SELECTION FOR SEXUAL DIMORPHISM IN BODY WEIGHT OF MICE*

By E. J. Eisen† and J. P. Hanrahan†‡

Abstract

A general prediction formula was developed to include maternal effects in selection for sexual dimorphism. This prediction equation was extended to the case of within-family selection.

Within full sib family selection for sexual dimorphism in 6-week body weight of mice was carried out for 10 generations in two replicates. Two lines were selected for large males–small females ($Mf1$, $Mf2$) and two lines for small males–large females ($mF1$, $mF2$). The observed pooled divergence ($Mf-mF$) in sexual dimorphism for 6-week body weight was $0 \cdot 183$ g per generation which agreed with the predicted divergence of $0 \cdot 190$ g. There was no apparent asymmetry in the sexual dimorphism response. However, the observed divergence within each sex did not agree with that predicted. The observed divergence in mean body weight was such that the mF lines increased while the Mf lines decreased. This result was thought to be due to an environmental maternal effect.

I. INTRODUCTION

Predicting selection response and interpreting selection experiments involving quantitative traits generally are based on the assumption that direct additive variance is the only genetic parameter of importance. Theoretical developments indicate that selection response may be influenced by the genetic variance in sexual dimorphism (Becker, Sinha, and Bogyo 1964; Griffing 1966; Eisen and Legates 1966; Frankham 1968a). Rahnefeld et al. (1963) and Eisen and Legates (1966) have suggested that the genetic correlation between the sexes for post-weaning growth rate in mice was less than unity. Hanrahan and Eisen (1972) concluded that a small selection response for sexual dimorphism in this trait should be possible. Further information on the amount of genetic variability in sexual dimorphism of quantitative traits and the extent to which the dimorphism can be modified by artificial or natural selection would be useful. It may, for example, be desirable to change the sexual dimorphism in the growth curve of beef cattle toward a desired optimum (Cartwright 1970). Natural selection for sexual dimorphism in body size of birds has been shown to play an important role in mating behavior (Jehl 1970).

Few selection experiments designed to exploit genetic variability in sexual dimorphism for a quantitative character have been reported. Selection for sexual dimorphism has been moderately successful for abdominal bristle number in *Drosophila melanogaster* (Harrison 1953; Frankham 1968b) and body weight in mice (Korkman

1957). Frankham (1968a) found that single-sex selection changed the sexual dimorphism for abdominal bristle number in *D. melanogaster* since selection response was consistently greater in the selected sex.

The present study reports the findings of a selection experiment designed to alter sexual dimorphism for 6-week body weight of mice. Predicted response to selection for sexual dimorphism is generalized to account for genetic maternal effects, which are known to be important in mammalian growth (Willham 1963; Eisen, Legates, and Robison 1970).

II. MATERIALS AND METHODS

The base population of mice was an outbred strain (ICR) obtained from the Institute of Cancer Research, Philadelphia, Pa., and is maintained as a control in our laboratory with about 25 males and 50 females per generation. Estimates of genetic parameters have been given by Hanrahan and Eisen (1972).

The trait used to measure sexual dimorphism was 6-week body weight. The following replicate selection lines each were initiated with 16 randomly chosen male–female pairs from the ICR control: (1) selection for an increase in sexual dimorphism by choosing the largest male and smallest female within each family (*Mf*1, *Mf*2); and (2) selection for a decrease in sexual dimorphism by choosing the smallest male and largest female within each family (*mF*1, *mF*2). Selection was practiced within full sib families to minimize inbreeding effects. Paired matings of selected males and females within each line were made at random except for avoiding full sib matings. The expected inbreeding coefficient under this system of mating is 7·8% after 10 generations of selection. Only virgin females between 8 and 10 weeks of age at time of mating were used. Matings for replicate 2 followed replicate 1 by 2 weeks in each generation. Omission of the replicate designation indicates that data were pooled over replicates. No control population was maintained as such in this study since the major interest was divergence between lines in sexual dimorphism. It was assumed that the selected lines served as adequate controls for each other.

Male–female pairs were kept in polypropylene cages for 16 days after which females were removed to individual maternity cages and checked for litters beginning on day 19. Litters were standardized to eight mice at 5 days of age to minimize differences in suckling stimulus. As nearly as possible, four males and four females were randomly saved from each litter. Total litter weight was recorded at 12 days of age. Mice were weaned at 3 weeks of age and individual body weights recorded to the nearest tenth of a gram at 3, 6, and 8 weeks of age. Weight gains from 3 to 6 weeks (post-weaning gain) and from 6 to 8 weeks also were tabulated.

Although 16 male–female pairs were selected from all lines in each generation, three additional pairs per line were selected as reserve matings, to be used as substitutes only in cases of sterile matings or loss of a litter. The mean number of male and female progeny scored for 6-week body weight per generation–replicate–line subclass was 60·3 and 60·2, respectively.

Females were fed *ad libitum* on a high energy ration (Old Guilford, Emory Morse Co.) during pregnancy and lactation, and on a general diet (Purina Laboratory Chows, Ralston Purina Co.) from weaning until mating. The laboratory was maintained at $22 \pm 2°C$ and $50 \pm 5\%$ relative humidity with a cycle of 12 hr artificial illumination followed by 12 hr darkness.

III. RESULTS AND DISCUSSION

(a) *Predicting Selection Response for Sexual Dimorphism at Autosomal Loci in the Presence of Maternal Effects*

The underlying genetic model given by Hanrahan and Eisen (1972) is restated here for the sake of clarity:

$$P_j = \mu_j + A_{o_j} + A^d_{m_j} + E_j,$$

where P_j = phenotype of an individual of the jth sex, μ_j = population mean, A_{o_j} = additive genotypic value for direct effects, $A_{m_j}^d$ = additive genotypic value of the dam of the individual for maternal effects, and E_j = environmental effect. The developments which follow are based on the above model.

A general form for predicting response to mass selection in males and females, respectively, may be written as

$$\Delta G_1 = \tfrac{1}{2}[i_1(h_{o_1}^2 + \tfrac{1}{2}h_{m_1}^2 + \tfrac{3}{2}h_{o_1}h_{m_1}r_{o_1 m_1})$$
$$+ i_2(h_{o_1}h_{o_2}r_{o_1 o_2} + \tfrac{1}{2}h_{m_1}h_{m_2}r_{m_1 m_2} + \tfrac{1}{2}h_{o_1}h_{m_2}r_{o_1 m_2} + h_{o_2}h_{m_1}r_{o_2 m_1})]\sigma_{p_1},$$

$$\Delta G_2 = \tfrac{1}{2}[i_2(h_{o_2}^2 + \tfrac{1}{2}h_{m_2}^2 + \tfrac{3}{2}h_{o_2}h_{m_2}r_{o_2 m_2})$$
$$+ i_1(h_{o_1}h_{o_2}r_{o_1 o_2} + \tfrac{1}{2}h_{m_1}h_{m_2}r_{m_1 m_2} + h_{o_1}h_{m_2}r_{o_1 m_2} + \tfrac{1}{2}h_{o_2}h_{m_1}r_{o_2 m_1})]\sigma_{p_2},$$

and response in sexual dimorphism is given by

$$\Delta G_D = \Delta G_1 - \Delta G_2,$$

where

$h_{s_j}^2$ = heritability of the s effects in the jth sex; s = direct (o) or maternal (m) additive genetic effects, respectively, and j = males (1) or females (2),

$r_{s_j t_k}$ = genetic correlation between the s effects in the jth sex and the t effects in the kth sex; i.e. $r_{o_1 o_2}$ is the genetic correlation between direct additive genetic effects of males and females,

σ_{p_j} = phenotypic standard deviation of the jth sex,

i_j = standardized selection differential of the jth sex.

Expressing response in standardized units and assuming $i_1 = -i_2 = i$, the sexual dimorphism response becomes

$$\Delta G_D' = i\{[\tfrac{1}{2}(h_{o_1} - h_{o_2})^2 + (1 - r_{o_1 o_2})h_{o_1}h_{o_2}]$$
$$+ [\tfrac{1}{4}(h_{m_1} - h_{m_2})^2 + \tfrac{1}{2}(1 - r_{m_1 m_2})h_{m_1}h_{m_2}]$$
$$+ \tfrac{3}{4}[h_{o_1}h_{m_1}r_{o_1 m_1} + h_{o_2}h_{m_2}r_{o_2 m_2} - h_{o_1}h_{m_2}r_{o_1 m_2} - h_{o_2}h_{m_1}r_{o_2 m_1}]\},$$

and if $h_{o_1}^2 = h_{o_2}^2 = h_o^2$, $h_{m_1}^2 = h_{m_2}^2 = h_m^2$, $r_{o_1 m_1} = r_{o_2 m_2} = r_{o_2 m_1} = r_{o_1 m_2}$, then

$$\Delta G_D' = i[(1 - r_{o_1 o_2})h_o^2 + \tfrac{1}{2}(1 - r_{m_1 m_2})h_m^2].$$

The above prediction equations for male and female responses may be modified for within full sib family selection as follows:

$$\Delta G_{w_1} = \tfrac{1}{4}[i_1(h_{o_1}^2 + h_{o_1}h_{m_1}r_{o_1 m_1}) + i_2(h_{o_1}h_{o_2}r_{o_1 o_2} + h_{o_2}h_{m_1}r_{o_2 m_1})]\sigma_{p_1}K_1,$$

$$\Delta G_{w_2} = \tfrac{1}{4}[i_2(h_{o_2}^2 + h_{o_2}h_{m_2}r_{o_2 m_2}) + i_1(h_{o_1}h_{o_2}r_{o_1 o_2} + h_{o_1}h_{m_2}r_{o_1 m_2})]\sigma_{p_2}K_2,$$

where $K_j = [(n_j - 1)/n_j(1 - t_j)]^{\frac{1}{2}}$, and n_j and t_j are number of progeny per full sib family and phenotypic correlation among full sibs for the jth sex, respectively. The sexual dimorphism response within families is

$$\Delta G_{w_D} = \Delta G_{w_1} - \Delta G_{w_2}.$$

Clearly, the sign and magnitude of the genetic correlation between direct and maternal effects may play an important role in determining response even when selection is practiced within full sib families.

In the present experiment reasonably valid assumptions are that $i = i_1 = -i_2$, $K = K_1 = K_2$, $n = n_1 = n_2$, and $t = t_1 = t_2$, so that the predicted responses are

$$\Delta G_{w_1} = \tfrac{1}{4}i(h_{o_1}^2 + h_{o_1}h_{m_1}r_{o_1m_1} - h_{o_1}h_{o_2}r_{o_1o_2} - h_{o_2}h_{m_1}r_{o_2m_1})\sigma_{p_1}K,$$

$$\Delta G_{w_2} = -\tfrac{1}{4}i(h_{o_2}^2 + h_{o_2}h_{m_2}r_{o_2m_2} - h_{o_2}h_{o_1}r_{o_1o_2} - h_{o_1}h_{m_2}r_{o_1m_2})\sigma_{p_2}K.$$

Estimates of parameters for 6-week body weight in the ICR base population (Hanrahan and Eisen 1972) are summarized in Table 1. The genetic correlation

TABLE 1

BASE POPULATION STATISTICS FOR 6-WEEK BODY WEIGHT

Statistic	Males	Females	Difference*
Mean ($\bar{X}_j$)	$31 \cdot 81 \pm 0 \cdot 06$	$26 \cdot 53 \pm 0 \cdot 05$	$5 \cdot 28 \pm 0 \cdot 06$
Phenotypic variance ($\sigma_{p_j}^2$)	$7 \cdot 61 \pm 0 \cdot 26$	$5 \cdot 43 \pm 0 \cdot 18$	$9 \cdot 33 \pm 0 \cdot 09$
Additive genetic variance ($\sigma_{Ao,j}^2$)	$2 \cdot 96 \pm 0 \cdot 95$	$2 \cdot 78 \pm 0 \cdot 68$	$0 \cdot 69 \pm 0 \cdot 82$
Heritability of direct effects ($h_{o_j}^2$)	$0 \cdot 39 \pm 0 \cdot 12$	$0 \cdot 51 \pm 0 \cdot 11$	$0 \cdot 07 \pm 0 \cdot 09$
Correlation among full sibs (t_j)	$0 \cdot 35 \pm 0 \cdot 02$	$0 \cdot 35 \pm 0 \cdot 02$	$0 \cdot 11 \pm 0 \cdot 02$
Heritability of maternal effects ($h_{m_j}^2$)	$0 \cdot 75 \pm 0 \cdot 46$	$0 \cdot 31 \pm 0 \cdot 41$	—

Genetic correlation between sexes ($r_{o_1o_2}$) $= 0 \cdot 87 \pm 0 \cdot 09$
Genetic correlation between direct and maternal effects ($r_{o_jm_k}$) $= -0 \cdot 55$

* Refers to expectation of difference between the sexes for each statistic; i.e. $\sigma_{p(1-2)}^2 = \sigma_{p_1}^2 + \sigma_{p_2}^2 - 2\sigma_{p_1}\sigma_{p_2}r_{p_1p_2}$.

between the sexes was less than 1 (or alternatively the heritability of the sex difference was greater than zero). Therefore, a selection response in sexual dimorphism would be anticipated. Substituting the values of Table 1 and $i = 1 \cdot 03$, $n = 4$ into the preceding formulas and assuming that $r_{o_jm_k} = -0 \cdot 55$ for all j and $k = 1,2$, yields $\Delta G_{w_1} = 0 \cdot 034$, $\Delta G_{w_2} = -0 \cdot 061$, $\Delta G_{w_D} = 0 \cdot 095$, and divergence $= 0 \cdot 190$ g. These predictions must be interpreted with caution since the sampling variance of the predicted response is quite large. This is because the genetic parameter estimates themselves have standard errors of significant magnitude.

(b) Observed Response in Sexual Dimorphism

The divergence between lines ($Mf - mF$) in the sex difference for 6-week body weight is shown in Figure 1 for both replicates. Table 2 gives the regression coefficients of divergence in the sex difference for 6-week body weight on generations of selection. The pooled divergence was significant ($P < 0 \cdot 01$), and there was no significant difference between replicate regressions. The pooled divergence of $0 \cdot 183$ g per generation is in good agreement with the predicted divergence of $0 \cdot 190$ g. Figure 2 indicates that the Mf and mF lines showed a clear difference in sexual dimorphism for 6-week weight from generations 6 through 10 in both replicates.

Response to selection for sexual dimorphism may be influenced by scaling effects (Eisen and Legates 1966; Frankham 1968b). Frankham (1968a, 1968b) defined the sex dimorphism ratio as male mean/female mean and stated that it should be free of

scale effects. Although the ratio is only scale-free under certain restrictive assumptions, it is reported here for comparative purposes since Korkman (1957) reported
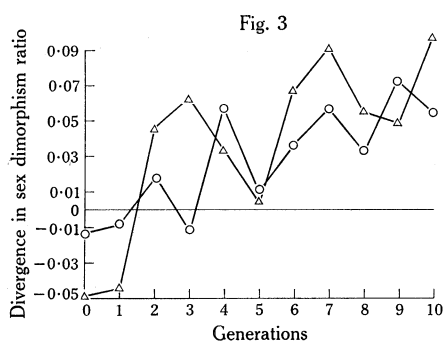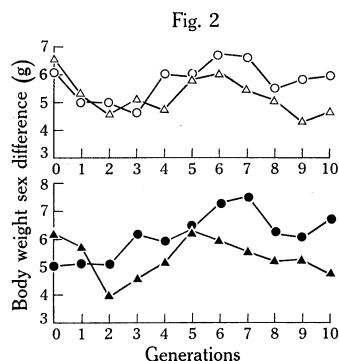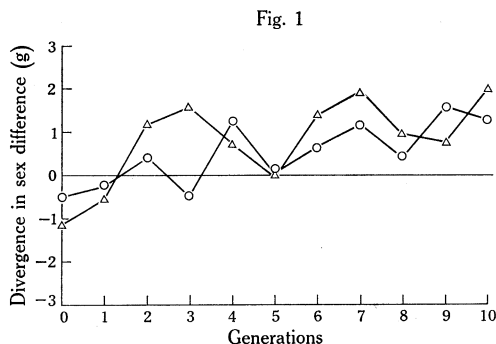

Fig. 1

Fig. 2

Fig. 3

Fig. 1.—Divergence $(Mf-mF)$ in the sex difference for 6-week body weight.
○ Replicate 1 $(Mf1-mf1)$.
△ Replicate 2 $(Mf2-mF2)$.

Fig. 2.—Response in the sex difference for 6-week body weight in $Mf1$ (○), $Mf2$ (●), $mF1$ (△), $mF2$ (▲).

Fig. 3.—Divergence $(Mf-mF)$ in the sex dimorphism ratio for 6-week body weight.
○ Replicate 1 $(Mf1-mF1)$.
△ Replicate 2 $(Mf2-mF2)$.

results of a selection experiment designed to alter the sex dimorphism ratio in body weight of mice.

TABLE 2

REGRESSION COEFFICIENTS OF THE DIVERGENCE $(Mf-mF)$ IN THE SEX DIFFERENCE AND IN THE SEX DIMORPHISM RATIO (MALE WEIGHT/FEMALE WEIGHT) ON GENERATION NUMBER

Trait	Sex difference			Sex dimorphism ratio		
	Replicate 1	Replicate 2	Pooled	Replicate 1	Replicate 2	Pooled
3-week weight (g)	0·047	0·010	0·028±0·023	0·0034	0·0013	0·0024±0·0017
6-week weight (g)	0·170**	0·196*	0·183±0·046**	0·0075**	0·0113**	0·0094±0·0019**
8-week weight (g)	0·218*	0·152*	0·185±0·055**	0·0095**	0·0091*	0·0093±0·0021**
Post-weaning gain (3–6 weeks) (g)	0·123*	0·183**	0·153±0·030**	0·0129**	0·0208**	0·0169±0·0029**
6–8 week gain (g)	0·047	−0·019	0·014±0·028	0·0615	−0·0021	0·0297±0·0227

* $P < 0·05$.   ** $P < 0·01$.

Figure 3 illustrates the divergence in the sex dimorphism ratio for 6-week body weight plotted against generation number. The pooled regression of divergence $(Mf-mF)$ on generation number (Table 2) of 0·0094 per generation was significant $(P < 0·01)$ and close to the predicted divergence in the sex dimorphism ratio of

$$[(\bar{X}_1+\Delta G_{w_1})/(\bar{X}_2-\Delta G_{w_2})]-[(\bar{X}_1-\Delta G_{w_1})/(\bar{X}_2+\Delta G_{w_2})] = 0·0081.$$

Korkman (1957) obtained a divergence in the sex dimorphism ratio of $0 \cdot 0125$ per generation (approximate value calculated from Table 3 of his paper), which is similar to that found in the present study.

The responses for divergence in the sex dimorphism ratio for each body weight and gain trait provided results similar to that obtained for the sex differences (Table 2). Therefore, there was no evidence to suggest that the sex dimorphism ratio removed any scale effect which may exist in the present data.

The realized cumulative selection differentials for each line are summarized in the following tabulation:

Line	Males (g)	Females (g)	Difference
$Mf1$	$8 \cdot 40$	$-7 \cdot 56$	$15 \cdot 96$
$Mf2$	$8 \cdot 77$	$-7 \cdot 48$	$16 \cdot 25$
$mF1$	$-9 \cdot 15$	$8 \cdot 03$	$-17 \cdot 18$
$mF2$	$-9 \cdot 78$	$8 \cdot 02$	$-17 \cdot 80$
Expected	$\pm 9 \cdot 94^{*}$	$\pm 8 \cdot 40^{*}$	$\pm 18 \cdot 34$

* $T(\frac{1}{2})i\sigma_{p_{w},j}$, where $T = 10$ generations, $i = \pm 1 \cdot 03$ standard selection differential units, and $\sigma_{p_{w_1}} = 1 \cdot 93$, $\sigma_{p_{w_2}} = 1 \cdot 63$ are phenotypic standard deviations within families for males and females, respectively.

The selection differentials are slightly larger for males due to the larger phenotypic standard deviation of males. The realized selection differentials for each sex were obtained by weighting the deviation of the selected individual's 6-week body weight from its full sib family mean by the number of progeny at 6 weeks. The weighted selection differentials did not differ greatly from the unweighted selection differentials and only the latter are presented. Thus, there was no suggestion that artificial selection was opposed by natural selection. The absolute values of the realized selection differentials were consistently less than the expected selection differential for both sexes, but the magnitude was not thought to be large enough to cause any serious bias in the predicted response.

The heritability of the sex difference, defined by Eisen and Legates (1966) as

$$h^2_{o(1-2)} = \sigma^2_{Ao(1-2)}/\sigma^2_{p(1-2)},$$

where $\sigma^2_{Ao(1-2)}$ and $\sigma^2_{p(1-2)}$ are additive direct genetic and phenotypic variances of the sex difference, equalled $0 \cdot 074$ in the base population (Table 1). The expected value of the heritability of the sex difference for within full sib family selection in the presence of maternal effects is modified to

$$h^2_{w_D} = \Delta G_{w_D}/S_w,$$

where

$$S_w = \tfrac{1}{2}i(\sigma_{p_{w_1}} + \sigma_{p_{w_2}}),$$

the expected within family selection differential. Substituting the parameter estimates for i and $\sigma_{p_{w},j}$ (see above tabulation) into this formula yields a value of $0 \cdot 052$ for the heritability of the sex difference based on within full sib family selection.

The realized heritability of the sex difference for 6-week body weight ($h^2_{w_D}$), calculated from divergence ($Mf-mF$) in response regressed on divergence in cumulative selection differential, is $0 \cdot 051 \pm 0 \cdot 015$ ($P < 0 \cdot 01$) for replicate 1 and

0·059±0·023 for replicate 2 ($P < 0·05$). Although the pooled realized heritability is relatively small (0·055±0·014), it is significant ($P < 0·01$), and there is close agreement between the realized heritability estimates from the two replicates. In addition, the realized heritability is not greatly different from the heritability predicted from the base population parameters. These results indicate that the additive genetic variance of the sex difference present for adult body weight of the mouse can be successfully exploited by means of artificial selection.

Using divergence between lines to measure selection response and realized heritability provides no information on asymmetry of response. The pooled responses in the sex difference and the sex dimorphism ratio for 6-week body weight regressed on generation number in the Mf and mF lines are given in Table 3. Correlated

TABLE 3

POOLED RESPONSE TO SELECTION FOR INCREASED (Mf) AND DECREASED (mF) SEXUAL DIMORPHISM REGRESSED ON GENERATION NUMBER

Trait	Sex difference		Sex dimorphism ratio	
	Mf lines	mF lines	Mf lines	mF lines
6-week weight (g)	0·126±0·043**	−0·058±0·049	0·0057±0·0014**	−0·0037±0·0017*
8-week weight (g)	0·060±0·046	−0·125±0·041**	0·0030±0·0013*	−0·0063±0·0014**
Post-weaning gain (3–6 weeks) (g)	0·087±0·034*	−0·067±0·042	0·0089±0·0031**	−0·0080±0·0033*

* $P < 0·05$.   ** $P < 0·01$.

responses are also given for 8-week body weight and post-weaning gain since they are highly correlated genetically with 6-week body weight. These estimates must be viewed with caution as they are not corrected for environmental effects. All of the responses were in the expected direction with the Mf lines showing an increase in sexual dimorphism for body weight and the mF lines showing a decrease (Fig. 2). The null hypothesis used to test whether the responses in the sex difference were symmetric for each trait was that the sum of the regression coefficients equals zero. In no case was this sum significantly different from zero, and it was concluded that selection for increased and decreased sexual dimorphism was not asymmetric.

TABLE 4

REGRESSION COEFFICIENTS OF DIVERGENCE ($Mf - mF$) IN MALE AND FEMALE 6-WEEK BODY WEIGHT (g)

Sex	Replicate 1	Replicate 2	Pooled	Predicted
Males	−0·022	−0·218**	−0·120±0·030**	0·068
Females	−0·192**	−0·414**	−0·303±0·023**	−0·122
Males−females	0·170**	0·196*	0·183±0·046**	0·190

** $P < 0·01$.

Selection experiments for sexual dimorphism require the evaluation of male and female responses separately. For example, it is conceivable that observed and predicted divergence in sexual dimorphism may agree, whereas observed divergence in each sex separately may not agree with that predicted. Examination of Table 4 indicates that this is what occurred in the present study. As already discussed, the

observed and predicted divergences in sexual dimorphism were in accord. However, the absolute pooled divergence in females was more than twice that predicted, and the pooled male divergence was negative rather than positive. The latter result is completely contrary to expectation. For example, the males from the mF lines were actually larger than males from Mf (Fig. 4) at the conclusion of the study. In contrast, Figure 4 shows that, as expected, females of the mF lines were larger than those from Mf. This outcome may be the result of a divergence in maternal environment between the lines, which is discussed in the next section.
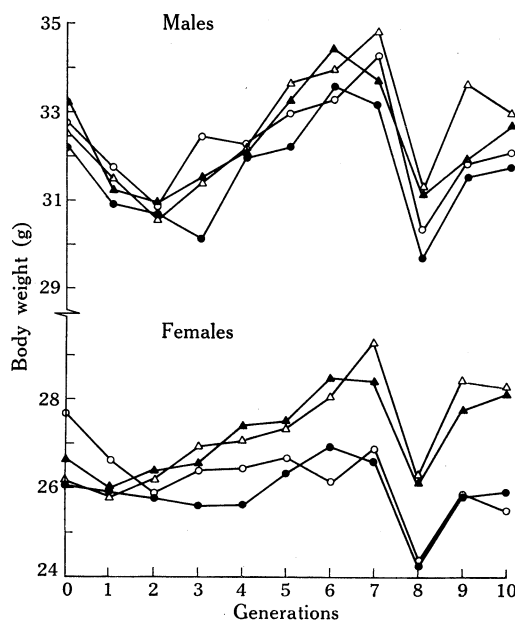

Fig. 4.—Response in male and female 6-week body weights.
● $Mf1$. ○ $Mf2$. ▲ $mF1$. △ $mF2$.

(c) Correlated Responses

Correlated responses in divergence $(Mf-mF)$ for the sex difference and the sex dimorphism ratio in the other body weight traits are presented in Table 2. Significant $(P < 0.01)$ positive correlated responses in pooled divergence were found for 8-week body weight and post-weaning gain but no significant responses were observed for 6- to 8-week weight gain and 3-week weight. These results were expected for the first three traits mentioned since there is a high positive genetic correlation between 6- and 8-week weight and between 6-week weight and post-weaning gain (Hanrahan and Eisen 1972), while the genetic correlation between 6-week weight and gain from 6 to 8 weeks is near zero (Young and Legates 1965). The absence of a significant correlated response for the dimorphism in 3-week body weight was not anticipated based on the high positive genetic correlation between 3- and 6-week weights. However, Hanrahan and Eisen (1972) reported a negative covariance between additive maternal effects on weaning weight and additive direct effects on 6-week weight, which would tend to cancel the influence of the positive correlation between additive direct effects.

Correlated responses in mean 6-week body weight, i.e. $\frac{1}{2}(\Delta G_{w_1} + \Delta G_{w_2})$, for the Mf and mF lines were also considered. The regression of the pooled divergence $(Mf-mF)$ for 6-week weight on generations of selection was significantly ($P < 0.01$) negative in both replicates (Table 5). The replicate responses were heterogeneous with

TABLE 5

REGRESSION COEFFICIENTS OF THE DIVERGENCE $(Mf-mF)$ IN MEAN BODY WEIGHT
AND LITTER TRAITS ON GENERATION NUMBER

Trait	Replicate 1	Replicate 2	Pooled
3-week weight (g)	0·013	−0·114*	−0·050±0·025
6-week weight (g)	−0·107**	−0·316**	−0·211±0·018**
8-week weight (g)	−0·157**	−0·357**	−0·257±0·024**
Post-weaning gain (3–6 weeks) (g)	−0·122**	−0·203**	−0·163±0·026**
6−8 week gain (g)	−0·062	−0·056	−0·059±0·023*
Number born	−0·07	0·12	0·02 ±0·06
12-day litter weight (g)	−0·02	−0·34	−0·18 ±0·12

* $P < 0.05$.   ** $P < 0.01$.

replicate 2 showing three times the divergence in mean 6-week body weight when compared with replicate 1. A similar negative divergence was observed for the other growth traits, with significant heterogeneity between replicates for 3- and 8-week weights. The relatively large negative divergence for mean 6-week body weight contrasts with a predicted divergence near zero. The reason for the discrepancy may be related to the fact that dams of the mF lines provided a superior environmental maternal effect which is reflected in larger post-weaning body weights of individuals in the mF lines. If this were the case, 12-day litter weight and 3-week individual weight, both highly influenced by maternal effects, should be larger in the mF line. Table 5 shows that there were no significant linear trends in the pooled divergence for these traits. However, examination of the data provides support for the contention that an environmental maternal effect was present since after the first generation of selection, 12-day litter weight was consistently higher in the mF lines, the mean divergence being 1·7 g in replicate 1 and 3·5 g in replicate 2. In addition, mean 3-week body weight did show a significant ($P < 0.05$) negative divergence in replicate 2.

Possible changes in fitness of the selected populations were measured by number born and 12-day litter weight. Results presented in Table 5 show no significant time trend in these traits, indicating that fitness was probably not affected adversely during the course of selection.

IV. ACKNOWLEDGMENT

V. REFERENCES

BECKER, W. A., SINHA, S. P., and BOGYO, T. P. (1964).—The quantitative genetic relationship of sexual dimorphism of birds. *Genetics, Princeton* 50, 235. (Abstr.)

CARTWRIGHT, T. C. (1970).—Selection criteria for beef cattle for the future. *J. Anim. Sci.* 30, 706–11.

EISEN, E. J., and LEGATES, J. E. (1966).—Genotype-sex interaction and the genetic correlation between sexes for body weight in *Mus musculus*. *Genetics, Princeton* **54**, 611–23.

EISEN, E. J., LEGATES, J. E., and ROBISON, O. W. (1970).—Selection for 12-day litter weight in mice. *Genetics, Princeton* **64**, 511–32.

FRANKHAM, R. (1968a).—Sex and selection for a quantitative character in *Drosophila*. I. Single-sex selection. *Aust. J. biol. Sci.* **21**, 1215–23.

FRANKHAM, R. (1968b).—Sex and selection for a quantitative character in *Drosophila*. II. The sex dimorphism. *Aust. J. biol. Sci.* **21**, 1225–37.

GRIFFING, B. (1966).—Influence of sex on selection. II. Contributions of autosomal genotypes having different values in the two sexes. *Aust. J. biol. Sci.* **19**, 593–606.

HANRAHAN, J. P., and EISEN, E. J. (1972).—Sexual dimorphism and maternal genetic effects on body weight in mice. *Theoret. appl. Genet.* (In press.)

HARRISON, B. J. (1953).—Reversal of a secondary sex character by selection. *Heredity* **7**, 153–64.

JEHL, J. R., JR. (1970).—Sexual selection for size differences in two species of sandpipers. *Evolution* **24**, 311–19.

KORKMAN, N. (1957).—Selection with regard to the sex difference of body weight in mice. *Hereditas* **43**, 665–78.

RAHNEFELD, G. W., BOYLAN, W. J., COMSTOCK, R. E., and SINGH, M. (1963).—Mass selection for post-weaning growth in mice. *Genetics, Princeton* **48**, 1567–83.

WILLHAM, R. L. (1963).—The covariance between relatives for characters composed of components contributed by related individuals. *Biometrics* **19**, 18–27.

YOUNG, C. W., and LEGATES, J. E. (1965).—Genetic, phenotypic, and maternal interrelationship of growth in mice. *Genetics, Princeton* **52**, 563–76.