

## Selection response for litter size at birth and litter weight at weaning in the first parity in mice

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Received August 20, 1988; Accepted June 12, 1990

Communicated by E. J. Eisen

**Summary.** Five 60-pair lines of mice were selected for seven generations for the following criteria: number born alive (LSO), random selection of litters (LC), number born alive divided by the weight of the dam at 9 weeks (LSO/DWT), total litter weight weaned divided by the weight of the dam at 9 weeks (LWT/DWT), and weight of litter weaned (LWT). All traits were measured in the first parity only and litters were not standardized. Realized heritabilities for LSO, LWT, LSO/DWT, and LWT/DWT were  $0.10 \pm 0.06$ ,  $0.11 \pm 0.07$ ,  $0.22 \pm 0.04$ , and  $0.22 \pm 0.08$ , respectively. Selection response for the two ratio lines was due to correlated responses in the respective numerators, LSO and LWT, as DWT did not decrease. In terms of improving LWT, selection for LWT/DWT was three times as effective as selection for LSO/DWT.

**Key words:** Selection – Mice – Litter size – Litter weight – Reproductive performance

### Introduction

Female reproductive performance has a major influence on the efficiency of many animal production systems (Dickerson 1970). In those systems where the primary effort is directed towards maximizing meat production, reproductive performance is best measured by some function of weight of progeny weaned.

The mouse has been used as a model for domestic livestock species in numerous studies on various components of reproductive performance, including ovulation rate (Land and Falconer 1969), embryo survival (Bradford 1969), litter size at birth (McCarthy 1982), and post-natal maternal performance (Nagai et al. 1978), all mea-

sured in the first parity. In all of the above studies selection was successful. Less well established are the genetic relationships between these traits and weight of litter weaned.

In many selection experiments, litter size was standardized at birth or simply no measurements were recorded at weaning. Selection for numbers and weight of litter weaned, in contrast to selection for their component traits, has not been successful (Steane and Roberts 1982). The lack of success has been attributed largely to negative maternal environmental effects (Eisen 1981). Falconer (1965) proposed that these effects could be explained by a negative relationship between the size of the litter a female was reared in and her body weight which, if small, adversely affected her subsequent litter size. In general, the results from selection studies involving female body weight or litter size have indicated a positive relationship between the two traits (McCarthy 1982).

In the present study, four lines were selected firstly, to evaluate direct and indirect responses to selection for two components of reproductive performance, number born and weight of litter weaned, and secondly, to determine whether accounting for the dam's body weight would affect either or both responses.

### Materials and methods

#### *Mice*

The lines originated from a heterogeneous population that was established from crosses between ten lines that had been previously selected for either maternal performance, the ability to defeat unfamiliar mice in fights – expressed as dominance value (Beilharz and Beilharz 1975), or shape of growth curve (Luxford 1987). One hundred and fifty pairs of mice were mated randomly with the restriction that their mate was from another line. Two hundred and forty males and females were then randomly select-

ed from all progeny produced by this initial set of matings. These mice were mated randomly, avoiding brother-sister matings. Generation 0 for the five lines discussed in this paper was established using the progeny of this mating. Six mice, where possible three males and three females, were chosen at random from each of one hundred and twenty litters. One mouse from each litter was then allocated at random to each of the five lines to provide 60 pairs in each line. The remaining 60 pairs were allocated in identical manner to a sixth line (IC), the performance of which will be discussed in a separate paper. Seven generations of selection were then carried out in the upward direction, using the following performance criteria measured in the first parity in the different lines:

LSO – number born alive;  
 LSO/DWT – number born alive/9-week weight of the dam;  
 LWT/DWT – total weight of litter weaned/9-week weight of the dam;  
 LWT – total weight of litter weaned;  
 LC – unselected control.

In the four selected lines, six mice, where possible three males and three females, were randomly chosen from each of the top 20 litters according to the appropriate criterion. In the unselected control line, litters were chosen at random. If six mice were not available from any litter, mice were taken from the 21st litter and so forth, to make up the numbers.

In the sixth line (IC), 60 males and 60 females were chosen at random from all mice alive at 9 weeks of age in each generation. This line was used only as a second replicate control line for estimating heritability within generations.

Throughout the experiment a commercial pellet feed and tap water were supplied ad libitum. The temperature in the mouse room ranged from 21 to 25°C. Mice were mated between 9 and 11 weeks of age, with selected males allocated to females at random. Males were left with the females for 18 days and then removed. Progeny were identified individually at 10 days of age by toe clipping and weaned at 3 weeks of age. Until selection, weaned males and females were separated into cages that held seven males or females, or fewer, depending on post-weaning mortality.

#### Measurements

The following data were routinely collected for all dams mated: date of mating, parturition and weaning of each litter; litter size at birth, defined as the number of young born alive (LSO) and litter size at weaning (LS21); weight of litter at weaning (LWT); total number born per 9-week weight of dam (LSO/DWT); total weight weaned per 9-week weight of dam (LWT/DWT); average weaning weight of offspring (LWT/LS21). Conception rate (CR), i.e., percentage of females producing a litter, was calculated for each line in each generation. For progeny, individual body weights were taken at 3, 6, and 9 weeks of age. Six-week weights were not analyzed for this paper. The 9-week weights provided the denominator used in appropriate performance criteria for dams of the next generation.

#### Analysis of generation means

All regression analyses were done using SPSSX software (SPSSX 1983). Realized heritabilities for the selected traits were calculated as twice the regression coefficient of the deviation of the generation mean of the selected trait from the value of the control line, on cumulated selection differential. In addition, the changes in a number of reproductive traits were compared among the lines by regressing generation means on generation number. Whether correlated responses occurred was seen from regressions on generation number, of the mean deviations from the control line of the traits in question in the selected lines.

Selection and secondary selection intensities per generation were calculated as the selection differential divided by the standard deviation of the particular trait in generation 0.

#### Analyses within generations

Data from the control line (LC) and the replicate control line (IC) were pooled and all analyses were done within line and generation by transforming the data into deviations from the appropriate line-by-generation subgroup mean. Heritability estimates were calculated from daughter-dam regression.

Genetic correlations were calculated as  $Cov_{xy}/\sqrt{(Cov_{xx} \cdot Cov_{yy})}$ , where  $Cov_{xy}$  is the dam-offspring covariance between the two traits calculated as the mean of the two possible covariances, and  $Cov_{xx}$  and  $Cov_{yy}$  are the dam-offspring covariances for the two traits separately. The standard error for the genetic correlation was calculated using the formula outlined by Reeves (1955). Phenotypic correlations were calculated as product-moment correlations.

#### Inbreeding

Rate of inbreeding,  $\Delta F$ , was estimated as  $1/2(Ne)$ , where  $Ne$  per generation was approximated by  $4N/(V_k + 2)$ , and  $N$  is the number of individuals that contributed progeny who became parents in the next generation, and  $V_k$  is the variance of family size. For each line, an average  $Ne$  over the whole selection experiment was calculated using the harmonic mean calculated from  $Ne$  in each generation (Falconer 1981).

## Results

The regression coefficients for generation means on generation number are presented in Table 1 for all traits in the five lines. The majority of the estimates were not significantly different from zero. A negative trend is evident for most of the traits in the control line, LC.

Realized heritabilities in each of the lines LSO, LWT, LSO/DWT, and LWT/DWT and heritability estimates

**Table 1.** Regressions of generation means on generation number

Line	LC	LSO	LSO/ DWT	LWT/ DWT	LWT
Trait					
LSO (no.)	-0.10 (0.08)*	0.03 (0.09)	0.10 (0.08)	0.18** (0.06)	-0.10 (0.08)
LS21 (no.)	-0.09 (0.08)	-0.00 (0.12)	-0.00 (0.15)	0.13 (0.09)	-0.19 (0.15)
DWT (g)	-0.02 (0.15)	-0.12 (0.11)	-0.00 (0.16)	0.09 (0.18)	-0.03 (0.14)
LWT/ LS21 (g)	-0.05 (0.20)	-0.18 (0.15)	-0.21 (0.15)	-0.06 (0.15)	0.03 (0.17)
CR (%)	0.10 (0.13)	0.24 (0.15)	0.08 (0.14)	0.45*** (0.11)	0.20 (0.14)
LWT (g)	-1.70 (2.00)	-1.18 (1.98)	-0.63 (2.35)	1.31 (1.86)	-0.30 (2.72)

\* Standard error

\*\*  $P < 0.05$

\*\*\*  $P < 0.01$

based on daughter-dam regression for the same traits in the control populations LC and IC are presented in Table 2. As shown by the realized heritabilities, selection was clearly more successful for the two composite ("ratio") traits compared to the lines where selection was simply for LSO or LWT. Predicted responses from daughter-dam estimates of heritability were similar to predicted response, except that that for LWT was higher.

In a subsequent analysis using the control line LC, female reproductive efficiency was expressed as a phenotypic covariate index. The index was in the form  $I = P_L - bP_D$  where  $P_L$  is either number born alive or weight of litter weaned,  $P_D$  is the weight of the dam at 9 weeks and  $b$  is the phenotypic regression of  $P_L$  on  $P_D$ . The correlation between these index values and the respective ratio values estimated in this experiment were 0.99 for both reproductive traits.

Percentage rise in inbreeding coefficient was 8.1, 8.3, 8.0, 8.4, and 8.4 for the lines LSO, LC, LSO/DWT, LWT/DWT, and LWT, respectively. This represents an average increase in  $F$  per generation of just over 1%.

Table 3 presents selection and secondary selection indices for all primary traits (i.e., excluding the ratio traits selected in two of the lines) for every selected line. In lines LSO and LSO/DWT, where number born was the principal trait of selection, the secondary selection intensities observed for LS21 and LWT were high, while the value for LWT/LS21 (i.e., average weaning weight) was negative, though only small in line LSO/DWT. Where LWT was the principal trait of selection (lines LWT and LWT/DWT), similarly high secondary selection intensities were observed for numbers born and weaned, and positive values, though smaller in magnitude, were recorded for LWT/LS21.

In Table 4 regression coefficients for deviation from control line LC, on generation mean, are presented for all traits in the selected lines. The significant ( $P < 0.01$ ) responses observed for LSO/DWT and LWT/DWT resulted from positive correlated responses in the numerators, rather than from any change in DWT. These correlated responses for LSO and LWT in lines LSO/DWT and LWT/DWT were also greater than the direct selection responses recorded for the same traits in the lines LSO and LWT, respectively.

The significant ( $P < 0.05$ ) increase in LWT observed in line LWT/DWT was associated with an increase in number born and consequently number weaned, while average weaning weight of the progeny remained constant. The increase in numbers born exhibited in lines LSO and LSO/DWT did not result in any significant improvement in weaning performance traits. Indeed, the average weaning weight of progeny in line LSO decreased significantly ( $P < 0.05$ ). The increase in numbers and litter weight at weaning recorded in line LWT/DWT

**Table 2.** Realized and daughter-dam heritability estimates for the four selected traits

	Line (= Trait selected)			
	LSO	LWT	LSO/ DWT	LWT/ DWT
Realized $h^2$	0.10 (0.06)*	0.11 (0.07)	0.22*** (0.04)	0.22*** (0.08)
Daughter-dam $h^2$	0.04 (0.10)	0.24** (0.10)	0.21** (0.10)	0.15 (0.12)

\* Standard error

\*\*  $P < 0.05$

\*\*\*  $P < 0.01$

**Table 3.** Cumulative selection differentials, and selection and secondary selection intensities per generation. Cumulative selection differentials are expressed in the units of the selected traits; all other values are in units of standard deviation per generation

Line	LSO (no.)	LSO/ DWT (no./g)	LWT/ DWT (g/g)	LWT (g)
Item				
Cum. sel. diff.	17.6	0.48	5.94	185.9
Sel. intens./gen.	0.88	0.67	0.66	0.73
Sec. sel. int. (LS0)/gen.	—	0.63	0.43	0.51
Sec. sel. int. (LS21)/gen.	0.82	0.58	0.58	0.71
Sec. sel. int. (LWT/LS21)/gen.	—0.41	—0.06	0.21	0.22
Sec. sel. int. (DWT)/gen.	0.32	0.14	0.10	0.32
Sec. sel. int. (LWT)/gen.	0.48	0.42	0.68	—

**Table 4.** Regression coefficients of deviation from control on generation number

Line	LSO	LSO/ DWT	LWT/ DWT	LWT
Trait				
LSO (no.)	0.132 (0.074)*	0.200*** (0.045)	0.285*** (0.067)	0.001 (0.001)
LS21 (no.)	0.089 (0.123)	0.089 (0.101)	0.226** (0.063)	—0.096 (0.107)
LWT (g)	0.517 (1.272)	1.072 (1.071)	3.010** (0.947)	1.405 (1.147)
LWT/LS21 (g)	—0.135** (0.063)	—0.161 (0.099)	—0.013 (0.078)	0.075 (0.114)
DWT (g)	—0.105 (0.113)	0.014 (0.128)	0.107 (0.189)	0.061 (0.074)
CR (%)	0.140 (0.110)	—0.018 (0.158)	0.349** (0.127)	0.100 (0.137)
LS0/DWT (no./g)	0.006 (0.004)	0.007** (0.003)	0.009** (0.004)	0.001 (0.003)
LWT/DWT (g/g)	0.027 (0.053)	0.033 (0.043)	0.092** (0.035)	0.051 (0.037)

\* Standard error,

\*\*  $P < 0.05$

\*\*\*  $P < 0.01$

**Table 5.** Heritabilities, and genetic and phenotypic correlations for LS0, LS21, LWT, and DWT calculated within pairs of generations. (Heritability values are on the diagonal, with genetic correlations above and phenotypic correlations below the diagonal)

Traits	LS0	LS21	LWT	DWT
LS0	0.04 (0.10)*	1.08	2.13	-0.70 (0.40)
LS21	0.79 (0.03)	0.18 (0.11)	1.05	0.04 (0.04)
LWT	0.42 (0.03)	0.71 (0.03)	0.24 (0.10)	0.95 (0.35)
DWT	-0.04 (0.03)	0.33 (0.04)	0.28 (0.04)	0.28 (0.09)

\* Standard error

was also accompanied by a positive change in fertility, i.e., percentage of females producing a litter (CR).

Daughter-dam heritability estimates, daughter-dam genetic correlations, and phenotypic correlations for LSO, LS21, LWT, and DWT, pooled over lines LC and IC, are shown in Table 5. The heritability estimates for litter sizes were low, and two of the genetic correlations with number born were greater than one. The two estimates of the daughter-dam covariances that constituted the numerator in the estimation of the genetic correlation varied greatly in magnitude and in some cases sign. Such variation may arise from maternal effects and sampling variability.

## Discussion

Comparison of Tables 1 and 4 shows that the unselected control line (LC) tended towards lower performance in most reproductive traits measured, while the selected lines varied, but in general did better than the control. The positive selection responses shown by the selected lines (Table 4) arise, therefore, partly because they did better than a slowly deteriorating control line. This suggests that there has been an inbreeding decline affecting all lines during the progress of this experiment.

Beilharz (1982) analyzed the performance of the original control population of this mouse colony (line 1). This population was propagated by 20 pairs of mice per generation, which makes it similar in size to the present selection and control lines (progeny of 20 litters selected from 60). In line 1 a systematic effort was made to keep all 20 families present represented in future generations. This means that the rate of inbreeding in line 1 must have been lower than that of the present lines. Beilharz (1982) found that an overall measure of performance (total 9-week weight of young per female mated) decreased by about 4% per 1% rise in  $F$ . Decreases in component traits were lower in magnitude.

**Table 6.** Estimates of dispersion variance ( $\sigma_d^2$ ), error variance ( $\sigma_e^2$ ), and unbiased standard errors for realized  $h^2$  in each selected line

Line	LS0	LWT	LS0/ DWT	LWT/ DWT
$\sigma_d^2$	0.0048 $\sigma^2$	0.0052 $\sigma^2$	0.0098 $\sigma^2$	0.0098 $\sigma^2$
$\sigma_e^2$	0.0158 $\sigma^2$	0.0158 $\sigma^2$	0.0148 $\sigma^2$	0.0148 $\sigma^2$
SE ( $h^2$ )	0.024	0.094	0.129	0.131

In the five lines of this experiment, inbreeding coefficient ( $F$ ) rose by just over 1% per generation. The trend towards lower values seen in Table 1 (in units per generation) for line LC was almost 2% for LWT, about 0.5% for LWT/LS21, and about 1% for each of LSO and LS21. These tendencies are, therefore, entirely compatible with what inbreeding is expected to cause in populations of such size. Comparing the performance of each selected line as a difference from control will, therefore, give a good estimate of the response, due to the selection practiced in this experiment.

Because resources were limited in our mouse house, we made a deliberate decision to work with relatively large selection lines (60 pairs measured), even though this meant that the lines were unreplicated. These lines gave us reasonable selection intensities (proportion selected was 1 in 3, which led to average selection intensities per generation of 0.66 to 0.88 standard deviation units, as shown in Table 2), while maintaining effective population sizes close to 40. Hill (1972, and earlier papers) has shown that simple regression estimates of standard errors of realized heritabilities are often biased downwards. He further provided formulae to estimate variance due to genetic dispersion, and to estimate unbiased standard errors of realized heritabilities when estimates of heritability and phenotypic variance are available. Using the estimates of realized heritability from Table 2 and phenotypic variance from generation 0, the values shown in Table 6 can be calculated from Hill's formulae for the conditions of our experiment (selection in one direction with control population).

Table 6 shows that the dispersion variances are not large compared with error variances. The resulting unbiased estimates of standard errors influenced as they are by heritability estimates, are larger in the lines in which a higher realized heritability was found, yet they remain of the same order of magnitude as the simple estimates calculated directly from the regression statistics. Strict application of the unbiased standard errors of Table 6 would suggest that the larger realized responses found were not significant, while the smallest response, in line LSO, was significant. This is an absurd result, which suggests that caution is required in the application of the estimates, including the estimates of standard errors, and

in the interpretation of the selection responses that we found.

There is a clear pattern of responses to selection in this set of selection lines. The larger of these responses was greater than expected by chance on a null hypothesis, when what actually happened is measured as regressions of cumulative differences from the unselected control on generations, or on cumulative selection differential for the heritability estimates. It would be unproductive, and bad science, to claim that no effect occurred. What follows is our comparative discussion and interpretation of the results, in full appreciation of the difficulties and unreliabilities of all selection experiments, including this one.

Realized heritabilities, obtained for numbers born (Bakker et al. 1978) and litter weight weaned (Dalton and Bywater 1963; Steane and Roberts 1982), were similar to the estimates recorded for these two traits in the lines LSO and LWT in this experiment. As in this study, litter size was not standardized at birth in any of the above selection experiments. The realized heritabilities for the ratio lines, LSO/DWT and LWT/DWT, were much higher than those achieved for the lines LSO and LWT. In the two ratio lines, the response to selection was due to positive correlated responses in the respective numerators, litter size at birth and litter weight at weaning, while the denominator, 9-week weight of the dam, remained constant or, if anything, tended to increase (line LWT/DWT). Selection was, therefore, far more successful for litter size at birth and litter weight at weaning when both traits were divided by dam's 9-week weight.

This result is initially surprising, as several selection studies have shown that adult body weight is positively correlated with litter size at birth (McCarthy 1982). Body weight has also been found to be positively correlated with postnatal maternal performance (Nagai et al. 1978). Eisen (1978), in a comparison of selection lines where litter size was standardized at birth, found that the selection response for litter size was substantially reduced when included in an index with 6-week body weight selected in the opposite direction.

However, litter weight at weaning and numbers born alive are complex traits, which have been shown to be influenced by both direct and maternal genetic effects, as well as by maternal environmental effects (Hanrahan et al. 1973; Eisen 1978). The use of dam's 9-week body weight in the denominator has obviously altered one or several of these effects. Falconer (1955, 1965) demonstrated that the heritability obtained for litter size at birth could be effectively reduced to zero via a negative correlation between the breeding value or phenotype of the mother for litter size and the subsequent litter size of the offspring. This negative correlation was the result of an adverse maternal environmental effect. Falconer suggested that the major part of the negative maternal effect

operated through the growth of the daughters as expressed in their adult weight.

The higher realized heritabilities achieved in the ratio lines may be explained because dividing the numerators, litter size at birth, and litter weight at weaning by the dam weight has corrected for the maternal effect by standardizing both traits for female body weight. As the analysis using the index  $I = P_L - bP_D$  showed, division by the dam's weight has produced an effect very similar to that of a linear index. Standardizing litter size at birth will also remove this type of maternal effect. The correlated responses per generation for litter size at birth, where the trait was selected as a ratio in this experiment, were similar to the direct responses obtained for selection for numbers born where litter size was standardized at birth (Joakimsen and Baker 1977; Eisen 1978).

The primary aim of the experiment included determining whether the correlated responses of the component traits that contribute to weight of litter weaned varied among the selection lines. The pattern of correlated responses differed markedly between the two lines LSO/DWT and LWT/DWT. In the line selected for LWT/DWT there was a significant positive correlated response in numbers born alive, with a concomitant increase in number weaned, while average weaning weight of the progeny remained the same. This resulted in a significant increase in litter weight weaned.

In contrast, in the line selected for LSO/DWT the significant response in numbers born was accompanied by only a marginal response in numbers weaned which, coupled with a negative correlated response in average weaning weight of the young, resulted in only a very small increase in litter weight weaned. This result indicates that the genetic relationship between litter weight weaned and its components is asymmetrical.

If there is no genetic relationship between litter size at birth and postnatal maternal performance, asymmetry may be observed because the phenotypic relationship between numbers born and average weaning weight has been shown to be negative, and the relationship between numbers born and numbers weaned is curvilinear, due to a negative relationship between numbers born and survival (Nelson and Robinson 1976; Eisen and Saxton 1984). In this situation response to selection on litter size at birth by itself would result in "apparent" negative, genetic correlated responses in average weaning weight of the offspring and, depending on the mean litter size and the shape of the curve, a decreasing correlated response in both numbers and litter weight weaned. However, if maternal performance was improved simultaneously with litter size at birth, the "apparent" genetic correlations between the various traits would be quite different, as was the case in selection of LWT/DWT.

Studies of the genetic relationship between numbers born and postnatal maternal performance have pro-

duced conflicting results (Eisen et al. 1979; Robinson et al. 1974; Joakimsen and Baker 1977). Where positive correlated responses were reported, associated increases in adult body weight were also noted. The positive relationship between numbers born and maternal performance may be the result of positive relationships between body weight and both traits rather than of any direct association. As would be expected, there was no such positive change in adult body weight with selection for LSO/DWT.

A separate cross-fostering study has been done using the lines selected for LWT and LWT/DWT, together with the replicate control line IC, to evaluate the contribution of prenatal and postnatal effects to any response in weaning weight (Wilkinson 1986). The results indicated that both selected lines were superior with regard to postnatal maternal performance compared to the control. There was no prenatal effect evident. Whether differences in lactation performance had contributed to the postnatal effect was determined in a subsequent milk production study using the same lines (J. L. Wilkinson, unpublished data). Females of both selection lines produced more milk than those of the control line, with the line selected solely on litter weight weaned having the highest production. Steane and Roberts (1982), in their selection study, noted that the correlated response in average weaning weight of the offspring was larger than any response in number weaned. A similar pattern of correlated responses was found for line LWT. Another important correlated response with selection for LWT/DWT was the positive change in fertility, i.e., percentage of females producing a litter. Eisen (1972) noted a similar correlated response for selection on standardized 12-day litter weight.

Our experiment has shown that a significant response to selection can be obtained for litter size at birth and litter weight at weaning, provided that adverse maternal effects can be accounted for. However, correlated responses of the different reproductive component traits varied substantially with the two selection criteria, LSO/DWT and LWT/DWT. In terms of improving total litter weight weaned, direct selection for the trait was far more effective than indirect selection using litter size at birth. This result has obvious and important implications for efforts to improve productivity in sheep and pigs.

*Acknowledgements.* We thank the Australian Meat and Livestock Research and Development Corporation and the Pig Research Committee for the provision of financial support. Two anonymous referees gave important, constructive input towards improvements of this paper.

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