1-1-2001

Two-stage Selection for Ovulation Rate and Litter Size in Swine — An Effective Procedure to Increase Reproductive Rate

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Summary and Implications

Litter size continues to be an important economic variable in pig production. Two determinants of litter size are ovulation rate and uterine capacity, where uterine capacity is defined as the maximum number of pigs a female can carry to parturition. When the number of fertilized ova exceeds uterine capacity embryo/fetal losses during gestation reduce litter size to that sow's uterine capacity. This experiment tested whether litter size can be increased by direct selection for ovulation rate and uterine capacity. It was accomplished by selecting for ovulation rate (OR) and number of fully formed pigs at birth (FF) in two stages. All gilts from 50% of the largest litters were selected in Stage 1, and then 50% of these gilts were selected on OR in Stage 2. Litter size at birth in gilts with high ovulation rate was considered a measure of their uterine capacity. Selected gilts were mated to boars selected from the upper one third of the litters for FF. Selection in each of two lines for eight generations was practiced. One of the lines, designated IOL, was started from a line previously selected for increased ovulation rate and embryonic survival, and thus began with a base of high litter size. The other line, designated COL, began from an unselected population. Responses in these lines were compared to those in a randomly selected control line (Line C). The genetic increases per generation for OR and FF were .27$\pm$.07 ova/generation (P<.01) and .35$\pm$.06 pigs/generation (P<.01) in line IOL and .30$\pm$.06 ova/generation (P<.01) and .29$\pm$.05 pigs/generation (P<.01) in line COL. In previous experiments, only 25 to 50% of the increase in OR was realized as a pig at birth. In this experiment OR and FF increased equally, indicating that increased litter size resulted in approximately equal increases in both ovulation rate and uterine capacity. Furthermore, the responses were similar in both lines indicating that the selection procedure will work effectively in populations with varying base levels of ovulation rate, uterine capacity and litter size. The selection procedure is still not practical in most breeding programs because the surgical procedure of laparotomy or laparoscopy is used for accurate measurement of OR. However, if a noninvasive procedure to measure OR is developed, this procedure can be effectively applied in industry breeding programs. Other changes that occurred as a result of this selection were decreased age at puberty, increased number of pigs born alive, and increased number of stillborn and mummified pigs. Two-stage selection for FF and OR is an effective procedure to improve litter size in swine.

Introduction

Ways to enhance selection response in litter size is a goal of pig breeders because litter size is an important economic variable in pig production. In females with high ovulation rate, litter size at birth is expected to closely represent uterine capacity. The hypothesis tested in this experiment was that selection with emphasis on ovulation rate (OR) and uterine capacity would cause litter size to increase. The objective was to quantify direct and correlated responses in ovulation rate, litter size and other production traits to two-stage selection for these traits.

Animals and Selection Procedure

Three genetic lines were used. Selection lines IOL and COL were derived from the Index and Control lines, respectively, developed at the University of Nebraska. The population is a composite developed from a Large White-Landrace base. Line IOL originated from the Index line that had previously been selected eight generations for increased ovulation rate and embryonic survival. Line COL was derived from the randomly selected

Table 1. Number of observations (n) and unadjusted phenotypic means for ovulation rate (ova) and number of fully formed pigs by line-generation

	Line IOL		Line COL		Line C	
Generation	n	Mean	n	Mean	n	Mean
			Ovulation rate			
1	57	17.1	66	12.7	66	12.7
2[a]	101	17.3	92	13.0	—	—
3[a]	84	17.4	96	13.3	—	—
4[b]	—	—	—	—	—	—
5	83	17.0	92	13.7	35	12.5
6	96	18.5	88	14.2	52	13.0
7	87	18.4	97	14.7	41	12.3
8	90	19.0	99	15.1	51	12.9
			Number of fully formed pigs			
0[c]	42	13.4(11.3) [c]	36	9.8(8.1)[c]	36	9.8(8.1)[c]
1[d]	44	11.1	38	10.2	41	9.4
2	52	11.8	56	10.3	36	9.0
3	43	12.2	45	9.8	36	9.3
4	43	11.8	42	10.8	45	8.8
5	41	12.7	43	10.4	39	8.5
6	48	13.4	44	11.5	35	8.9
7	43	13.4	45	11.8	37	9.6
8	42	12.5	42	10.3	35	7.4

[a]Ovulation rate was not measured in Generations 2 and 3 in line C.
[b]Ovulation rate was not measured in Generation 4 gilts.
[c]Mean number of fully formed pigs in 2nd parity sows. Means for these same sows at first parity are in parenthesis.
[d]Beginning in Generation 1 number of fully formed pigs was recorded in gilts.

control line (line C). Line IOL started from a base with greater ovulation rate and litter size than Line COL. Line C was continued with random selection to serve as a control for both selection lines.

Lines IOL and COL underwent eight generations of two-stage selection. In Stage 1 all gilts born in 50% of the largest litters were selected. Laparotomy was performed on these gilts ten days after their second estrus to measure OR by counting number of corpora lutea. Approximately 50% of these gilts were selected on OR in Stage 2. Boars in each line were selected from the highest ranking 15 litters for number of fully formed pigs (FF). Although we did not know each gilt's uterine capacity, it was believed that the number of fertilized ova in gilts selected on OR exceeded their uterine capacity. Then during gestation, embryo/fetal losses due to insufficient uterine capacity reduced the number of fetuses for that sow. Thus, litter size at birth was considered a measure of uterine capacity in the gilts selected on OR. In line C at least one gilt per litter and one boar per half-sib family were randomly selected. Each line had approximately 40 litters per generation.

Traits Measured and Analyzed

Number of corpora lutea (OR) present during the second estrous cycle in gilts of lines IOL and COL was measured in all generations except the third one. In line C gilts, OR was recorded only in the first and in the last four generations. Prenatal loss (PL) was calculated as the difference between OR and FF. Number of pigs born alive (BA), number of stillborn pigs (SB), number of mummified pigs (M), and individual birth weight (BW) and litter birth weight (LBW) were recorded at birth. Number of pigs weaned (NW), individual weaning weight (IWW), and litter weaning weight (LWW) were recorded at weaning. Age at puberty (AP) was recorded when the gilt first stood immobile to back pressure in the presence of a boar. Weight of gilts was measured on average at 125 d of age (W1). Weight of boars and gilts was recorded approximately at 178 d of age (W2). Backfat was recorded when average weight of pigs in the pen was approximately 209 lb.

Data Analysis

Genetic parameters and direct and correlated responses were estimated with an animal model that calculated the estimated breeding values for each pig. Depending on the trait, models included the fixed effects of generation and sex, and the random additive direct and maternal genetic effects. Direct and correlated responses were estimated with regressions of estimated breeding values on generation number to estimate responses per generation.

Results and Discussion

Generation means

Mean ovulation rate and number of fully formed pigs per litter are shown by line and generation in Table 1, and means for number of live, stillborn and mummified pigs are in Table 2. Development of these lines from the Index selection lines began with litters from second parity sows. Thus, litter size data for Generation 0 females are for these second parity sows. Data for these same females as first parity sows are in parentheses. All litter size data for Generations 1 through 8 are for first parity sows. Ovulation rate and number of fully formed pigs increased steadily in both lines IOL and COL, but remained relatively unchanged in line C. Number of live pigs per litter increased in the selection lines, but both number of stillborn and mummified pigs per litter also increased.

Genetic trends

Estimated genetic trends in ovulation rate and litter size are illustrated

(Continued on next page)

in Figure 1. Genetic responses (Table 3) for number of pigs per litter were substantial in both line IOL (.35±.06 pigs/generation, P<.01) and line COL (.29±.05 pigs/generation, P<.01). Genetic responses for ovulation rate were .27±.07 ova/generation (P<.01) in line IOL and .30±.06 ova/generation (P<.01) in line COL.

In line COL, number of pigs per litter increased 97% as rapidly as ovulation rate. In line IOL, litter size increased 130% compared with ovulation rate, although this greater rate of response in line IOL was not significantly more than that in line COL. The control line from which line COL was derived had no antecedents of selection, neither for component traits nor directly for litter size. Line IOL already had increased ovulation rate (4.2 ova) and litter size (2.0 fully formed pigs) at Generation 0 of two stage selection due to previous selection. Responses for ovulation rate, number of fully formed pigs, and number born alive were comparable in both selection lines (Figure 1). Thus, rate of change in ovulation rate and uterine capacity did not depend on mean genetic level of the line. Similar responses can be expected in other genetic lines.

The estimated total genetic responses at Generation 8 in ovulation rate in line COL relative to line C were 2.32±.74 ova and 2.16±.57 fully formed pigs at birth. Responses in line IOL relative to line C were 2.08±.79 ova and 2.64±.62 fully formed pigs. Responses at Generation 8 in number of live pigs per litter were 1.84±.57 pigs in line COL and1.60±.62 pigs in line IOL. These comparisons suggest that at Generation 0, uterine capacity was more limiting in line IOL than in line COL because the number of fully formed pigs increased more rapidly than ovulation rate. If that was true, selection for fully formed pigs in line IOL should have resulted in a greater increase in uterine capacity than selection for number of fully formed pigs in line COL. Workers at USDA MARC have clearly shown that increased litter size will occur from changes in the most limit-

Table 2. Number of observations (n) and unadjusted phenotypic means for number of pigs born alive, stillborn, and mummified by line-generation.

Generation	Line IOL n	Line IOL Mean	Line COL n	Line COL Mean	Line C n	Line C Mean
		Number of pigs born alive				
0	42	11.7(9.2)[a]	36	9.1(7.6)[a]	36	9.1(7.6)[a]
1	44	9.6	38	9.7	41	9.0
2	52	10.8	56	9.7	36	8.4
3	43	10.2	45	9.1	36	8.9
4	43	9.7	42	9.8	45	8.1
5	41	11.0	43	9.6	39	8.1
6	48	9.5	44	10.6	35	8.6
7	43	11.1	45	10.8	37	9.0
8	42	10.6	42	9.7	35	6.6
		Number of stillborn pigs				
0	42	1.7(2.0)[a]	36	0.7(0.5)[a]	36	0.7(0.5)[a]
1	44	1.4	38	0.5	41	0.3
2	52	1.0	56	0.6	36	0.6
3	43	2.0	45	0.7	36	0.4
4	43	2.1	42	0.9	45	0.7
5	41	1.7	43	0.8	39	0.4
6	48	3.9	44	1.0	35	0.6
7	43	2.3	45	1.1	37	0.6
8	42	1.8	42	0.6	35	0.6
		Number of mummified pigs				
0	42	0.3(1.7)[a]	36	0.2(.5)[a]	36	0.2(0.5)[a]
1	44	0.3	38	0.2	41	0.2
2	52	0.4	56	0.3	36	0.2
3	43	0.5	45	0.4	36	0.1
4	43	0.3	42	0.5	45	0.2
5	41	0.5	43	0.6	39	0.2
6	48	0.6	44	0.5	35	0.2
7	43	0.5	45	0.5	37	0.2
8	42	1.2	42	1.2	35	1.0

[a]Generation means are for 2nd parity sows. Means for these same sows at their first parity are in parenthesis.

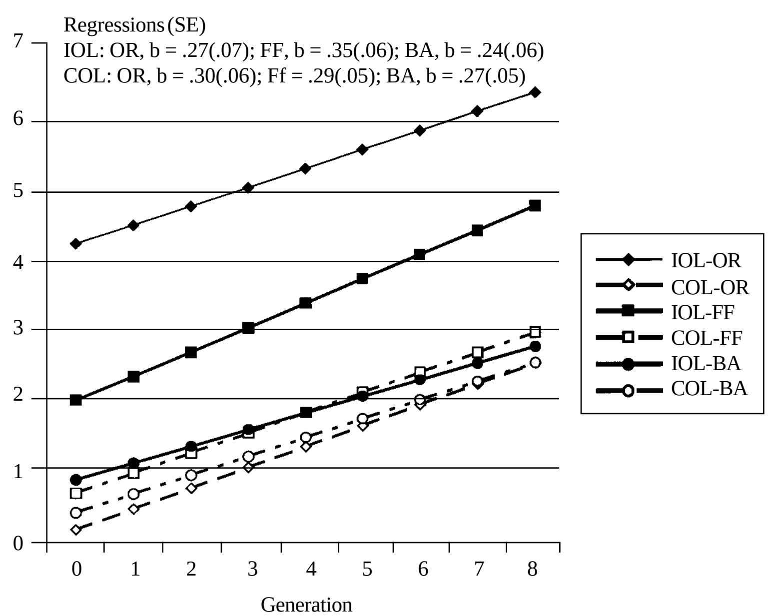

Figure 1. Genetic changes in lines IOL (solid lines) and COL(dashed lines) relative to line C for ovulation rate (OR) and number of fully formed (FF) and live (BA) pigs per litter.

Table 3. Coefficients (b) and standard errors (SE) of regressions of mean estimated breeding value on generation number by trait and line

	Line IOL		Line COL		Line C	
Trait[a]	b	SE	b	SE	b	SE
OR	0.27**	0.07	0.30**	0.06	0.01	0.07
FF	0.35**	0.06	0.29**	0.05	0.02	0.05
BA	0.24**	0.06	0.27**	0.05	0.04	0.05
M	0.04*	0.01	0.03*	0.01	0.00	0.01
SB	0.10**	0.03	0.03	0.02	0.01	0.02
AP	-2.37*	0.70	-2.03*	0.67	-0.00	0.72
BF, in	0.004	0.003	0.12**	0.003	-0.002	0.003
BW, lb	0.024**	0.007	0.013†	0.004	-0.002	0.004
LBW, lb	0.80**	0.15	0.42*	0.13	-0.07	0.13
LWW, lb	0.02	0.33	-0.09	0.31	0.13	0.29
NW	0.07	0.04	0.15**	0.03	-0.01	0.03
PL	0.15*	0.05	0.18**	0.05	0.00	0.05
W1, lb	1.19*	0.44	-0.26	0.42	-0.18	0.40
W2, lb	2.47**	0.53	-0.29	0.51	-0.40	0.53
IWW, lb	0.07†	0.02	-0.00	0.02	0.00	0.02

[a]OR=ovulation rate, FF=number of fully formed pigs, BA=number of pigs born alive, M=number of mummified pigs, SB=number of stillborn pigs, AP=age at puberty, BF=backfat thickness at 209.5 lb., BW=pig birth weight, LBW=litter birth weight, LWW=litter weaning weight adjusted for age weaned and to a standard number nursed, NW=number weaned per litter adjusted for age weaned and to a standard number nursed, PL=prenatal loss, W1=weight at 125 d, W2=weight at 178 d, and IWW=pig weaning weight.
** P<.01, * P<.05, † P<.10.

Table 4. Estimates of heritabilities[a] (h^2), phenotypic variances (σ^2), genetic correlations (r_g), and phenotypic correlations (r_p).

				r_g		r_p	
Trait[a]		h^2	σ^2	OR	FF	OR	FF
OR[b]		0.42±0.06	8.29	—	—	—	—
FF		0.18±0.08	10.76	0.52	—	.16	—
BA		0.23±0.06	9.81	0.14	0.83	.05	0.88
M		0.17±0.05	0.80	-0.11	0.79	.01	-0.08
SB		0.29±0.05	2.54	0.62	0.20	.23	0.33
AP		0.73±0.05	675.36	0.07	-0.41	.07	-0.12
BF, in		0.49±0.04	.018	-0.09	0.24	-.07	0.03
BW, lb	D[b]	0.04±0.03	0.44	0.44	0.22	.11	-0.05
	M[b]	0.43±0.03	—	-0.26	-0.95	—	—
LBW, lb	D	0.30±0.12	56.7	0.40	0.73	.08	0.85
	M	0.04±0.06	—	-0.14	0.19	—	—
LWW, lb		0.16±0.05	355.7	-0.24	0.06	-.07	-0.04
NW		0.24±0.06	4.54	-0.22	0.62	-.11	0.34
PL		0.12±0.09	14.83	0.83	-0.04	.59	-0.69
W1, lb	D	0.36±0.10	359.3	0.08	-0.03	.12	0.03
	M	0.21±0.05	—	-0.01	-0.37	—	—
W2, lb		0.58±0.04	597.5	0.02	-0.05	.14	0.07
IWW, lb	D	0.15±0.04	3.89	-0.18	0.18	.06	0.04
	M	0.25±0.03	—	0.11	-0.51	—	—

[a]See Table 3 for definition of traits.
[b]D= direct heritability, M=maternal heritability; heritability is direct for traits without D or M designation.

ing component and that when ovulation rate and litter size are in balance, changes in litter size will occur from uniform changes in both traits (Bennett and Leymaster, 1990, J. of Anim. Sci. 68:969). Our results are consistent with their findings.

In previous work at Nebraska (Cassady et al., 1999, J. Anim. Sci. 78:1430), we found that selection for increased plasma concentration of FSH can be used as an indirect selection criteria for ovulation rate. Although the genetic correlation between plasma FSH and ovulation rate was only moderate, indirect selection was nearly as effective (93%) in changing ovulation rate as direct selection because plasma concentration of FSH can be measured in both sexes. In our experiment, two-stage selection for ovulation rate and number of fully formed pigs was effective because litter size in gilts with increased ovulation rate was a good measure of uterine capacity. However, this procedure still requires laparotomy to record ovulation rate, a procedure that may not be practical in most breeding herds. A strategy to improve litter size could be to select for uterine capacity through litter size in a first stage and on plasma concentration of FSH in a second stage. Thus, the difficult task of measuring ovulation rate by surgical procedures is avoided. The efficacy of this selection procedure to enhance rate of response in litter size has not been tested directly.

Genetic parameters

Estimates of genetic parameters (heritabilites and genetic correlations) are needed to develop multi-trait selection programs. Heritability is the relative contribution of genetic effects (the heritable component) to total phenotypic variation that is due to both genetic and environmental effects. This heritable component of variation can be due to genes of the pig in which the trait was measured (direct heritability) or to genes of the dam for maternal effects on the pig's performance (maternal heritability). For some traits, such as ovulation rate and backfat thickness, the pig's own genes are responsible for genetic differences among animals and there is almost no effect of genes of the dam. But for other traits, such as pig birth and weaning weight, the pig's record is due to the effect of its own genes and to the effect of its dam on its development. Some of the dam's effect is due to her genes and is heritable.

Knowledge of the relative value of these heritabilities allows breeders to

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predict the response expected from selection for a trait. However, single-trait selection is almost never practiced because many traits contribute to economics of pig production. Therefore, it is also important to know genetic and phenotypic correlations among traits to predict correlated responses in other traits and to develop selection indexes to jointly improve all economic traits. Positive genetic correlations mean that selection for one trait will cause the other trait to increase in value while a negative correlation means that selection to improve one trait will cause the other trait to decrease. The strength of the association is determined by how close these correlations are to 1 or –1. When values of correlations are undesirable, such that single-trait selection to improve one trait will cause an undesirable change in another trait, selection indexes can be constructed to simultaneously improve both traits.

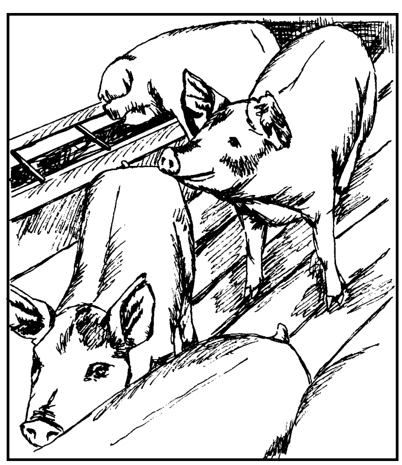
Estimates of genetic and phenotypic correlations and direct (h_d^2) and maternal (h_m^2) heritabilities are presented in Table 4. Most of the traits had considerable genetic variation. Direct heritability estimates ranged from .04±.03 for birth weight to .73±.05 for age at puberty. Maternal heritability estimates ranged from .04±.06 for litter birth weight to .43±.03 for individual pig birth weight.

The important genetic correlations in this study are those between ovulation rate and number of fully formed pigs, with other production traits. Many of these correlations were close to zero, indicating at most very weak associations with ovulation rate and litter size.

Correlated responses per generation in the other traits measured were also estimated. Averaged across selection lines, number of mummified pigs per litter increased by .035 per generation and number of stillborn pigs per litter increased by .065 per generation ($P<.05$). These responses explain the somewhat lower response in number of live pigs per litter (average of .255 across lines) compared with number of fully formed pigs per litter (average of .32). The increase in number of mummified pigs occurred because of its genetic correlation of .79 with number of fully formed pigs. The correlation between ovulation rate and mummified pigs was very low. On the other hand, the increase in number of stillborn pigs occurred because of its moderately high correlation of .62 with ovulation rate, although it was also positively correlated with number of fully formed pigs.

Prenatal loss, ova not represented by a pig at birth, increased at the rate of .165 embryos/fetuses per generation ($P<.05$). It was due entirely to its high genetic correlation (.83) with ovulation rate. Age at puberty decreased at the rate of 2.2 days per generation.

The selection practiced in this experiment significantly increased ovulation rate and litter size. Associated with these changes were greater numbers of stillborn and mummified pigs per litter. However, the increase in total born was sufficiently large to offset these changes so number of live pigs per litter increased significantly. The correlated decrease in age at puberty was a desirable change as there are economic benefits to pork producers from decreased age at puberty in gilts. The selection applied did not cause significant correlated responses in other production traits.



Conclusions

Two-stage selection was effective in improving ovulation rate and litter size. Approximately 97% of the increase in ovulation rate was realized as more pigs in line COL. In line IOL, previously selected for increased OR, litter size increased 130% more than OR, although the extra rate of response was not significant. Two-stage selection can be used to improve litter size in populations varying greatly in ovulation rate and litter size. Application would be enhanced by a non-invasive procedure to record ovulation rate. Because number of mummified and stillborn pigs increased along with increased litter size, selection criteria to increase litter size should include number and/or weight of live pigs rather than number of fully formed pigs at birth.

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