.74	0.74
4	150	21	15.95	13.24	11.49	9.52	0.73	0.73
5	127	43	17.02	14.02	11.89	10.91	0.71	0.78
6	164	22	17.98	13.09	12.70	9.91	0.73	0.84
7	169	24	18.87	14.46	13.03	11.29	0.73	0.79
8	155	22	21.23	14.41	13.08	9.73	0.67	0.69
9	156	19	20.70	13.00	12.99	10.00	0.67	0.79
10	162	48	20.46	13.77	13.64	10.33	0.72	0.76

[a] N = number of gilts, OR = number of corpora lutea, F = number of fetuses, ES = embryonal survival rate, I = Index select line, and C = control line.
[b] Laparotomy not done on base generation Line C gilts.

lated to 257.9 Index points, 25.5 ovulations, 14.7 fetuses at 50 days gestation, and -.02 embryonal survival rate.

Number of observations and phenotypic means for traits at 50 days of gestation are in Table 2. The difference between Lines I and C at generation 10 was 6.7 OR, 3.3 F and -.04 ES. Mean estimated breeding values are plotted in Figure 1. Estimated genetic responses in Line I relative to Line C averaged .67 OR ($P<.01$), .35 F ($P<.01$) and -.008 ES ($P<.05$) per generation. Expected responses based on base generation parameter estimates were an increase in ovulation rate and a slight decline in embryonal survival rate, which was expected to maximize the response in litter size. The observed results at 50 days gestation agreed well with expected responses.

Number of litters and phenotypic means for birth and weaning traits are in Table 3. The estimated genetic difference between Line I and C at generation 10 was 3.1 pigs. However, the difference in number born live was 1.6 pigs. The differences in generation 11, which represented total index selection applied and a random sample of gilts selected to farrow, were 1.3 fully formed pigs and .4 pigs born live. Litter birth weight tended to be greater for Line I; however, the difference between lines did not increase significantly with generations.

Number of stillborn and mummified pigs per litter were greater in Line I than Line C each generation during index selection. The differences were 1.51 stillborn and .83 mummified pigs at generation 10 and .93 stillborn and .53 mummified pigs at generation 11. Part of the increase in number of mummified pigs was due to the laparotomy procedure. The effect of laparotomy was estimated to be a reduction of .97 $\pm$ .26 fully formed pigs, .81 $\pm$ .26 pigs born live, and increase of .44 $\pm$ .12 mummified pigs. The difference in this effect on fully formed and mummified pigs is due to fetal deaths occurring after 50 days gestation and not detected as a mummified pig at birth. The laparotomy procedure did not significantly affect number of stillborn pigs. There was a reduction in number of mummified pigs in both lines during generations 11 to 14 when laparotomy was not practiced.

Genetic response in Line I relative to Line C over all generations averaged an increase of .21 $\pm$ .04 fully formed pig, .10 $\pm$ .04 live pig, .12 $\pm$ .03 stillborn pig, .03 $\pm$ .02 mummified pig and .2 $\pm$ .13 lb litter birth weight per generation (Figures 2 and 3). Responses were significant except those in mummified pigs and litter birth weight. Multiplying these values by 14 generations of selection produces predicted genetic responses of 2.95 fully formed and 1.4 live pigs. Mean differences during generations 12 to 14 were somewhat greater than these values, averaging 4.1 total and 2.1 live pigs per litter.

Mean number of pigs weaned and litter weaning weight are in Table 4. Means are adjusted for number after

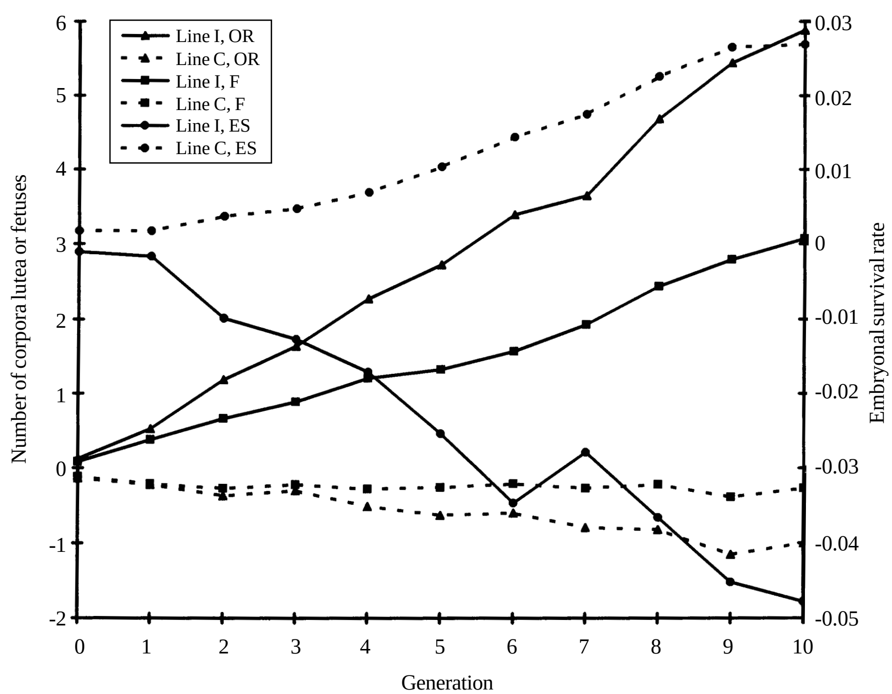

Figure 1. Mean estimated breeding value plotted against generation (genetic trend) for ovulation rate (OR), number of fetuses at 50 days gestation (F), and embryonal survival to 50 days gestation (ES).

Table 3. **Mean number of fully formed (FF), live (NBA), stillborn (SB), and mummified (MUM) pigs, and weight of FF pigs at birth (LBW)[a]**

	No litters		FF		NBA		SB		MUM		LBW, lb	
Gen	I	C	I	C	I	C	I	C	I	C	I	C
-1	42	41	10.3	9.5	9.9	9.3	0.43	0.22	0.17	0.05	29.7	28.6
0	43	41	11.0	10.4	10.5	10.2	0.49	0.20	0.56	0.24	30.8	28.8
1	43	40	10.8	9.1	10.3	8.8	0.56	0.25	0.95	0.38	20.4	24.2
2	44	42	10.5	9.3	9.7	8.9	0.75	0.41	1.34	0.67	27.1	25.1
3	44	42	10.6	8.3	9.3	8.0	1.23	0.34	1.86	1.17	26.2	22.4
4	44	43	10.7	8.9	9.0	8.6	1.75	0.30	1.20	0.61	27.5	24.6
5	48	43	11.6	9.2	9.8	8.2	1.79	1.00	1.56	1.21	27.5	24.4
6	44	44	11.7	9.8	10.1	9.1	1.57	0.70	2.57	0.31	29.5	29.3
7	45	41	11.6	10.0	10.4	9.2	1.20	0.78	1.76	0.63	26.2	27.5
8	51	42	11.2	8.1	9.2	7.6	2.04	0.53	1.65	0.50	25.1	21.6
9	47	36	11.8	9.3	10.2	8.6	1.62	0.76	1.55	0.21	24.9	25.1
10	53	39	12.6	9.5	10.7	9.2	1.87	0.36	1.19	0.36	26.6	24.0
11	60	47	11.2	9.4	9.6	9.2	1.65	0.72	0.70	0.17	26.4	25.1
12	47	41	13.8	9.8	11.5	9.0	2.30	0.80	0.60	0.46	31.5	25.1
13	79	47	13.3	8.8	10.4	8.5	2.90	0.30	0.49	0.17	30.1	23.3
14	97	43	13.4	9.7	11.4	9.3	2.05	0.37	0.47	0.30	29.7	24.6

[a]Gen = generation, I = index select line, C = control line.

crossfostering and weaning age. Records for sows whose pigs were all fostered to other sows were not included. Sows given pigs to nurse and all pigs subsequently died were given a value of zero for both traits. Another line farrowed contemporary to these lines and fostering was practiced across all three lines. Thus, number nursed was less than number of live pigs for Line I. There was a tendency for Line I sows to wean fewer pigs with less weight at weaning than Line C sows. Average response in Line I relative to Line C was -.05 ± .02 ($P < .05$) pigs weaned and -.4 ± .42 lb litter weight per generation (Figure 4).

Estimates of genetic parameters are in Table 5. Heritabilities ranged from .08 for number weaned to .32 for litter birth weight. Heritabilities of number of fetuses, number of fully formed pigs, number of live pigs and number of stillborn pigs were from .16 to .18. Heritability of number of mummified pigs was .12. All values are somewhat greater than most values found in the literature, which for these traits are mostly in the range of .05 to .15.

Ovulation rate was negatively correlated with embryonal survival but positively correlated with number of fetuses, number of fully formed pigs, number of stillborn pigs and number of mummified pigs. It was not correlated with number of live pigs, but was negatively correlated with number weaned. Embryonal survival was positively correlated with number born but was not correlated with other traits. Number of fetuses was positively correlated with total born and live pigs at birth. Number of stillborn pigs also was positively correlated with number of fetuses.

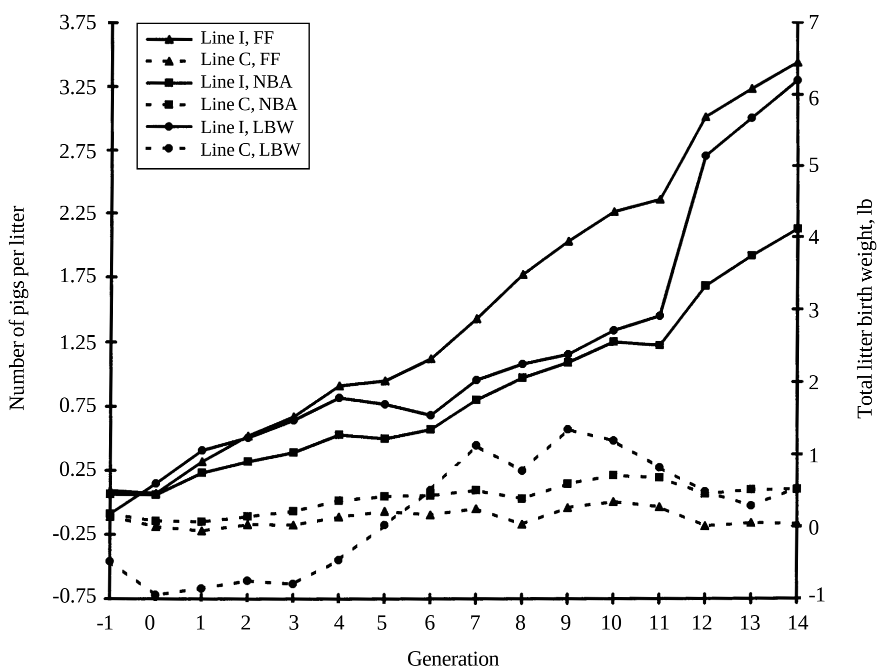

Figure 2. Mean estimated breeding value plotted against generation (genetic trend) for number of fully formed pigs (FF), number of live pigs (NBA), and weight of fully formed pigs (LBW) at birth.

Discussion

The selection index was designed to maximize litter size response. This result probably was achieved for number of fetuses at 50 days gestation, but response in litter size at birth was less. The response in number of fetuses was .35 per generation, approximately 30

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Table 4. Mean number weaned per litter and total weight of litter weaned, adjusted for number after crossfostering and weaning age[a]

	Number weaned per litter		Litter weaning weight, lb	
Gen	Line I	Line C	Line I	Line C
-1	8.2	8.4	124.7	132.0
0	9.4	9.2	132.0	128.5
1	8.1	7.6	111.1	108.5
2	8.2	8.3	117.7	119.5
3	7.8	8.4	115.7	124.3
4	8.2	8.2	116.2	114.8
5	8.3	8.3	119.7	114.4
6	8.6	8.9	115.5	121.0
7	8.4	9.0	108.5	119.9
8	7.9	8.6	111.1	119.7
9	8.1	8.5	103.6	113.3
10	8.5	8.9	105.2	115.7
11	8.1	8.3	111.1	107.1
12	8.3	9.0	51.3	57.2
13	8.3	9.2	55.4	60.5
14	8.6	9.6	58.1	66.0

[a]Gen = generation, Line I = index select line, Line C = control line.

percent greater than expected response for selection directly on number of fetuses. However, the response in number born per litter was .21 pig per generation, approximately 15 percent greater than response expected from direct selection for litter size, but only 60 percent of the observed response in number of fetuses.

When the experiment was designed, we believed most embryonal/fetal loss had occurred by 50 days gestation and that number of fetuses and litter size were highly correlated. Since then, researchers at the US Meat Animal Research Center reported significant fetal loss occurs late in gestation. This experiment verifies those results. Increased number of mummified pigs and losses of fetuses after 50 days gestation occurred in Line I. The losses were greater in sows carrying larger numbers of fetuses. Genetic improvement in uterine capacity after 50 days of gestation did not keep pace with the increase in number of fetuses and late gestation losses increased.

All expressions of litter size, including number of stillborn and mummified pigs, had greater heritabilities than most values in the literature. Greater genetic variation for these traits in this population may be due to the selection response in ovulation rate. As ovulation rate increased, uterine capacity became the limiting variable in litter size. Measures of litter size are, then, measures of effects of uterine capacity on fetal survival rate, especially those in late gestation. Selecting on component traits of litter size probably would have been more effective if ovulation rate and a measure of uterine capacity to term were used.

Two other important findings in this study are the correlated responses of increased number of stillborn pigs and decreased number weaned in Line I. Increased incidence of stillborn pigs seems partly related to birth weight. Averaged over generations, birth weight of live pigs averaged 2.46 lb in Line I and 2.73 lb in Line C. Average birth weight of stillborn pigs was less than weight of live pigs in both Line I and C (.51 and .42 lb, respectively). This difference between live and stillborn

Table 5. Heritabilities and genetic correlations

		Genetic correlation		
Trait	Heritability	OR	F	ES
OR	0.24			
F	0.18	0.44		
ES	0.14	-0.86	0.47	0.14
FF	0.16	0.24	0.85	0.36
NBA	0.17	-0.02	0.61	0.36
SB	0.17	0.34	0.67	-0.01
MUM	0.12	0.27	0.17	0.00
LBW	0.32	-0.10	0.47	0.24
NW	0.08	-0.37	-0.18	0.07
LWW	0.25	-0.18	0.12	0.16

[a]OR = number of corpora lutea, F = number of fetuses, ES = embryonal survival, FF = total number of pigs born per litter, NBA = number born alive, SB = number of stillborn pigs, MUM = number of mummified pigs, LBW = litter birth weight, NW = number weaned, and LWW = litter weaning weight.

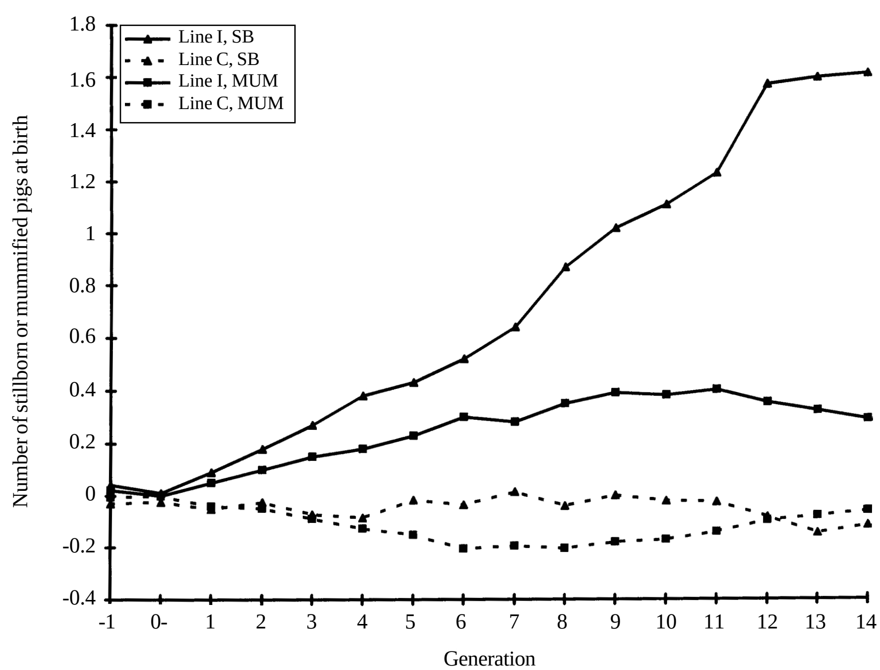

Figure 3. Mean estimated breeding value plotted against generation (genetic trend) for number of stillborn (SB) and mummified pigs (MUM) per litter.

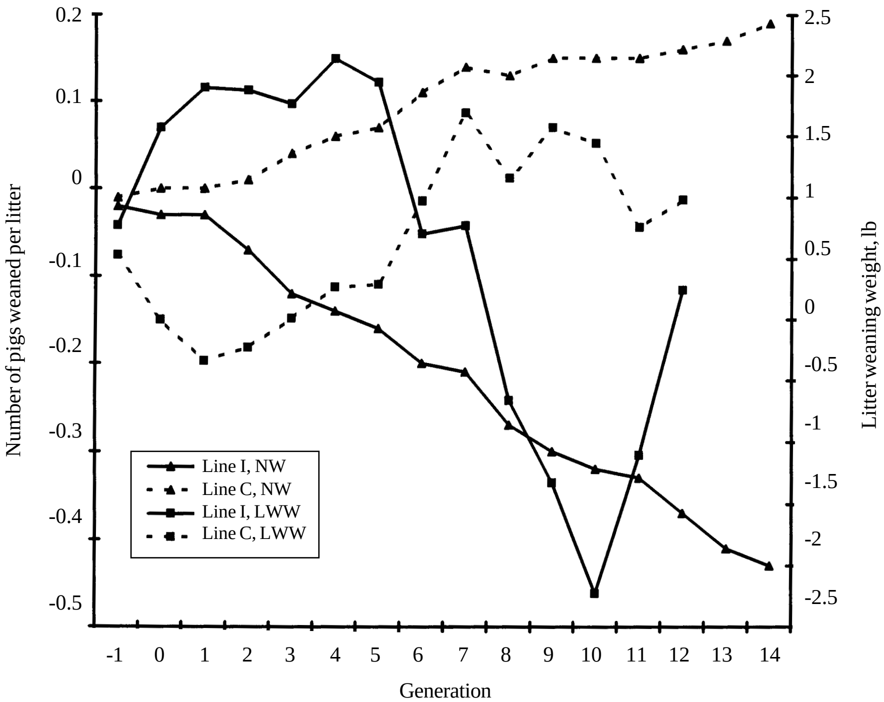

Figure 4. Mean estimated breeding value plotted against generation (genetic trend) for number of pigs weaned (NW) and 28-day litter weaning weight (LWW).

pigs remained consistent throughout the experiment. Average birth weight decreased in Line I with selection for increased litter size. Therefore, there were more small pigs and more of them were stillborn. Other factors, such as length of parturition, which may be longer in large litters, also may be involved in the increase in stillborn pigs.

Decreased weight of live pigs might have contributed to greater preweaning mortality in Line I. Although crossfostering was practiced, Line I sows frequently nursed only Line I pigs. If birthweight was related to viability, more deaths of Line I pigs were expected. Survival rate from birth to weaning was analyzed, including the genetic effect of the pig and of its nurse dam. Direct heritability, that due to genes of the pig, was 3 percent, whereas maternal heritability, that due to genes of the nurse dam, was 7 percent. The trend in breeding values was negative for both components in Line I. The combination of decreased genetic trend in both direct and maternal effects on pig survival caused the significant negative trend in number weaned. Selection did not significantly affect maternal effects on milk production as measured by litter weaning weight.

Inbreeding increased in both lines during the experiment, but it increased more in Line I. Mean inbreeding in generation 14 was .18 (range from .15 to .26) in Line I and .12 (range from .09 to .17) in Line C. Increased inbreeding of both dam and pig are known to decrease pig viability. Therefore, the decrease in pig survival to weaning and decrease in number weaned in Line I were likely related to both decreased birth weight and to increased inbreeding.

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