

SECOND THOUGHTS ON SELECTION FOR COMPONENTS OF REPRODUCTION IN SWINE

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SUMMARY

Selection for components of litter size are reviewed. Although ovulation rate responded to direct selection, half of the advantage was lost by day 30 and fetal mortality continued thereafter until about 20% of the increased ovulation rate was realized as greater litter size. Selection for litter size in high ovulating gilts was effective due to increases in ovulation rate and uterine capacity. Emphasis on ovulation rate and prenatal survival to day 50 of gestation was optimized by index selection, producing changes in components that were less hostile than direct selection for ovulation rate. Measurement of uterine capacity by use of a surgical procedure was validated. A conceptual model of litter size partitioned prenatal mortality into embryonic and fetal phases. Fetal mortality occurs due to the interaction of uterine capacity with ovulation rate and potential embryonic viability. Selection for litter size is equivalent to selection for components by fixed independent culling levels. Genetic information is accruing on control of ovulation rate, prenatal survival, and uterine capacity.

INTRODUCTION

Because litter size is a lowly heritable trait, expressed only by sexually mature females, geneticists long believed that selection for litter size in swine would be ineffective. However, litter size increased due to selection in mice, with ovulation rate identified as the mechanism (Falconer, 1963). Selection experiments for ovulation rate in mice were subsequently conducted during the mid-1960's (Bradford, 1969; Land and Falconer, 1969). Direct selection for a component of litter size, ovulation rate, was first practiced in swine in 1967 (Zimmerman and Cunningham, 1975), before selection for litter size itself was attempted. At that time, the scientific merit of the ovulation rate experiment was generally viewed with much skepticism (Lavon Sumption, personal communication). During the ensuing quarter of a century since the now acclaimed classical experiment was started, researchers integrated genetic and physiological concepts of interactive components to elucidate the genetic basis of litter size. The improved understanding of litter size was accompanied by significant statistical and computing developments, leading geneticists to forecast that litter size will receive increasingly greater emphasis in the future; e.g., Hill and Webb (1982), Haley et al. (1988), de Vries and Sorensen (1990), and Ollivier et al. (1990). The present objectives are to provide an historical perspective on the development of selection procedures for components of litter size in swine and to suggest opportunities for future research.

TERMINOLOGY

Ovulation rate is the sum of corpora lutea counted on both ovaries. The prenatal period is divided into two phases, embryonic and fetal. The embryonic phase occurs from fertilization to about day 25 of gestation, whereas the fetal phase describes the remainder of gestation; day 25 is an approximation of the age when differentiation ceases (Dziuk, 1987). Uterine capacity is the

maximum number of fully formed fetuses that can be carried to term when ovulation rate is not limiting (Christenson et al., 1987) and the level to which litter size is reduced when the uterus is challenged by more embryos and fetuses than can be nurtured to birth. Litter size is the number of fully formed fetuses at birth given natural ovulation rate and a completely functional uterus.

SELECTION FOR OVULATION RATE

Selection for ovulation rate was practiced in a 14-breed composite population (Zimmerman and Cunningham, 1975). Select and control lines were produced annually from approximately 40 litters and 20 boars each. Mid-ventral laparotomies were performed 9 to 11 days after second estrus to record ovulation rate at a common stage of sexual development. Boars of both lines were selected randomly, whereas control gilts were chosen in a stratified manner to represent the distribution of ovulation rate. Selection on ovulation rate was applied to gilts of the select line for ten generations.

Direct response to selection for ovulation rate produced an increase of $.49 \pm .10$ ova per generation and realized heritability was estimated as $.46 \pm .10$ (Johnson et al., 1984). Although ovulation rate was measured at second estrus, over 95% of gilts conceived at later estrous cycles. Hansen et al. (1976) reported that the line difference in ovulation rate at second estrus (3.2 ova) was maintained during the third through fifth (2.5, 3.6, and 2.9 ova, respectively) estrous cycles of generation 8 gilts. Likewise, after ten generations, Johnson et al. (1984) estimated the line difference as 3.8, 4.8, and 4.1 ova at first, second, and third estrous cycles, respectively. The correlated response in litter size was estimated as $.089 \pm .058$ pigs per generation (Lamberson et al., 1991). This value is about 50% greater than the original estimate (Cunningham et al., 1979); the recent value was estimated from a larger data set than previously used. The increase in litter size was therefore about 18% of the increase in ovulation rate ($.089/.49$).

Generation 9 litters from both lines were also produced from second parity sows to populate new facilities (Johnson et al., 1984). Based on regression coefficients, estimated line differences in ovulation rate and litter size of generation 9 gilts were 4.41 ova and .80 pigs, respectively; the corresponding observed differences were 3.71 ova and 1.25 pigs (Cunningham et al., 1979). Selection for ovulation rate ceased and 11 generations of relaxed selection followed. Ovulation rates were recorded in generations 12, 15, and 18 (generations 3, 6, and 9 of relaxed selection), with the line difference averaging 2.86 ova (Lamberson et al., 1991). During each generation of relaxed selection, litter size of the ovulation rate line was greater than the control line, averaging $.74 \pm .20$ pigs more per litter. Clearly, nine generations of selection for ovulation rate did increase litter size.

During relaxed selection, the line difference in ovulation rate was perhaps 65 to 77% ($2.86/4.41$ or $2.86/3.71$) of the difference established by selection through generation 9. This apparent reduction may indicate that selection was exploiting epistatic effects present in the composite population (Lamberson et al., 1991). The difference between lines in litter size during the relaxed selection phase (.74 pigs) agreed well with the difference estimated by regression at the end of selection (.80 pigs). The observed line difference in litter size at generation 9, 1.25 pigs, was much greater than differences during the preceding four generations (Cunningham et al., 1979) and may reflect variation due to sampling. During the relaxed selection phase, about 26% ($.74/2.86$) of the line difference in ovulation rate was realized as increased litter size.

Although litter size did increase somewhat due to selection for ovulation rate, the correlated response in prenatal survival was approximately $-1.6 \pm .5\%$ per generation (Johnson et al., 1984). Studies were conducted to determine when prenatal losses were occurring. Survival of fetuses to 30

days was significantly lower in ninth generation gilts (-5.5%) and sows (-8.5%) of the ovulation rate line. Samples of tenth generation gilts indicated 5.2% lower survival to 30 days of gestation for ovulation rate gilts; the difference increased to -10.6% by 70 days of gestation. These studies revealed that roughly half of the ovulation rate advantage of select line gilts was lost by 30 days of gestation and that fetal mortality thereafter was also greater in the ovulation rate line.

Cunningham et al. (1979) suggested that increased ovulation rate of the select line might be exploited by using favorable effects of crossbred gilts on prenatal survival. Two experiments were conducted to test the idea (Johnson et al., 1984). First, generation 9 sows were mated to Landrace, Large White, and Lean Growth (a line split off from generation 2 of the 14-breed composite) boars. F₁ gilts were artificially inseminated with Duroc semen and reproductive data were collected on 107 gilts at 30 days of gestation. Crossbred ovulation rate gilts had more ova (2.7) and fetuses (.5), but lower survival (-8.2%). Second, select and control sows of generation 2 of relaxed selection were mated pure or to Large White boars. Daughters were artificially inseminated with Duroc semen and 230 gilts were slaughtered at 30, 50, and 70 days of gestation. Select minus control pure line differences in ovulation rate and in number of fetuses at 30, 50, and 70 days were 1.5, 2.8, -.4, and -.4, respectively. Corresponding values for crossbred gilts were 1.2, -1.2, 1.2, and -.9.

The crossbreeding experiments yielded interesting results. The difference between select and control crossbred gilts in ovulation rate met expectations in the first experiment, but differences between both pureline and crossbred gilts were less than expected in the second experiment. Also, there was no consistent evidence that crossbred females could accommodate additional embryos or fetuses. However, selection was practiced in a 14-breed composite population that was already highly heterozygous before F₁ females were produced in the evaluation phase.

SELECTION FOR LITTER SIZE

Litter size was traditionally considered the product of two component traits, ovulation rate and prenatal survival. Cunningham et al. (1979) recognized that selection for litter size is a type of index selection. Consequently, simultaneous selection for both components through the "index" of litter size might overcome the apparent antagonistic genetic relationship between ovulation rate and prenatal survival that restricted the correlated response of litter size to selection for ovulation rate.

After two generations of relaxed selection, the ovulation rate line was sampled in 1979 to initiate selection for litter size. Selection was based on the litter size into which pigs were born. About 40 litters were produced annually, with replacement boars and gilts selected from the 15 and 17 largest litters, respectively. The original control line and the relaxed selection, ovulation rate line were each maintained as contemporaries with about 40 litters and 15 sires per generation. The total response to eight generations of selection for litter size was estimated as 1.06 pigs, about .13 pigs per generation (Lamberson et al., 1991). The estimate of realized heritability of litter size in a high ovulating line was $.15 \pm .05$.

Relationships of ovulation rate with prenatal survival and litter size led Johnson et al. (1985) to speculate that selection for litter size in a high ovulating line would automatically shift selection pressure towards prenatal survival and away from ovulation rate. Later, Johnson and Neal (1988) suggested that uterine capacity may have limited the correlated response of litter size to selection for ovulation rate and hypothesized that effective selection for litter size in the high ovulating line was achieved due to increased uterine capacity. These concepts were addressed by estimating the correlated changes in ovulation rate and uterine capacity to selection for litter size (Gama and

Johnson, 1993). Random samples of the litter size and relaxed selection, ovulation rate lines were crossed with a Large White X Landrace composite line to produce F_1 and backcross gilts. The estimated straightline response in ovulation rate was $1.44 \pm .73$ ova at second estrus and $1.15 \pm .79$ ova at the estrus of conception. Gilts were surgically altered to estimate uterine capacity and slaughtered between 93 and 100 days of gestation; the advantage in uterine capacity was $.66 \pm 1.28$ pigs for the litter size line. Thus, increases in ovulation rate of about 1.30 ova and in uterine capacity of .66 pigs were associated with the direct response in litter size of $1.21 \pm .38$ pigs, averaged over three parities. The estimated straightline response in litter size of gilts was $.83 \pm .34$ pigs, in good agreement with the cumulative response of 1.06 pigs achieved by gilts during selection.

Selection for litter size in a high ovulating line was effective. Litter size increased about .13 pigs per generation and the estimate of realized heritability was .15. The increase in litter size was associated with increases in both ovulation rate and uterine capacity, the latter result providing evidence for genetic regulation of uterine capacity in swine.

INDEX SELECTION FOR OVULATION RATE AND PRENATAL SURVIVAL

Johnson et al. (1984) advanced the concept of litter size as a natural index of ovulation rate and prenatal survival by understanding that variation in litter size was phenotypically determined rather than genetically. Consideration of the genetic variance-covariance structure to optimize weightings of components would produce a selection index more efficient than direct selection for litter size. The strategy is to increase ovulation rate rapidly while restricting the decrease in prenatal survival.

The traditional index equations were formed with the economic values of ovulation rate and prenatal survival equal to the mean of the other component. Parameters for genetic and phenotypic variance-covariance matrices were estimated from data collected during selection for ovulation rate. The heritabilities of ovulation rate and prenatal survival were .45 and .15, respectively; the genetic correlation was -.75. The emphasis on ovulation rate relative to prenatal survival is 68:32% based on the selection index approach, compared to 42:58% for the natural weightings reflected in litter size. The natural index of litter size is influenced too much by prenatal survival, the most variable trait, which is threefold less heritable than ovulation rate. Theoretically, the selection index approach is about 53% more efficient than direct selection for litter size.

Index selection for litter size began in 1981 in a Large White X Landrace composite population (Neal et al., 1989). All gilts raised in the index line, about 150, are mated to sons of the 15 highest indexing dams. At about day 50 of gestation, laparotomies are performed to record ovulation rate and number of fetuses; survival to day 50 is calculated and the index value determined. The 40 gilts with the highest index values are allowed to farrow. Performing laparotomies at day 50 permits roughly four times as many gilts to be evaluated as conventional selection for litter size. Consequently, the selection intensity for dams of replacement males is increased, i.e., selecting 15 out of 150 rather than 15 out of 40 (Johnson et al., 1985). A control line is maintained with about 40 litters by 15 sires per generation.

Results of five generations of index selection for litter size were reported by Neal et al. (1989). The regressions of line differences on generation number were $.57 \pm .11$ ova, $-1.3 \pm 1.0\%$ survival to day 50, $.20 \pm .20$ fetuses, and 5.10 ± 1.76 index points. Realized heritability of the index, $.30 \pm .09$, was in close agreement with the theoretical value of .35. Johnson et al. (1984) predicted that intensity of selection would average about 1.52 per generation for selected dams. The intensity actually achieved was about 1.30, roughly 86% of predicted. Taking into account the lower selection

intensity, observed responses in ovulation rate, prenatal survival, and number of fetuses were approximately 80 to 85% of the responses predicted.

The selection index for litter size was developed because response due to direct selection for ovulation rate (.49 ova per generation) was largely offset by decreased prenatal survival (-1.6% per generation). The index objective was to optimize the genetic changes in components, thereby maximizing the increase in litter size. Index selection for litter size produced responses of .57 ova and -1.3% prenatal survival (day 50) per generation. It seems likely that index selection produced a better balance of genetic changes in components relative to direct selection for ovulation rate.

The ultimate objective of the selection index for litter size is to increase the number of pigs born. During evaluation of lines from the ovulation rate experiment, serial slaughter of pregnant gilts indicated that a high proportion of prenatal mortality occurred by day 50 (Johnson et al., 1984), a result consistent with earlier studies. It was assumed that the genetic correlation between number of fetuses at day 50 and litter size approached unity. This information provided the basis for counting fetuses at day 50 of gestation. Preliminary estimates of responses in number of fetuses at day 50 and in litter size were $.20 \pm .20$ and $.19 \pm .14$ pigs per generation, respectively. There is now convincing evidence that fetal losses occur during late gestation when ovulation rate is high (Leymaster et al., 1986; Christenson et al., 1987). If such losses are genetically regulated, index selection using prenatal survival to day 50 will produce less change in litter size than expected.

The paper by Johnson et al. (1984) had a significant impact on research by contemplating the genetic regulation of prenatal survival and its apparent antagonistic genetic correlation with ovulation rate. The research brought to light new opportunities to increase litter size by selection and consequently stimulated other geneticists to conduct research on prenatal survival. For example, an experiment with mice directly compared effects of litter size and index selection (Clutter et al., 1990; Gion et al., 1990; Kirby and Nielsen, 1993; Clutter et al., 1994), while genetic parameters for components were estimated in rabbits (Blasco et al., 1993a). Several recent reviews have addressed components of litter size in swine; e.g., Legault (1985), Eisen (1986), Haley et al. (1988), van der Lende and Schoenmaker (1990), and Blasco et al. (1993b).

THE CONCEPT OF UTERINE CAPACITY

Fetal mortality, particularly during late gestation, is often overlooked because much of prenatal mortality is due to embryonic losses. Yet, the mechanisms responsible for embryonic and fetal mortality clearly differ. Perhaps the heritability of prenatal survival is low, in part, simply because it is a composite trait. Partitioning of prenatal survival into components may allow development of more effective selection schemes, analogous to accounting for components of litter size.

The concept of uterine capacity implies there is a limit to the number of fetuses that the uterine environment can support. Various effects of uterine capacity can be studied only if uterine capacity is measurable. Leymaster et al. (1986) and Christenson et al. (1987) reported the evaluation of unilateral hysterectomy-ovariectomy (UHO) as a surgical procedure to measure uterine capacity. They concluded that the number born to UHO gilts did estimate uterine capacity of a single uterine horn, therefore, total uterine capacity can be estimated as twice the number born to UHO gilts.

Other results of the UHO evaluation experiment provided insight into interactive effects of ovulation rate and uterine capacity. Significant fetal loss occurs during late gestation if the uterus is challenged by more fetuses than it can support. Therefore, the normal distribution of ovulation rate limits the expression of uterine capacity in a portion of females, suggesting that ovulation rate

and uterine capacity interact to affect prenatal mortality and litter size. Due to the interaction, the correlation of ovulation rate with number of fetuses decreases as gestation advances, whereas the correlation between uterine capacity and number of fetuses increases. As ovulation rate increases, litter size approaches a plateau that is equal to uterine capacity. Ovulation rate and uterine capacity are phenotypically independent, or nearly so. Finally, ovulation rate and uterine capacity both limit litter size, suggesting simultaneous selection for each component to increase litter size.

INTEGRATION OF COMPONENTS OF LITTER SIZE

Results of the UHO evaluation experiment provided the impetus for Bennett and Leymaster (1989) to develop a model of litter size based on ovulation rate, potential embryonic viability, and uterine capacity. The three components are independent, but interact to determine prenatal mortality and litter size. Prenatal mortality can occur in two distinct phases, each due to different mechanisms. The first phase of mortality, essentially embryonic mortality, may reduce ovulation rate to potentially viable embryos. Several known causes of this reduction are considered inherent to the ovum/embryo and not directly associated with limitations of the uterine environment. It is assumed that each ovum has the same probability, called potential embryonic viability, of surviving this phase. Consequently, potentially viable embryos are binomially distributed within each ovulation rate class. The second phase of mortality, basically fetal mortality, occurs only if the number of potentially viable embryos exceeds uterine capacity. In this model, prenatal survival can be complete and litter size can be less than both ovulation rate and uterine capacity.

The model was phenotypically and genetically calibrated for intrapopulation parameters and simulated results not used for calibration were compared to experimental results to validate the model. The value of potential embryonic viability was .82 with a heritability of 0.00; heritabilities of ovulation rate and uterine capacity were .25 and .15, respectively. Response surfaces were simulated to predict effects of changes in ovulation rate and uterine capacity on distributional properties of prenatal survival and litter size and on correlations of composite traits with component traits. Changes in either component alone will not greatly affect litter size because continual change causes litter size to plateau. If initial means of components are comparable, the most effective way to increase litter size is to make similar changes in each component.

Implications of different genetic models to describe characteristics of the simulation model of litter size were discussed by Bennett and Leymaster (1990a). It was shown that selection for litter size is equivalent to selection for potentially viable embryos and uterine capacity based on fixed independent culling levels. Due to selection index theory, an index of components should be the most efficient method to select for litter size. Correlations among ovulation rate, uterine capacity, prenatal survival, and litter size are not pleiotropic in nature, but rather arise from interactions among components, causing nonlinear relationships of components with litter size and prenatal survival. The model predicts asymmetry of realized heritabilities and of correlated responses of components due to divergent selection for litter size. Various selection strategies were also simulated (Bennett and Leymaster, 1990b). The simulated results agreed qualitatively, if not quantitatively, with observed experimental results in swine, mice, and sheep.

Experimental research to define and measure uterine capacity and conceptual, simulation, and theoretical research to integrate components have improved understanding of the genetic basis of litter size. Particularly, the dynamic effect of uterine capacity on fetal mortality has been insightful. The technique to measure uterine capacity was incorporated into selection experiments in swine

(K.A. Leymaster), mice (Clutter et al., 1994), and rabbits (Blasco et al., 1993b) and used to evaluate line or breed effects in swine (Gama and Johnson, 1993; Haley and Lee, 1993). Realized heritability of uterine capacity in mice was estimated as $.08 \pm .01$ by Kirby and Nielsen (1993) and evidence was recently published indicating large heterosis effects for uterine capacity in Large White X Meishan F_1 gilts (Haley and Lee, 1993). Recent reviews included sections on uterine capacity (Haley et al., 1988; Ollivier et al., 1990; Wilmot et al., 1990).

OPPORTUNITIES FOR FUTURE RESEARCH

Physiological mechanisms affecting variation in uterine capacity are unknown, while estimates of within and between breed genetic variation and heterosis effects are needed to refine the conceptual model of litter size. Selection lines and breeds are sources of variation that can be used to study the genetic nature of uterine capacity. Lines selected solely for uterine capacity would be very informative, but require considerable time to develop. Chinese breeds can presently be studied, however results will require careful interpretation. Regardless of the approach taken, experiments must be well designed to account for the large coefficient of variation associated with uterine capacity. It is not known if relevant genetic variation exists for potential embryonic viability, but data published by Haley and Lee (1993, table 4) may indicate that the Meishan breed is exceptional. Ovulation rate, potential embryonic viability, and uterine capacity were considered genetically and phenotypically independent in the conceptual model of litter size. Nonetheless, it is important to determine if pleiotropic effects are indeed present.

A porcine genetic linkage map was published by Rohrer et al. (1994) and maps will rapidly become more dense. Litter size, being a lowly heritable, sex-limited trait expressed first at a year of age, is an excellent example of a trait that could benefit from marker-assisted selection. Searches for markers that cosegregate with loci affecting litter size will be undertaken. However, due to the interaction among components, it may be difficult to identify markers for litter size. It seems more probable to find markers for ovulation rate or uterine capacity. Research is underway at the University of Nebraska (F_2 generation involving the selection index line) and at MARC (reciprocal Meishan backcrosses) to find markers for components of litter size. Wilmot et al. (1990) indicated a project to markers linked to loci responsible for prenatal survival in a Large White X Meishan F_2 population.

Accurate, non-surgical procedures to measure ovulation rate and uterine capacity would permit practical application of index selection for components. Rodger Johnson is testing a two-stage selection scheme, with initial selection based on ovulation rate at second estrus and subsequent selection based on litter size. It is reasoned that litter size of high ovulating gilts would approximate uterine capacity. If heterosis effects on uterine capacity are sufficiently large, then selection in maternal lines might ignore uterine capacity and litter size, focusing on ovulation rate. Crosses between high ovulating maternal lines might bring the components into balance, increasing litter size. This is only a short-term approach that may work until more basic information is provided by research currently underway at several institutions.

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