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The University of Nebraska - Lincoln, 1990

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PREVIEW

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**CORRELATED RESPONSES TO SELECTION
FOR REPRODUCTIVE TRAITS IN SWINE**

by

Luis L.T. Gama

A DISSERTATION

Presented to the Faculty of
The Graduate College in the University of Nebraska
In Partial Fulfillment of Requirements
For the Degree of Doctor of Philosophy

Major: Animal Science

Under the supervision of Professor Rodger K. Johnson

Lincoln, Nebraska

November, 1990

DISSERTATION TITLE

CORRELATED RESPONSES TO SELECTION FOR REPRODUCTIVE TRAITS IN SWINE

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CORRELATED RESPONSES TO SELECTION FOR
REPRODUCTIVE TRAITS IN SWINE

Luis L.T. Gama, Ph.D.

University of Nebraska, 1990

Advisor: Rodger K. Johnson

Correlated responses to selection for increased litter size or decreased age at puberty in swine (eight generations) after previous selection for ovulation rate (nine generations) were evaluated. Selection for litter size resulted in an increase of $.83 \pm .35$ fully formed pigs per litter in first parity gilts, and the response was maintained in second and third parity sows. Litter size response was due to an increase of $1.30 \pm .54$ eggs in ovulation rate and $.66 \pm 1.28$ pigs in uterine capacity, but no significant changes were observed in uterine dimensions. About 25% of the increase in litter size could be explained by a reduction in the number of mummified pigs at birth, an indication that uterine capacity in late gestation was increased.

Selection for litter size resulted in no change in litter weight at birth, but in a reduction in both number of pigs weaned and individual weaning weight. Pigs selected for litter size had delayed growth to 90 kg and delayed puberty in females, but little change in backfat thickness. Selection for decreased age at puberty resulted in minor changes in litter size, but in a reduction in litter weight at birth and weaning, even though number of pigs weaned was not affected. Pigs selected for younger age at puberty had increased backfat

thickness but little change in growth rate to 90 kg.

Genetic parameters for embryonic survival to 50 days of gestation estimated in a line of pigs selected for an index of ovulation rate and embryo survival were .01 to .04 for the heritability of direct effects, .01 to .04 for the heritability of maternal effects and -.21 to -.72 for the correlation between direct and maternal effects.

PREVIEW

DEDICATION

This dissertation is dedicated to Manuela and Madalena, for their love, support and patience.

Thank you.

PREVIEW

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PREVIEW

INTRODUCTION

Two major approaches have been used to define components of litter size in swine. The first one considers litter size as the product of ovulation rate and embryonic survival (Johnson et al., 1984) while the second approach regards litter size as the minimum of ovulation rate and uterine capacity (Bennett and Leymaster, 1989). In the last model, embryonic survival is just the result of ovulation rate (or number of viable embryos) exceeding or not uterine capacity, and thus, mean litter size depends on the mean of its two components plus their interaction. When selection for litter size is practiced in a line where the two components are unbalanced, e.g., a high ovulating line, more of the selection pressure will be placed on the more limiting component. Selection for litter size in a line previously selected for high ovulation rate was successful (Lamberson et al., 1990), and it is important to investigate how the components of litter size contributed to the selection response.

In swine, a decrease of 20% in age at puberty or an increase of 20% in litter size result in a reduction in costs of production of, respectively, 2% and 2 to 5% (Tess et al., 1983). These estimates, obtained from modelling work, assume that other traits are held constant, and are of importance in the definition of breeding goals in swine. However, when evaluating the overall biological and economic efficiency of a selection program, changes in other traits associated with the selected trait(s) should be considered. It is therefore

important to evaluate how selection for either increased litter size or decreased age at puberty affects other economically important traits.

Survival of a litter during gestation, measured as the proportion of potential embryos that survive to term, is an important component of litter size, and accounts for more of the variation in this trait than ovulation rate does (Johnson et al., 1984). Even though it is usually regarded as a trait of the dam, variation in embryonic survival results from variation in uterine environment provided by the dam and from variation among individual embryos in their ability to survive, dependent on their own genes.

The objectives of this work were to 1) analyze responses in ovulation rate, uterine dimensions and uterine capacity in swine selected for litter size, 2) investigate how much of the response in litter size could be explained by a reduction in number of mummified pigs at birth, 3) examine if the increase in litter size obtained by selection practiced in first-parity gilts was maintained in later parities, 4) analyze correlated changes in individual and maternal traits following selection for increased litter size or decreased age at puberty, and 5) estimate the magnitude of maternal and individual genetic effects on embryonic survival in swine.

LITERATURE REVIEW

1. Components of litter size

Litter size in pigs is limited by the number of eggs shed at mating and the proportion of those eggs which develop to term (Hammond, 1921). Fertilization occurs for nearly all ova (Wrathall, 1971, Archibong et al., 1987), and therefore it does not contribute much to variation in litter size.

Two major approaches have been used to define components of litter size in swine. The first one considers litter size as the product of ovulation rate and embryonic survival (Johnson et al., 1984) while the second approach regards litter size as the minimum of ovulation rate and uterine capacity (Bennett and Leymaster, 1989). In the last model, embryo survival is just the result of ovulation rate (or number of viable embryos) exceeding or not uterine capacity, and thus mean litter size depends on the mean of its two components plus their interaction.

1.a. Ovulation rate

Ovulation rate sets the upper limit for litter size and is usually estimated by the number of corpora lutea present in the ovary, counted either *in vivo* (laparoscopy, laparotomy) or after slaughter. Possible sources of error in estimating ovulation rate result from the presence of polyovulatory follicles (Bidanel, 1989) or a possible miscounting of corpora lutea due to deep corpora lutea in the ovarian

tissue. The possible existence of monozygotic twins is usually ignored in swine, but in some cases females carry more embryos than their corpora lutea number (Blichfeldt and Almlid, 1982).

It is usually assumed that all ova have the same probability of being fertilized and that, indeed, fertilization occurs for all or none of the eggs in pigs. This may not be entirely true, at least when ovulation rate is higher than usual. When gonadotropins are used to cause superovulation, immature ova (primary oocytes) are released (Wrathall, 1971) and the same may be true in gilts selected for increased ovulation rate (Koenig et al., 1986). These immature ova are not fertilized or polyspermy occurs, and thus normal development does not proceed (Bolet, 1986).

1.b. Embryonic survival

Sir John Hammond (1914, 1921) first reported on the relationship between ovulation rate and embryonic survival in swine, and estimated that embryonic-fetal mortality results in a 25-50% loss of potential pigs. In their review of the literature, Pope and First (1985) indicated that 40-50% of the potential embryos are lost before farrowing. Embryonic survival, measured as the proportion of potential embryos that survive to term or the ratio of number of pigs born to corpora lutea number, is therefore an important component of litter size.

Variation in embryonic survival results from variation in uterine environment provided by the dam and in the ability of the embryo to

survive, dependent on its own genes. It is also possible that an interaction exists between the genotypes of the embryo and the dam, as shown in mice by Moler et al. (1980).

Breed differences in embryonic survival are quite important. Young et al. (1976) reported a mean embryonic survival to 30 d of gestation of 70% for Hampshire and 84% for Yorkshire sows. Chinese breeds of pigs are well known for their much lower embryonic mortality than European breeds, even though they have similar ovulation rates (Bolet et al., 1986, Bazer et al., 1988b). On the other side, Large White sows screened for high prolificacy have much higher ovulation rates and lower embryonic survival than unselected sows (Legault, 1985, Bolet et al., 1986).

Genetic parameter estimates for embryonic survival are more scarce than for ovulation rate. Johnson et al. (1984) reported an estimate of .15 for the heritability of embryonic survival regarded as a trait of the dam, while Neal et al. (1989) reported an estimate of .18 for the same trait. The fact that crossbred litters have higher embryonic survival than purebred litters (Johnson and Omtvedt, 1973) indicates that individual genetic variation for embryonic survival does exist, even though it may be mostly non-additive.

1.c. Uterine capacity

The concept, factors involved and measurement of uterine capacity are discussed later in this review. Information on genetic and phenotypic parameters for uterine capacity in swine is not available

at this point. In a selection-simulation study, Bennett and Leymaster (1990b) assumed a heritability between .15 and .20 for uterine capacity in pigs. The realized heritability for the same trait in mice was .08 (Gion et al., 1990).

1.d. Relationship between litter size and its components

Bidanel (1989) reviewed several reports of the relationship between litter size and its components. The average correlations from those reports are summarized in Table 1.

TABLE 1. AVERAGE CORRELATIONS AMONG LITTER SIZE AND ITS COMPONENTS
(from review by Bidanel, 1989)^a

	OR	ES	LS
OR		-.25	.29
ES	-.40		.79
LS	.28	.73	

^a OR = ovulation rate, ES = embryonic survival, LS = litter size; phenotypic correlations above the diagonal, genetic correlations below.

Embryonic survival tends to decline linearly as ovulation rate increases (Blichfeldt and Almlid, 1982, Johnson et al., 1985) and this decline tends to be more pronounced as gestation proceeds (Wrathall, 1971), an indication that uterine capacity is playing a more important

role in late gestation. Breed differences in the relationship between ovulation rate and embryonic survival have been reported by Davis et al. (1987).

The relationship between ovulation rate and litter size is curvilinear, litter size tending to reach a plateau at ovulation rates around 25 eggs (Johnson and Neal, 1988). This non-linear relationship could explain some of the discrepancies in estimates of phenotypic correlations, ranging from .06 (Young et al., 1978) to .57 (Davis et al., 1987).

Relationships between uterine capacity and litter size or ovulation rate in pigs have not been documented in the literature. In their simulation work, Bennett and Leymaster (1990b) assumed that ovulation rate and uterine capacity are uncorrelated, both genetically and phenotypically, and that uterine capacity has a phenotypic correlation with litter size of .61 and a genetic correlation of .75. A selection experiment for uterine capacity in mice (Gion et al., 1990) resulted in increased litter size and a very slight increase in ovulation rate.

Given the relative variation in embryonic survival and ovulation rate and their relationships with litter size, Johnson et al. (1984) derived an index of components that was expected to be 53% more efficient than direct selection for litter size. After five generations of selection, response was .19 pigs/litter/generation (Neal et al., 1989). The same principle of selecting on an index of components was later applied in mice (Clutter et al., 1990). After 13

generations of selection, response per generation was 13% higher in the line selected on the index than in a line selected for litter size (Gion et al., 1990), but this advantage was not maintained after 21 generations of selection (Kochera et al., 1990), possibly because index weights were not recalculated to reflect changes in parameters.

Bennett and Leymaster (1989, 1990a, 1990b) proposed a model where litter size equals the minimum of ovulation rate (or, more precisely, number of viable embryos) and uterine capacity. Under this model, the two components are assumed uncorrelated, but interact to determine litter size. In a given population, mean litter size can be predicted by a mathematical model that includes the cubic effects of the two components and their interactions. If the means of the two components are balanced, changing the two components simultaneously is more effective in increasing litter size than changing either component individually, but would cause little change in embryonic survival. If the means of the two components are unbalanced, changing the component with the lowest mean has the greatest effect on litter size.

The same model predicts that the phenotypic correlation between ovulation rate and litter size decreases as ovulation rate increases relative to uterine capacity. Therefore, when the mean ovulation rate is high, litter size is determined mostly by uterine capacity and the correlation between ovulation rate and litter size is small. The correlation between ovulation rate and embryonic survival becomes more negative as ovulation rate increases relative to uterine capacity, but the negative correlation between those two traits represents not a

real antagonism, but rather results from the interaction between ovulation rate and uterine capacity.

The Bennett and Leymaster model further predicts that, when the means of the two components are unbalanced, the heritability (h^2) of litter size will approach the h^2 of the most limiting component. When the two components are balanced, the h^2 of litter size decreases because of the increased importance of the interaction between ovulation rate and uterine capacity. Selection for litter size would tend to balance the two components, because most pressure would be placed on the most limiting component.

Simulated response to selection (Bennett and Leymaster, 1990b) indicated that selection for an index of ovulation rate and uterine capacity would be 37% more efficient than direct selection for litter size, versus an advantage of only 21% for an index combining ovulation rate and embryonic survival.

One possible weakness of the Bennett and Leymaster model is that it does not consider any variation in potential embryonic viability, i.e. it assumes that any embryonic losses up to 30 d (independent of uterine capacity) are standard in all situations (18% in their model) and would result from ovulation of primary oocytes, fertilization failure, polyspermy, genetic lethals, etc. This is in disagreement with results from a selection experiment for ovulation rate, which resulted in higher embryonic loss to 30 d in the line selected for ovulation rate (Geisert et al., 1978, Johnson et al, 1984) possibly due to increased incidence of immature ova (Koenig et al., 1986).

2. Response to selection for litter size in swine and mice

2.a. Direct selection

Expected responses to selection for litter size in swine are as high as .47 pigs per generation (Avalos and Smith, 1987), but it is probably more realistic to expect responses of about .20 to .25 pigs per generation (Bichard and David, 1985, Bennett and Leymaster, 1990b). However, until recently, no experimental evidence existed to support the feasibility of selection for litter size in swine.

Ollivier (1982) and Bolet et al. (1989) reported results of 10 generations of selection for the mean litter size of the first two parities in swine. The realized h^2 of this measurement was $.04 \pm .13$ after 11 generations of selection. The possible reasons for the lower than expected response were discussed by Bolet et al. (1989). The regression of line differences on generation was $.12 \pm .04$ for ovulation rate and $.12 \pm .07$ for number of embryos at 30 d, both measured in third parity sows.

More recently, Lamberson et al. (1990) reported results of selection for litter size in a line previously selected nine generations for ovulation rate. After eight generations of selection for litter size, the response was about one additional pig at birth, with a realized heritability of $.15 \pm .05$.

Mice have consistently responded to litter size selection, with realized heritabilities averaging .16 (Eisen, 1986). Consistently, selection for increased litter size in mice has resulted in increased ovulation rate and no change or a slight improvement in embryonic