GENETIC ANALYSIS OF COMPETITION BETWEEN CAGE-MATES AS A FACTOR AFFECTING THE GROWTH OF MICE.

by

LUIS SIEUVE MONTEIRO

Lic. Vet. (Lisbon)
Dip. Anim. Gen. (Edin.)

Thesis presented for the Degree of Doctor of Philosophy
of the University of Edinburgh in
the Faculty of Science.

Edinburgh. September, 1964

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I. INTRODUCTION

The relation between environment and the phenotypic value of a metric character has received little attention in genetical studies. The main concern has been to study the genetic values of a character, the environmental variation being regarded as a disturbing factor which is usually reduced as much as possible.

Much of the study of the genetics of quantitative characters has been done with the number of bristles on certain parts of the body of Drosophila and with body weight of mice. Both these characters have been chosen partly for their convenience, but body weight is also relevant to problems of the improvement of economic characters of farm animals. Drosophila bristles are very little subject to the influence of external environmental circumstances though localized non-genetic factors in development play a large part in determining the number of bristles at any one site (Reeve and Robertson 1954). Body weight in mice, as in other mammals, is, however, very sensitive to environmental factors, which play a large part in determining the phenotypic value. It therefore seems important to investigate in detail some of the possible environmental variables and to find out whether they are important sources of variation of body weight and, if so, the manner in which they affect weight. The particular aspects of environment studied in this work were those associated with the presence of other individuals during growth and the effect of maternal ability and litter size on post-weaning growth.

The presence of members of the same species and of the her species which live in the same niche are part of the environment f an individual. Competition between such individuals therefore ffects environmental variation. Intra-specific competition, besides s role in natural selection of wild species, is particularly important domestic and laboratory animals. These animals are, usually, kept groups in limited spaces and conditions where interactions of this nd are more likely to occur.

The intra-specific competition can be due either to the umber of individuals per unit of environment available (space, food, tc., whichever is the limiting factor), to specific behaviour of the ndividuals, or to interaction between both effects. These types of ompetition might affect both the means and the variances of the erformance of the individuals kept together. When the number of ndividuals per group varies, other things being equal, obviously the roup mean will be directly related to the density of individuals. owever, if dominant and submissive social behaviour are displayed, he statistic affected will be the within group variance. As this ype of social behaviour is only present when individuals are kept in roups and its effect might be related to the density of individuals, ne would therefore expect the variance of group means to be proportional o the variance of group size and the within group variance to be roportional to the group size. This was shown by McBride (1959) using olsson data on postweaning gain in weight of pigs penned separately r in litter groups. The variance between litters was bigger when the nimals were penned together in litters of varying sizes than when they ere penned separately, but the within litter variance showed a change in the same direction as the between litter variance, suggesting that growth in pigs is affected by the type of pen mates.

The influence of the number of mice per cage on postweaning gain was studied by Barkema (1961). Mice were weighed and housed in numbers varying from one to five animals in cages of the same size when four weeks old and weighed again at eight weeks. In these conditions there was a minimal mean gain in weight per cage when three mice were caged together and for the same number per cage a significant increase in the within cage variance. This seems to indicate that social relationships between mice are particularly effective when the group size is three. It was also found that the correlation between initial and final weight increased with the number of mice housed together. The same problem was studied by Wolff (1962) in slightly different conditions. The numbers housed together were nine, eighteen or thirty-six mice. The cages were arranged in such a way as to provide each mouse with 6.7 sq.in. of floor space regardless of the number caged together. Gain from three to six weeks was measured and no difference was found in weekly gain depending on numbers caged together. The contradiction between the results of Barkema and Wolff seems to be due to the fact that the former used cages of uniform size independently of the numbers housed together, whereas the second used the same area per mouse for any number caged. This indicates that competition is solely dependent on the area available per mouse. Therefore, it would be expected the strain of social relationship to be directly related to the number caged together in cages of uniform size. This was not the case in Barkema's work, where he found that, although the maximum number per cage was five, the maximum effect was found when three mice were housed together. As the minimal number caged together by Wolff was nine mice, a possible explanation for the absence of competition in his experiment is given by the existence of an upper limit of mice housed together above which a settled social order cannot be established, as it was shown by Grant and Chance (1958). The influence of the number of mice per cage on variability of the response to anaesthesia was studied by Mackintosh (1962). The experiment consisted in caging together one, two or eight mice and measuring the duration of seconal anaesthesia after three and ten days of caging. The variance of time of recovery from anaesthesia depending on the number caged together before the experiment, was found to be minimal for mice caged in pairs. The variance was less after the mice had been caged together for ten days than after they had been together for only three days prior to the administration of seconal. The experiment was conducted on two inbred strains and their F_1 cross, and the variance of the inbreds kept in pairs was in the same range as the variance of the hybrids. It was suggested that variability of the response is related to the existence of "social homeostasis", this relationship being at an optimum when mice are caged in pairs.

The performance of laying hens in relation to the amount of feeding space available per bird was studied by Lee et al. (1952). The feeding space per one hundred birds was 24 and 48 sq. ft. It was found that the effect of the lower level of feeding space was to reduce feed intake, egg production and feed efficiency.

The effect of linear distance between plants and competitional ability on yield, which is comparable to the effect due to variable number of animals housed together, was studied by Sakai and Suzuki (1954). Two varieties of barley with different competitive abilities were planted with variable distances between adjacent plants either in pure stand plots or in mixed plots. It was found that in several characters closely related to yield there was a direct relationship between the performance and the distance between adjacent plants. It was also found that when both varieties were planted with a short space between each other (2 cm.) the performance in the variety with superior competitive ability was twice the performance of the same variety when in pure stand plots.

Distance between adjacent plants is not the only factor affecting competition. Plants of different genotype planted in mixed plots showed different competitive ability. This effect of competition was shown by Sakai (1953). Using three varieties of wheat, by their differential performance when planted in mixed plots and pure strain plots, he was able to rank the varieties according to their competitive ability in relation to their dry weight and the number of heads per plant. A substantial increase in variance was also found when plants were planted in mixtures in comparison with the variance in pure stand plots. The variance attributable to competition varied from 25 to 40% of the total environmental variance, the maximum variance being found when the best and the worst competitors were growing together.

Competition between individuals of different genotypes was demonstrated in poultry by King and Bray (1958) using several strains in pure and mixed flocks. It was found that although the heavy strains could successfully compete with the light ones, the effects of such competition were small and on the limit of biological importance. On the same aspect of competition, Tindell and Craig (1958) found that less competitive strains, when mixed with more aggressive strains, tended to mature later. They also found that within strains and flocks there were correlations between the social status and certain quantitative characters. Hens ranking high in social order tended to be heavier at five months, gain less thereafter, feed more often, mature earlier and have higher egg production rates.

The existence of competition during pre-weaning growth in pigs depending on the birth weight was demonstrated by Lodge and Pratt (1963). A crossfostering experiment was made where one sow of a pair received the heaviest and the other the lightest half of the combined litters. Although at birth the weight of the four lightest pigs of the new "heavy" litter was significantly larger than the weight of the four heavier pigs of the new "light" litter, this difference was no longer apparent at three, five or eight weeks of age. This indicates that in "heavy" litters the four lightest pigs were in competitive disadvantage, whereas in the "light" litters the four heavier pigs could compete successfully with their litter mates.

An experiment using cross-fostered litters in pigs was made by Cox and Willham (1962) in order to determine the role of post-natal maternal effects on body weight. Each sow from a group of three reared two of her own pigs and two of each of the other females of the set. Weights were taken individually at 21, 42, 98 and 154 days. The analysis shows, besides the main effects due to genotype, pre-natal and post-natal maternal effects, a significant interaction between litters as born and litters as reared. This interaction was proved not to be due to fostering. It suggested the existence of a specific influence of the pen environment on the growth of the pig, acting in such a way that its performance could not be predicted by the performance of their sibs in other pens. The pen environment being controlled by the sow and other individuals present suggests that this interaction can be attributed to an effect of their pen mates on growth. If pigs within a litter compete for a limited amount of milk, the larger animals will take all the milk they can for themselves, thus reducing the milk available for the smaller ones and magnifying possible existing genotypic differences in body weight. This effect would only be displayed in certain litters where, by chance, smaller pigs were fostered with bigger ones or *vice versa*, and not when fostering occurred between litters with pigs of the same size, leading therefore to the non-additive effect found in that experiment.

The same type of experiment was carried out by Cox, Legates and Cockerham (1959) with mice and no interaction was found. Competition between litter mates is competition in the restricted sense of the word, where animals strive for a substance available in limited amounts and no social order has to be invoked to explain this effect but only that larger animals are better competitors than smaller ones. By contrast, when a social order exists, even if food is in excess, the competition will not be for the food itself but for access to it. The results will be the same in both cases, i.e. increase in the within group component of the environmental variance.

The competition between individuals of different genotypes can be of great importance in evolution. Any new genotype appearing in a population, in order to survive and reproduce itself, might have to compete with the existing genotypes and, in this case, no new genotype without ability to compete can be selected, regardless of its other characteristics. The change in environmental variance due to competitive effects can lead to different estimates of the genetic parameters of the same population. It was shown by Sakai (1955), using several characters in rice, that substantial improvement in heritability estimation could be achieved if competitive factors were taken into account. The way in which these factors should be accounted for depends on the purpose of the experiment. If the purpose is to estimate genetic parameters in the best laboratory conditions, the experiment should be designed in such a way as to minimise the expression of competitive differences between animals, by keeping a constant number in each group and separating animals with extreme genotypes, thus reducing the environmental component of variation and giving better conditions for the expression of the genotype. If, as it is suggested by Biggers et al. (1958), the minimal environmental variance is obtained when animals are in environmental conditions which give the best performance for the character under study, a further improvement might be made by determining in which group size the animals give the best performance. If, on the other hand, the aim is to extrapolate from the results of the experiment to natural conditions, where competitive effects cannot be minimized, the control of these factors would introduce errors in such extrapolations.

One of the purposes of the work to be described was to study the effect of competition on the body weight of mice during their growth and to determine the proportion of the total variance in body weight attributable to this factor, thus enabling a decision to be made regarding the profitability of efforts to control this in genetical experiments.

To account for the radical change in environmental conditions from the pre- to the post-weaning growth periods, a division was made between these two periods and a separate study of competition was made in each of them. During post-weaning growth i.e. from 3 to 6 weeks of age, both the effects of number and genotype per cage on the environmental variation were studied. During pre-weaning growth, i.e. from birth to 3 weeks of age, the density effect is exclusively determined by the size of the litter. Both the variance due to this factor and that due to differences of maternal ability are usually estimated together and termed "the variance due to common environment" (Falconer (1960)). In order to decrease this variance, the usual procedure is to standardize litter size but, unless the standardization is made for the number in the smallest litter, some mice have to be fostered in order to make up the number chosen. If there is any important effect of the genotype of the litter mates on pre-weaning growth of mice, this cross-fostering might increase the within litter variation by an unpredictable amount.

The effect of an environmental factor on body dimensions has two aspects - immediate and subsequent. The most commonly studied aspect is the effect of the factor on body dimensions during the period when the factor is acting, or on body dimensions at the end of the period of action. This might be called the "immediate" effect of the environmental factor. For example, the immediate effects of maternal influence on the growth of the young will be studied by their effects on pre-weaning growth or on weight at weaning. The studies of competition described before were concerned with the immediate effects.

The environmental factors may, however, influence the character after it has ceased to act. This will be called the "subsequent" effect. For example, the subsequent effects of maternal influences would be studied by their effects on post-weaning growth or on body dimensions at some later stage. The studies to be described in this section are concerned with the subsequent effects of maternal ability and litter size, as environmental factors, on the body weight of the young. Post-weaning growth was studied in order to find out how the environmental effects changed and how the final, adult weight was ultimately affected.

The subsequent effects of maternal factors on the growth of the young may be quite different from their immediate effects. For example, if pre-weaning growth is depressed by a poor maternal environment, post-weaning growth may be increased, so that the subsequent effect of the pre-weaning environment is progressively reduced in the weights at later ages. This is often referred to as "compensatory growth". However, the reverse may equally well happen, increased pre-weaning growth being followed by reduced post-weaning growth, and the term "compensatory growth" will be used here to refer to the subsequent effects of the pre-weaning environment, regardless of whether this is an increase or a decrease of post-weaning growth.

There have been a few previous studies of compensatory growth, chiefly in cattle. Dickinson (1960) used as source of environmental variation differences of pre-natal maternal ability of cows of three different breeds. Comparisons between individuals obtained from reciprocal crosses were made for several body measurements. It was found that differences existing at birth were no longer apparent at two years of age. There was a close relationship between the time of maturity of the character and the duration of the maternal effect. Thus earlier maturing characters were the first in which earlier existing differences were reduced. The same results were found by Taylor (1962), studying within pair variance of identical twins at successive ages. A pattern of increase of variability followed by a decrease of variability was found in several body dimensions studied. In all cases the age of maturity of the character corresponded closely with the age at maximum variability. Crichton et al. (1960) also studied dairy cattle, but used as source of environmental effect different planes of nutrition. They found that significant differences in body weight at early ages were no longer apparent at five years of age. One character affected by the plane of nutrition was the age at sexual maturity, as indicated by the onset of the first oestrus. However, sexual maturity took place at a constant percentage of the mature weight in differently treated cows.

The growth of rats was studied by Widdowson and McCance (1960). By reducing the number of rats reared by a female, they were able to increase the growth of the remaining young rats compared with others reared in normal-sized litters. It was found that at 21 days of age rats from small litters were twice to four times the weight of those from normal-sized litters. Differences in weight were apparent at later ages. The sexual maturity, measured by the age at opening of the vagina, was found to change with the treatment. In fast-growing females, the vagina opened at 36 to 37 days with a weight range of 80 to 100 grammes, whereas in normal growing females the vagina opened ten days later at a weight range of 70 to 90 grammes. The conclusion is that sexual maturity is determined by size rather than by age.

The evidence referred to seems to point out the conclusion that the growth process leads to a compensation for environmental factors occurring before weaning age and affecting body dimensions, in such a way that both positive or negative effects of an early environment on the character are greatly reduced at maturity. Compensatory growth is the expression here used to refer to both positive and negative aspects of this growth effect.

Another way of describing compensatory growth is through changes in the environmental component of variance. If compensatory growth occurs, the environmental variance will decrease at some later stage as compared with the variance at the time when the environmental factors are acting.

An investigation of compensatory growth must take account of the mathematical nature of the growth process. The growth of an individual can, ideally, be divided into two phases, the exponential and the asymptotic. During the exponential phase the rate of growth continually increases, in proportion to the weight attained, and during the asymptotic phase the rate of growth decreases till it is zero when the individual has attained its final weight. The mathematical expressions for the growth curve in the two phases are

$$Y_t = Y_o e^{kt}$$

for the exponential, and

$$Y_t = B - (B-C)e^{-k't}$$

for the asymptotic phase, where Y_t is the weight, or other bodily dimension, at time t, Y_o is the initial weight, B is the final, adult weight and C is the weight at the beginning of the asymptotic phase; k and k' are the relative rates of growth in each phase. The two curves are connected at weight of C, and this is the inflection point, at which the direction of curvature changes from positive to negative (Brody, 1945). The problem is to determine in which of these two phases compensatory growth occurs. Compensation can only occur when the growth process allows the variance due to earlier causes to decrease.

During the exponential phase of growth the relationship between successive measurements separated by one unit of time interval is given by $Y_t = Y_{t-1} e^k$. From this it follows that the variance of the second weight, Y_t, is related to the variance of the first weight, Y_{t-1}, by

$$\text{Var } Y_t = \frac{\bar{Y}_t^2}{\bar{Y}_{t-1}^2} \text{ Var } Y_{t-1}$$

provided the relative growth rate, k, is the same for all individuals. This relationship merely expresses the constancy of the coefficient of variation of Y. As $\bar{Y}_t^2$ is always larger than $\bar{Y}_{t-1}^2$, during the exponential phase of growth, there is an increase of variance with time. The obvious conclusion is that compensatory growth does not occur during this phase and if it occurs at all it has to act during the asymptotic phase.

If compensatory growth occurs during the asymptotic phase, and if it has the maximum effect so that the adult value of the character is the same for all individuals, then the variance of a later measurement is related to the initial variance at the beginning of this phase by the expression:

$$\text{Var } Y_t = \frac{(B - \bar{Y}_t)^2 \text{ Var C}}{(B - \bar{C})^2}$$

where C is the value of the character at the beginning of the asymptotic phase, B is the adult value and Y_t is the value at time t.

Decrease in variance due to compensatory growth can occur in two different ways. Either the variance of Y_t decreases gradually with the increase in $\bar{Y}$ until eventually the variance is zero when $Y_t = B$ i.e. when the adult stage is attained; or the compensation occurs by a shift of the inflexion point of the growth curve, so that the variance of C is zero.

A decision between these two hypotheses and a probable mechanism for compensatory growth can be visualised from the evidence of the effect of early environment on sexual maturity given by Crichton et al. (1960) on cattle and Widdowson and McCance (1960) on rats. As was said before, they found that the weight at sexual maturity was nearly the same for all individuals but the age at which sexual maturity occurred depended on the previous treatment. In individuals having a small body weight for environmental reasons, sexual maturity was delayed, with the result that it occurred at the same body weight as in better treated animals. As individuals at sexual maturity are in the same developmental stage, it may be concluded that they are also in the same developmental stage when they have the same body weight, and that there is a direct relationship between body weight during growth and physiological age. Therefore, one result of environmental factors acting during growth is to change the relationship between chronological and physiological age, and the effect of compensatory growth is to normalise this relationship.

If, as it is suggested by Brody (1945), sexual maturity is closely related to the inflexion point of the growth curve, changes in age at sexual maturity can be regarded as equivalent changes in age at the inflexion point. As the inflexion point of the growth curve determines the end of the exponential phase of growth, the effect on growth of early environmental factors is to change the duration of this phase, in such a way that animals start their asymptotic phase of growth at the same physiological age. Therefore, compensatory growth is the result of an inverse relationship between the effect of early environmental factors on body size and the duration of the exponential phase of growth. The degree of compensation depends on the variability of the character at the inflexion point.

The hypotheses to be tested in this work are:

(1) That there is an adjustment of growth for earlier occurring environmental factors affecting body size. This adjustment reduces the variability of adult body size in comparison with variability at early ages.

(2) That this adjustment consists in changes of the duration of the exponential phase of growth in such a way that the inflexion point of the growth curve occurs within a small range of the body dimensions considered.

Maternal effects on body weight in mice have been studied by Cox et al. (1959), Young and Legates (1960) and Brumby (1960). They found that maternal effects are still apparent at 12 weeks of age. The proportion of the total variance attributable to maternal effects was found to decrease from over 60% at 3 weeks to 16% at 8 weeks of age. The measure of maternal effect here used is the average weight of the litter at 3 weeks of age.

In order to test the hypotheses made, the points to be analysed in this work are:

(1) Relationship between age and the variance of body weight due to maternal effects.

(2) Relationship between the inflexion point of the growth curve and sexual maturity.

(3) Relationship between maternal effect and sexual maturity.

II. COMPETITION

(1) Material and Methods

Two experiments were designed to evaluate the importance of competition between mice of different genotypes as a factor influencing growth. The effects on pre-weaning growth were studied in the first experiment and on post-weaning growth in the second, which also included a study of the effect of the number of mice per cage.

The broad outline of the experiments was as follows. Groups of mice of the same strain and groups belonging to different strains were kept together in the same conditions for a period of time. Individual mice were weighed at the beginning and end of that period. Competition between genotypes was measured by the differential performance of individuals of the same strain in pure and mixed strain groups.

(i) Effect of competition between genotypes on pre-weaning growth. In order to get different genotypes for testing competition, a selection programme was carried out. This consisted of selecting two lines respectively for large and small weaning weight. As was stated earlier, the weaning weight depends largely on maternal effects. To eliminate the bias due to this factor, within litter selection was used. This method consists in choosing from each litter two individuals with the greatest deviation from the litter mean at 3 weeks of age. In the case of selection for large weaning weight, the heaviest individual of each sex at 3 weeks of age was selected, and for small weaning weight the lightest one of each sex in the litter was selected. These animals were used as parents of the next generation. This procedure, besides eliminating the bias due to maternal factors, has the advantage of doubling the effective population size, and so halving the rate of inbreeding (Falconer, 1960).

The selected individuals were mated at random, avoiding mating between close relatives.

The base generation consisted of 35 matings of a random-bred strain known as Q strain. This strain originated from crosses between six different strains.

The selection was carried out in four generations in the large and small line and generations were kept in step for the two lines.

From the original 35 matings, 32 were mated in the large line and 30 in the small line at the fourth generation. Losses were due to death or infertility.

Mice were mated when the youngest was 7 weeks old. By this time the oldest was about 8 weeks old. The number of mice in the litter at birth and at weaning was recorded and the offspring were weaned, weighed and selected at 3 weeks of age. The selected ones were stored six per cage until mating. Also at weaning, prior to selection, three mice of each sex were chosen at random from each litter. These were kept in cages of six and weighed weekly until 7 weeks of age, the age and weight of females being recorded when their vagina opened.

From the lines selected for large and small body weight, a cross-fostering experiment was designed in order to determine the effect of competition between genotypes on pre-weaning growth.

During the pre-weaning period competition is likely to arise from body size differences rather than social behaviour. Selection for body weight at weaning, therefore, seems to be the right approach to obtain strains with different competitive ability. However, as will be seen later, the four generations of selection obtained were not enough to give a difference between lines that could show a clear-cut picture of competition during suckling.

Mice to become parents of the cross-fostered litters were obtained in the following way. From a litter of selected parents after selection had been made in the way described, a second choice of mice was made. This choice consisted in selecting in each litter the second largest mouse of each sex in the line selected for large body weight and the second smallest mouse of each sex in the small body weight line. These mice were mated at random within each line and their offspring cross-fostered. In large litters a third choice was made in order to increase the number of matings. This was repeated in each generation of selection.

The disadvantage of this method is that, in the majority of the litters, the second choice mice were little different in weaning weight from the litter means, resulting in a very small selection differential. Therefore, their offspring at any generation were nearly equivalent, in respect of the selection applied, to the selected line one generation before. An alternative way was to do the cross-fostering on the second litters of the selected strains. This alternative was not adopted because it would have either increased the generation interval, or two generations would have had to be kept at the same time.

The cross-fostering was carried out in matings of second choice mice in the following way. Two females from the same or different lines, giving birth on the same day, had their litters rearranged in such a way that they reared five of their own offspring and five offspring of the other female. All combinations between and within strains were used. The plan of the cross-fostering is as follows:-

		Litters as born	
		A	B
Litters as reared	A	$a_1 \ldots\ldots\ldots a_5$	$b_1 \ldots\ldots\ldots b_5$
	B	$a_6 \ldots\ldots\ldots a_{10}$	$b_6 \ldots\ldots\ldots b_{10}$

The two females giving birth on the same day are represented by the capital letters A and B. These two females can belong either both to the large or to the small line, or one to the large and the other to the small line. Each column represents the mice as they were born. The rows show the arrangement of individual mice as they were reared. To distinguish between mice as born and as reared, a full sib group reared by the same mother will be called sibship and the two sibships reared by the same mother will be called a litter. The number in each litter was standardized at ten to avoid possible influences of litter size on competition. The standardization to ten mice per litter was chosen because the modal litter size of the Q strain is ten. The cross-fostering was done at random within females giving birth on the same day. Individual mice were identified and weighed, and the litters were rearranged at birth. The mice were weighed individually every week until they were 3 weeks old. The same procedure was used on the 2nd, 3rd and 4th generation of selection. The first generation of selection was not used because, for the reasons given before, the second choice offspring of both lines were, on average, genotypically equivalent to the original stock.

As any sibship of either line could have been reared by a large or small line mother and have had large or small litter mates, the following notation is used throughout.

Each sibship is identified by three capital letters.

Designate the 1st: The strain of young whose growth is measured (subscript N or F, whether "natural" or "fostered").

2nd: The strain of litter mates providing competition (with subscript as above).

3rd: The strain of the female rearing the litter.

Thus, for example, $S_F/L_N/L$ means small strain mice fostered (S_F), with large strain mice not fostered (L_N), all being suckled by a large strain female (L).

(ii) Effect of competition on post-weaning growth. The experiment designed to estimate the effect of competition on body weight during post-weaning growth followed the same principles as the experiment described above. Mice with the same and different genotypes were kept together in cages and competitive effects estimated from the differential performance of mice having individuals of the same and different genotypes as cage mates. An attempt was also made to determine the influence of the number per cage on competition.

Mice from the four inbred strains, JU, RIII, CBA and C_{57}, were used in this study. Mice from each strain were weaned and weighed at three weeks of age and, at that age, caged with individuals of the same strain or any one of the other strains. All possible combinations of two strains per cage were used, making a total of sixteen different groups. For example, a mouse of the JU strain could either be caged with other JU individuals or with CBA, C_{57} or RIII. The same was done for the other strains. If they were caged with mice of the same genotype, the two sets were obtained from different litters. Within this framework, cages of two and of four mice were established. Sexes were caged separately. The mice were weighed again at 6 weeks of age to obtain the gain from 3 to 6 weeks of age, the criterion used in the analysis. Twenty-four mice of each sex were used for each of the sixteen combinations of strains for groups of four mice caged together, making a total of 384 mice of each sex. The same numbers were used for groups of two mice caged together.

The competitive ability of a strain was measured by its effect as cage mates. Thus, for instance, the competitive ability of CBA mice in relation to the JU's was measured by the difference between the performance of JU's when caged with other JU's and JU's when caged with CBA's.

(2) Results

(i) Effect of competition between genotypes during pre-weaning growth. Four different effects were estimated from the data obtained in the cross-fostering experiments. These are:

(a) Fostering effect.

(b) Effect of genotype on maternal ability.

(c) Joint effects of genotype and competition.

(d) Effect of competition.

These effects were evaluated by comparison of the mean growth of mice that differed in relation to the effect under study but were otherwise identical. The measure of growth used in these experiments was the first, second and third week weight. The weights were used rather than gain in weight from birth, because the differences in birth weight between groups compared were very small.

The effects (a), (c) and (d) could be measured by the performance of young reared either by large line females or small line females. As in certain cases an interaction between the line of the female and the effect under study was apparent, the analyses were made separately for each type of female.

(a) Fostering effect.

It is possible that females can discriminate between their own offspring and fostered young when both are reared together. This could lead to different treatment of each set of young and, therefore, to a different performance of natural and fostered offspring. In order to investigate this possibility, comparisons were made between the natural and fostered offspring of a litter. Both sets of young compared were from the same line and were reared by the same mother. Using the notation described before, comparisons were made of $L_N/L_F/L$ with $L_F/L_N/L$ mice and of $S_N/S_F/S$ with $S_F/S_N/S$ mice. As comparisons could be made between individuals reared by the same mother, the method of paired differences was used to test the significance between the means of natural and fostered offspring. The results are shown in Table 1.

None of the differences between natural and fostered offspring of a litter is significantly different from zero. Also, the differences seem to be positive or negative in a random fashion. These results indicate, therefore, that there is no discriminatory treatment by the female of her natural or fostered offspring.

(b) Effect of genotype of the females on their rearing ability.

The analysis used to detect this effect consisted in testing mean paired differences. A number of litters of both lines were split and five full sibs reared by their own mother and other five by a female of the other line, and vice versa. Therefore, it was possible to pair observations of a set of mice reared by a large female with another set of mice reared by a small female, provided that the two sets were born

TABLE 1. Fostering effect

Means and standard errors of paired differences between natural and fostered offspring. Weights in grams.

eneration of election	d.f.	Birth weight	1st week weight	2nd week weight	3rd week weight
		$L_N/L_F/L - L_F/L_N/L$			
2nd	18	0.05 ± 0.03 NS	0.03 ± 0.07 NS	0.06 ± 0.09 NS	-0.04 ± 0.25 NS
3rd	20	0.05 ± 0.03 NS	0.09 ± 0.07 NS	0.10 ± 0.08 NS	0.06 ± 0.22 NS
4th	21	-0.01 ± 0.03 NS	-0.01 ± 0.07 NS	0.03 ± 0.10 NS	-0.03 ± 0.22 NS
		$S_N/S_F/S - S_F/S_N/S$			
2nd	16	0.00 ± 0.02 NS	0.00 ± 0.07 NS	0.11 ± 0.09 NS	-0.04 ± 0.24 NS
3rd	21	0.01 ± 0.02 NS	0.06 ± 0.06 NS	0.08 ± 0.06 NS	0.10 ± 0.22 NS
4th	20	-0.01 ± 0.03 NS	-0.04 ± 0.06 NS	-0.12 ± 0.08 NS	0.11 ± 0.18 NS

NS = non-significant ($P > 0.05$)

in the same litter. The difference between the maternal ability of females of the two lines can be measured by the different performance of the large or the small young they rear. In this way the effect of the genotype of the females is confounded with the fostering effect of the young. However, from the evidence presented above, it is reasonable to treat the fostering effect as non-existent.

Although some sibships could not be used because of loss of some of their full sibs reared in the other litter, the method of paired differences proved to be more efficient than the comparison between randomized groups. The results in Table 2 are presented separately for comparisons between offspring of the large line and of the small line. From the results it can be seen that the majority of differences are not significantly different from zero. The few significant ones are to be expected by chance in view of the number of comparisons made. The conclusion is, therefore, that the difference in mothering ability between females of the large and small lines is either very small or non-existent. However, the differences are predominantly positive in one set of comparisons; i.e. the large females are better than small ones, when the mothering ability is measured by the weights of small line offspring, whereas when measured by the large line offspring the differences seem to be randomly positive or negative.

(c) Joint effect of genotype and competition.

These effects were evaluated by comparing the mean weight of mice of the large and small lines reared together by the same female. The comparisons were made separately for females of each line.

As both competition and selection could affect the within-sibship variance of weight, these were calculated, compared in the way described

TABLE 2 Effect of genotype on maternal ability

Mean and standard errors of the differences between the performance of young reared by large and small line females.

eneration of election	d.f.	Birth weight	1st week weight	2nd week weight	3rd week weight
		$L_N/S_F/L - L_F/S_N/S$			
2nd	12	0.02 ± 0.01 NS	0.41 ± 0.11**	0.59 ± 0.25*	0.94 ± 0.50 NS
3rd	13	0.01 ± 0.02 NS	0.07 ± 0.11 NS	-0.09 ± 0.23 NS	-0.13 ± 0.39 NS
4th	22	-0.01 ± 0.01 NS	-0.00 ± 0.12 NS	0.09 ± 0.19 NS	-0.17 ± 0.36 NS
		$S_F/L_N/L - S_N/L_F/S$			
2nd	11	0.02 ± 0.02 NS	0.27 ± 0.08**	0.45 ± 0.26 NS	0.84 ± 0.64 NS
3rd	13	0.07 ± 0.01**	-0.04 ± 0.11 NS	0.09 ± 0.26 NS	0.35 ± 0.46 NS
4th	21	0.02 ± 0.22 NS	0.11 ± 0.10 NS	0.30 ± 0.18 NS	0.39 ± 0.36 NS

NS $(P > 0.05)$

* $(P < 0.05)$

** $(P < 0.01)$

above, and tested by a two-tailed F- test. The results are presented in Table 3. The within-sibship variances of the two lines do not differ significantly except in a few cases that can be reasonably attributed to chance. Therefore, it can be concluded that neither selection nor competition affects the variance of weight.

The comparisons between means were made by the method of paired differences. The results are presented in Table 4, separately for mice reared by large and by small line females. The mean of differences between individuals of the two lines are consistently significant and increasing with the generation of selection. This shows that selection was effective over the four generations. However, these differences are very small, the largest being less than one gram at 3 weeks of age. The differences between lines increase with age, being greatest at 3 weeks. This is due to the fact that selection was applied at that age and also to the nature of the growth process, which increases earlier differences.

With the exception of the second generation of selection, the difference between the mean weight of the two lines at 3 weeks is slightly larger when mice are reared by small females than when mice are reared by large line females.

(d) Effect of competition.

The competitive effect was evaluated by comparing mice of one line reared by females of the same line but having different litter mates. The comparisons were made separately for offspring reared by large and by small line females.

Although the comparisons between the within full-sib variances for the joint effects of selection and competition indicate that neither

TABLE 3. Effect of genotype and competition

Within sibship variance of large and small offspring reared by the same female. The significance levels refer to the differences between the two lines.

Generation of selection	d.f.	Birth weight			1st week weight			2nd week weight			3rd week weight		
		$L_N/S_F/L$		$S_F/L_N/L$	$L_N/S_F/L$		$S_F/L_N/L$	$L_N/S_F/L$		$S_F/L_N/L$	$L_N/S_F/L$		$S_F/L_N/L$
2nd	64	0.0096	NS	0.0134	0.06	NS	0.07	0.15	NS	0.14	0.65	NS	.69
3rd	84	0.0096	NS	0.0088	0.07	NS	0.05	0.17	NS	0.10	0.80	NS	.64
4th	120	0.0084	NS	0.0094	0.09	*	0.06	0.12	NS	0.11	0.63	NS	.66
		$L_F/S_N/S$		$S_N/L_F/S$	$L_F/S_N/S$		$S_N/L_F/S$	$L_F/S_N/S$		$S_N/L_F/S$	$L_F/S_N/S$		$S_N/L_F/S$
2nd	65	0.0109	NS	0.0076	0.12	**	0.05	0.26	**	0.10	0.70	NS	0.44
3rd	72	0.0085	NS	0.0089	0.05	NS	0.06	0.13	NS	0.12	0.54	NS	0.58
4th	116	0.0108	NS	0.0082	0.09	*	0.06	0.15	NS	0.11	0.63	NS	0.70

NS $(P > 0.05)$

* $(P < 0.05)$

** $(P < 0.01)$

TABLE 4. Effect of genotype and competition

Means and standard errors of paired differences between large and small line offspring reared by the same female.

Generation of selection	d.f.	Birth weight	1st week weight	2nd week weight	3rd week weight
		$L_N/S_F/L - S_F/L_N/L$			
2nd	14	0.09 ± 0.05 NS	0.29 ± 0.05**	0.27 ± 0.06 **	0.63 ± 0.15 **
3rd	20	-0.00 ± 0.03 NS	0.17 ± 0.05 **	0.29 ± 0.08 **	0.57 ± 0.14 **
4th	29	0.03 ± 0.02 NS	0.26 ± 0.06 **	0.40 ± 0.07 **	0.64 ± 0.17 **
		$L_F/S_N/S - S_N/L_F/S$			
2nd	15	0.04 ± 0.03 NS	0.18 ± 0.06 **	0.22 ± 0.07 **	0.39 ± 0.24 NS
3rd	17	.0.03 ± 0.03 NS	0.14 ± 0.08 **	0.27 ± 0.12 *	0.71 ± 0.24 **
4th	28	0.03 ± 0.03 NS	0.29 ± 0.08 **	0.41 ± 0.09 **	0.82 ± 0.21 **

NS ($P > 0.05$)

* ($P < 0.05$)

** ($P < 0.01$)

of these effects had any influence on the variance, comparisons of within sibship variances were made for the competitive effect. The results are shown in Table 5.

Some of the variances differ significantly when comparisons are made within mice of the small line. However, the last generation shows no significant difference between the variances. In these circumstances, no sure conclusion can be drawn about the effect of competition on the variance.

The comparison between means for the evaluation of the competitive effect could not be made by the method of paired differences, because comparisons had to be made between offspring reared by a random set of females. The standard errors of the differences are, therefore, fairly large in relation to those estimated for the other effects.

The results are presented in Table 6. No significant differences were found and, therefore, the conclusion to be drawn from the results is that the competition effect is either very small or non-existent.

However, in small line mice reared by small mothers the differences in weight depending on the litter mates are larger than those of large mice reared by large females. The differences in this line also increase with the generation of selection whereas in the large line mice they seem to be randomly distributed over the three generations of selection studied. If the effect of competition exists, it seems to interact with either the genotype of the young measured or with the genotype of the females which rear these young.

Conclusions

From the cross-fostering experiment the only clear-cut results are those referring to the fostering effect and response to selection.

TABLE 5. Competition effect

Within full sibship variance of offspring of the same line reared by females of the same line, having large and small litter mates. Significance of the difference due to litter mates.

Generation of selection	d.f.		Birth weight		1st week weight		2nd week weight		3rd week weight	
	$L_N/S_F/L$	$L_N/L_F/L$	$L_N/S_F/L$	$L_N/L_F/L$	$L_N/S_F/L$	$L_N/L_F/L$	$L_N/S_F/L$	$L_N/L_F/L$	$L_N/S_F/L$	$L_N/L_F/L$
2nd	60	76	0.0134	0.0091	0.07	0.06	0.14	0.15	0.69	0.74
			NS		NS		NS		NS	
3rd	84	84	0.0088	0.0118	0.05	0.09	0.10	0.13	0.64	0.67
			NS		*		NS		NS	
4th	120	88	0.0094	0.0106	0.06	0.07	0.11	0.13	0.66	0.60
			NS		NS		NS		NS	
	$S_N/S_F/S$	$S_N/L_F/S$	$S_N/S_F/S$	$S_N/L_F/S$	$S_N/S_F/S$	$S_N/L_F/S$	$S_N/S_F/S$	$S_N/L_F/S$	$S_N/S_F/S$	$S_N/L_F/S$
2nd	68	64	0.0081	0.0109	0.05	0.12	0.14	0.26	1.05	0.70
			NS		**		**		*	
3rd	88	72	0.0079	0.0085	0.06	0.05	0.24	0.13	0.90	0.54
			NS		NS		**		*	
4th	84	116	0.0056	0.0108	0.07	0.09	0.19	0.15	0.83	0.63
			*		NS		NS		NS	

NS ($P > 0.05$)

* ($P < 0.05$)

** ($P < 0.01$)

TABLE 6 Competition effect

Means and standard errors of the differences between offspring of the same line, reared by females of the same line, having large and small litter mates.

Generation of selection	d.f.	Birth weight	1st week weight	2nd week weight	3rd week weight
		$L_N/S_F/L - L_N/L_F/L$			
2nd	32	0.02 ± 0.04 NS	0.33 ± 0.15*	0.34 ± 0.30 NS	0.86 ± 0.61 NS
3rd	40	-0.02 ± 0.04 NS	-0.04 ± 0.14 NS	-0.19 ± 0.24 NS	-0.46 ± 0.50 NS
4th	50	0.05 ± 0.03 NS	0.15 ± 0.14 NS	0.10 ± 0.23 NS	0.18 ± 0.49 NS
		$S_N/S_F/S - S_N/L_F/S$			
2nd	31	0.01 ± 0.03 NS	0.00 ± 0.15 NS	-0.17 ± 0.11 NS	-0.17 ± 0.36 NS
3rd	38	0.06 ± 0.03 NS	0.11 ± 0.13 NS	0.14 ± 0.22 NS	0.29 ± 0.47 NS
4th	48	-0.03 ± 0.04 NS	0.06 ± 0.14 NS	0.30 ± 0.20 NS	0.51 ± 0.38 NS

NS ($P > 0.05$)

* ($P < 0.05$)

The effect of fostering, if any, is negligible. Females do not discriminate between their own offspring and the fostered young. The same results were found by Brumby (1960).

The difference between the large and small line of second choice mice, measuring the response to selection, increased with the generation of selection, showing that selection was effective over the four generations. However, the response in both lines was very small. This was not expected from results obtained by Hull (1960), who used the same method of selection. However, as it will be seen later, the heritability of body weight at three weeks is quite small and selecting within litters only uses half of the additive variance. It seems worth mentioning the larger differences between lines observed in mice reared by small line females.

As the results for the effects of genotype on mothering ability and competition are not significant, the only conclusions that can be drawn from the experiment are that if these effects exist they are very small and unimportant. However, a tentative hypothesis will be made in order to account for the trend observed in the results.

The effect of genotype on maternal ability seems only to be effective when measured in small line offspring and no differences at all are found when large line offspring are used. As, in both cases, the same mothers are compared, the only possible explanation is that when young of the small line are reared with large line young, only the small offspring are affected by the poor mothering ability of the female. This indicates that when the supply of milk is slightly reduced, large mice still manage to get all they need, thus reducing the amount of milk available for the small mice. The results of competition agree with this hypothesis.

Although the performances depending on litter mates of small mice reared by small mothers are not significantly different, the differences in body weight are comparatively large, reaching 60% of the joint effect of competition and selection. Also in small mice, with the exception of the second generation of selection, the differences in body weight are consistently positive. Therefore it seems reasonable to conclude that, during suckling, competition is evident only when the supply of milk is limited and, in these conditions, the mice with inferior competitive ability show a worse performance than they do in non-competitive conditions. On the other hand, the mice with the best competitive ability are not affected by the same conditions. This view is substantiated by the differences found in the joint effects of response to selection and competition between mice reared by large and small females. As the average genotype is the same in both cases, the larger differences between lines found when the mice are reared by small females have to be due to competition, thus showing that competition is effective only when a limiting environmental factor is present.

As has been stated, these conclusions are only tentative and to test them it would be necessary to repeat the experiment using mice with wider genotypic differences than those used here.

(ii) Effect of competition on post-weaning growth.

The influences of competition between individuals of different genotypes and of the number per cage on post-weaning growth are studied in this section. Post-weaning growth was measured by the gain in weight between 3 and 6 weeks of age. Competition was evaluated by the effect of the different competitive conditions on means and variances of gain.

It was found that gain in weight from 3 to 6 weeks of age was pendent on the 3 week weight. This implies that a certain proportion the variance of gain can be attributed to the variance in 3 week ight. This, of course, increases the error variance, thus decreasing e efficiency of the analysis. It was then decided to remove the effect 3 weeks weight on gain. The method used is described by Fisher (1958) d consists in using as error variance the mean square deviations from e regression line of gain on 3 week weight. Random differences in mean week weight of mice receiving different treatments are also removed.

The regression coefficients of gain on 3 week weight, of each x, number per cage and strain are presented in Table 7. There are rge differences between males and females in the regression coefficients. les have positive regression coefficients whereas females, with the ception of the CBA strain, have either zero or negative regression efficients. The number per cage also influences the regression efficient which is larger when four mice are caged together. There e also large differences between the regression coefficients of strains. erefore the correction for 3 weeks weight was made separately for each x, strain and number per cage. Corrections were not used for the cases ere the regression coefficient was not significantly different from ro, as the reduction in error variance would not be compensated by e loss of degrees of freedom.

The variances depending on strains and cage mates and pooled r number per cage are presented separately for females and males in able 8. Comparisons were made for each strain between mice reared in ure strain and mixed strain cages.

TABLE 7. Regression coefficients of gain on three week weight.

Strains	Females		Males	
	2/cage	4/cage	2/cage	4/cage
JU	-0.28 ± 0.10**	-0.03 ± 0.09	0.23 ± 0.13	0.53 ± 0.15**
RIII	-0.02 ± 0.08	-0.07 ± 0.10	0.30 ± 0.11**	0.41 ± 0.13**
CBA	0.17 + 0.07 *	0.68 + 0.11**	0.50 + 0.11**	0.97 ± 0.15**
C57	-0.06 ± 0.03	-0.25 ± 0.18	0.70 ± 0.18**	0.63 ± 0.16**

* $(P < 0.05)$

** $(P < 0.01)$

TABLE 8. Variance depending on strain and on cage mates. Significance of the difference between the variance of each strain in pure and mixed strain cages.

	STRAINS				
age-mates	JU	RIII	CBA	C_{57}	Variance according to cage-mates
	Females				
JU	0.94	0.76 NS	1.17 *	3.73 **	1.65
RIII	0.62 NS	0.64	0.86 **	0.88 NS	0.75
CBA	1.41 NS	1.18 *	2.04	2.26 *	1.72
C_{57}	2.14 **	1.30 *	1.83 NS	1.20	1.62
ariance f strains	1.28	0.97	1.47	2.01	
	Males				
JU	2.96	1.84 NS	4.59 NS	3.47 NS	3.22
RIII	2.77 NS	2.32	3.84 NS	3.36 NS	3.07
CBA	2.15 NS	1.61 NS	3.37	1.88 *	2.25
C_{57}	2.01 NS	2.89 NS	2.37 NS	3.31	2.65
ariance f strains	2.48	2.17	3.54	3.01	

NS ($P > 0.05$)
* ($P < 0.05$)
** ($P < 0.01$)

The homogeneity of the variance was tested for the within rain variance and the variance due to cage mates by the Bartlett test nedecor, 1956). The variance of gain differed with the strain in both emales ($\chi^2_3 = 24.08$) and males ($\chi^2_3 = 12.74$), whereas the variance due o cage mates was significantly heterogeneous for females ($\chi^2_3 = 35.48$) t not for males ($\chi^2_3 = 7.69$). The heterogeneity of the variance due o cage mates in females is clearly due to the very low variance that ice of the RIII strain induce in their cage mates of all strains. lthough the overall variance due to other cage mates does not differ, n some specific combinations of strains caged together there are ubstantial differences between the variances of females of the same train when in pure and mixed cages. These are the C_{57} females when aged with JU's, the C_{57} females when caged with CBA's, and the JU emales when caged with C_{57}'s. Also the CBA's in pure cages have a arger variance than any combination of CBA's caged with other strains.

The variance of each strain according to the number caged ogether, and the overall variance according to the number per cage, re presented in Table 9. The overall strain variance of both males nd females is independent of the number caged together. This is equally rue when the comparisons between variance according to the number per age are made separately for each strain, with the exception of mice of he CBA strain. In this strain the variance of gain is significantly arger in both males and females when four are kept in the same cage s compared with two per cage.

The pooled variances of gain for the four strains classified ccording to the strain of their cage mates and to the number per cage re presented in Table 10.

TABLE 9. Variance of gain in weight according to the strains and number per cage. Significance of the difference between two and four mice per cage.

	STRAINS				
umber er cage	JU	RIII	CBA	C_{57}	Variance according to number per cage
		Females			
/cage	1.44 NS	1.09 NS	0.90 **	1.66 NS	1.27 NS
/cage	1.12	0.86	2.05	2.37	1.60
		Males			
/cage	2.61 NS	2.08 NS	2.39 **	3.51 NS	2.68 NS
/cage	2.34	2.25	4.70	2.36	2.91

NS $(P > 0.05)$

** $(P < 0.01)$

TABLE 10. Variance of gain classified according to cage mates and number per cage. Significance of the difference between two and four per cage.

	STRAIN OF THE CAGE MATES			
Number per cage	JU	RIII	CBA	C_{57}
		Females		
2/cage	1.66 NS	0.85 NS	1.02 **	1.55 NS
4/cage	1.64	0.65	2.42	1.69
		Males		
2/cage	2.83 NS	3.21 NS	2.02 NS	2.68 NS
4/cage	3.60	2.94	2.49	2.62

NS ($P > 0.05$)

** ($P < 0.01$)

The effect of the strains on the variance of gain of their cage mates is the same with two mice per cage as with four, in both males and females, with one exception: female mice that have CBA females as cage mates are significantly more variable in cages of four mice than in cages of two.

To study the overall effect on mean gain in weight from 3 to 6 weeks of age of different competitive conditions set by the strain of cage mates and number per cage, an analysis of variance was conducted. This method is not strictly valid in this case, as there are differences in the variance of each strain and, in females, of the variance due to cage mates. The conclusions, however, are not likely to be seriously affected. The analysis of variance is presented in Table 11.

The significance of the mean squares due to number per cage and cage mates in both males and females shows that the effect of competition between individuals of different genotypes and the number per cage affects the mean post-weaning gain. The significance of the mean squares due to strains merely reflects the genetic differences between the strains. The only significant interaction in the analysis is the interaction between number per cage and strains. This shows that the number caged together does not affect all the strains in the same way. The non-significance of the interaction between strains and cage mates indicates that the competitive ability of a strain is independent of the type of the strain they are competing with. The same result obtained for the interaction between cage mates and number per cage implies that the competitive ability of a strain is the same either when two or four mice are kept in the same cage.

From the percentages of total variance attributable to competitive factors, it can be seen that the effect of these factors is

Source of variation	FEMALES d. f.	Sums of squares	Mean square	Component of variance	Percentage of total variance	MALES d.f.	Sums of squares	Mean square	Component of variance	Percenta of tota varianc
Number per cage	1	14.42	14.42**	0.04	1.4%	1	59.52	59.52**	0.15	3.0%
Strains	3	705.66	235.22**	1.21	42.0%	3	1026.56	342.19**	1.76	36.0%
Cage-mates	3	28.90	9.63**	0.04	1.4%	3	64.58	21.53**	0.09	1.9%
N/cage x strain	3	21.14	7.05**	0.05	1.7%	3	42.07	14.02**	0.11	2.3%
N/cage x cage mates	3	5.55	1.85 NS	-	-	3	13.29	4.43 NS	-	-
Strain x cage mates	9	23.85	2.65 NS	-	-	9	36.88	4.09 NS	-	-
N/cage x strain x cage mates	9	26.79	2.98 NS	-	-	9	41.70	4.63 NS	-	-
Litters	541	985.41	1.82**	0.67	23.0%	536	1741.89	3.23**	1.11	23.0%
Individuals	192	169.61	0.88	0.88	30.0%	192	315.23	1.64	1.64	34.0%
Total corrected for 3 week weight	764	1981.33				759	3341.72			
Regressions	3	73.00				8	426.63			
Total	767	2054.33				767	3768.35			

NS $(P > 0.05)$

** $(P < 0.01)$

very small. All together they account for no more than about 5% of the total variance of gain in females and about 7% in males. In contrast, the genotypic variance is 42% in females and 36% in males and the remainder of the environmental variance is approximately 55% in both sexes. As a proportion of the non-genetic variance, the competitive factors contribute about 8% in females and 11% in males.

The effect of competition between different strains can be examined in detail by the mean gain in weight of mice of each strain classified according to the strain of their cage mates and also by the mean difference in gain of mice of the same strain when in pure- or mixed-strain cages. Means and standard errors of gain are presented in Table 12. The differences between pure and mixed cages and the standard error of the difference are presented in Table 13.

From Table 12 the relative competitive ability of a strain can be ascertained by the mean gain of all four strains according to the cage mates. The lowest gain is observed when mice are caged with C_{57} strain, and the largest gain is observed when their cage mates are of the RIII strain in females and CBA in males. Mice having JU's as cage mates have the second lowest mean gain in both males and females. From Table 13 the differences between mixed- and pure-strain cages stress the fact that having C_{57} mice as cage mates reduces the gain of all other strains. It is therefore possible to rank the four inbred strains for competitive ability in the following order:

$$C_{57} > \text{JU} > \text{CBA} \geqslant \text{RIII}.$$

The relationship between the post-weaning growth of a strain and its competitive ability is illustrated in Fig. 1, which represents the data of Table 12 in graphical form. There seems to be an inverse relationship

TABLE 12. Mean and standard error of gain of the strains classified according to their cage mates.

Cage-mates	STRAINS JU	RIII	CBA	C_{57}	Mean gain according to cage mates
			Females		
JU	9.41 ± 0.14	8.78 ± 0.13	8.04 ± 0.15	6.30 ± 0.28	8.13 ± 0.09
RIII	9.52 ± 0.12	8.65 ± 0.12	8.11 ± 0.14	7.15 ± 0.14	8.36 ± 0.06
CBA	9.57 ± 0.17	8.46 ± 0.16	7.74 ± 0.21	6.90 ± 0.22	8.17 ± 0.09
C_{57}	9.05 ± 0.21	8.07 ± 0.16	7.49 ± 0.19	6.67 ± 0.16	7.82 ± 0.09
Mean gain of strains	9.39 ± 0.08	8.49 ± 0.07	7.85 ± 0.09	6.76 ± 0.10	
			Males		
JU	11.60 ± 0.25	11.27 ± 0.22	9.97 ± 0.31	8.59 ± 0.27	10.36 ± 0.13
RIII	12.16 ± 0.24	11.12 ± 0.22	10.28 ± 0.28	8.38 ± 0.27	10.49 ± 0.13
CBA	12.16 ± 0.21	11.11 ± 0.18	9.93 ± 0.27	9.31 ± 0.20	10.63 ± 0.11
C_{57}	11.17 ± 0.20	10.30 ± 0.25	9.53 ± 0.22	8.44 ± 0.26	9.68 ± 0.12
Mean gain of strains	11.77 ± 0.11	10.95 ± 0.10	9.93 ± 0.13	8.68 ± 0.13	

TABLE 13. Mean and standard errors of differences between mixed and pure strain cages.

	STRAINS			
Cage mates	JU	RIII	CBA	C_{57}
		Females		
JU	-	+0.13 ± 0.17	+0.30 ± 0.27	-0.37 ± 0.31 ?
RIII	+0.11 ± 0.18	-	+0.37 ± 0.25	+0.48 ± 0.21*
CBA	+0.16 ± 0.22	-0.19 ± 0.19	-	+0.23 ± 0.27
C_{57}	-0.36 ± 0.26	-0.58 ± 0.20**	-0.25 ± 0.28	-
		Males		
JU	-	+0.15 ± 0.29	+0.04 ± 0.40	+0.15 ± 0.38
RIII	+0.56 ± 0.35	-	+0.35 ± 0.39	-0.06 ± 0.37
CBA	+0.56 ± 0.32	-0.01 ± 0.29	-	+0.87 ± 0.32**
C_{57}	-0.43 ± 0.32	-0.82 ± 0.32*	-0.40 ± 0.35	-

* ($P < 0.05$)

** ($P < 0.01$)

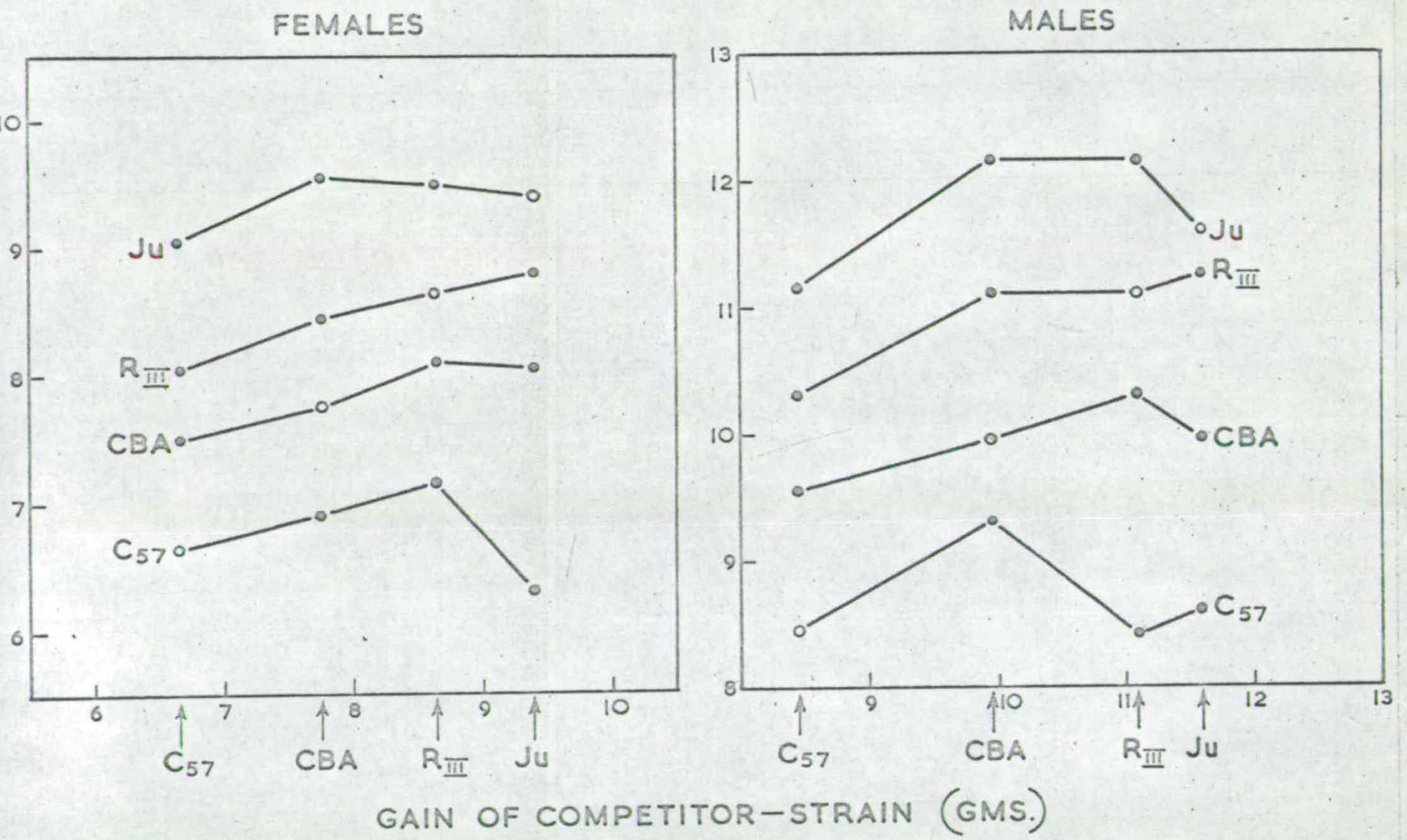

FIG. 1 Relationship between the gain in weight of a strain and its competitive ability. The gain of a strain when in pure cages is plotted against the gain they induce in their cage mates. Pure strain cages are represented by open circles, mixed cages by closed circles.

etween the post-weaning growth of a strain, measured by its mean gain n pure cages, and its competitive ability, measured by the mean gain of ts cage mates. This is certainly the case with the C_{57} strain which, eing the smallest, reduces the growth of its cage mates of other strains. his relationship also holds for the CBA and RIII strains. However, the JU train, which is the largest, is ranked as the second best competitor. his position is due to the specific effect of the JU and C_{57} strains, which, hen caged together, both have their growth reduced, whereas the JU strain hen with either CBA or RIII has very little effect on their growth.

Besides the effect of strain of cage mates, the effect of number er cage and the interaction between number per cage and strain are the ompetitive factors which in the analysis of variance proved to be ignificant sources of variation. These effects can be examined in detail y comparing the mean gain of each strain when caged in pairs with the mean ain of the same strain when in four per cage. The mean gain of each strain lassified according to number per cage and the difference between these eans are presented in Table 14. In both males and females the gain ecreases when mice are caged in groups of four as compared with two per age. An exception is given by the mice of the JU strain, where the ifferences, although not significant, suggest that both sexes grow better hen caged in groups of four than in groups of two. This explains the nteraction between number per cage and strain observed in the analysis f variance.

TABLE 14. Means and standard errors of gain of mice of each strain classified according to number per cage.

Number per cage	STRAINS JU	RIII	CBA	C_{57}	Mean gain according to number per cage
			Females		
2/cage	9.27 ± 0.12	8.59 ± 0.11	8.11 ± 0.09	7.06 ± 0.13	8.26 ± 0.06
4/cage	9.51 ± 0.11	8.39 ± 0.09	7.58 ± 0.14	6.46 ± 0.16	7.98 ± 0.07
			Males		
2/cage	11.68 ± 0.16	11.29 ± 0.15	10.24 ± 0.16	9.23 ± 0.19	10.61 ± 0.08
4/cage	11.87 ± 0.15	10.61 ± 0.15	9.61 ± 0.22	8.13 ± 0.16	10.05 ± 0.09

Means and standard errors of the differences of gain between two and four mice caged together.

Number per cage	STRAINS JU	RIII	CBA	C_{57}	Overall mean difference
			Females		
2-4/cage	-0.24 ± 0.16	0.20 ± 0.14	0.53 ± 0.17**	0.60 ± 0.20**	0.28 ± 0.09**
			Males		
2-4/cage	-0.19 ± 0.22	0.68 ± 0.21**	0.63 ± 0.27**	1.10 ± 0.25**	0.56 ± 0.04**

** ($P \leq 0.01$)

clusions

The general conclusion from this experiment is that post-
ning growth of mice is affected by the number per cage and by the
otype of their cage mates. The effect of competition due to the geno-
e of the cage mates on mean gain in weight is very small. These
fects are all less than one gram where the average gain is around
n grams.

As would be expected, the mean gain in weight is affected by
e size of the group caged, being larger for groups of two per cage than
r groups of four. The differences, however, are very small and about the
me magnitude as those determined by the genotype of cage mates. Probably
e effect of number per cage will become more important when larger groups
r cage are used. The optimum number per cage, however, seems to depend
a certain extent on the genotype. As mice of the JU strain grow better
en caged in groups of four than in groups of two, it seems reasonable
expect the optimum number per cage in this strain to be larger than in
y other of the strains studied.

From the results obtained in this experiment, it seems that the
st important effect of competition is the effect of the genotype of cage
tes on the within strain variance of gain in females, as this variance
n increase four times depending on the strain of their cage mates.
his is the case of C_{57} females caged with RIII's, where the variance of
$_{57}$ is 0.88 gram^2 and the same strain caged with JU's has a variance of
.73 gram^2.

For the effect of the RIII females lowering the variance of all
he strains they are caged with, the expression "Social homeostasis" used
y Mackintosh (1962) can be applied. The relationship between the

ompetitive ability of a strain and its effect on the within strain ariance of its cage mates is illustrated graphically in Fig. 2. n the case of females, the competitive ability of a strain, measured y the reduction in mean growth of its cage mates, seems to be associated ith an increase of the within strain variance of its cage mates. The III strain ranks the lowest as far as competitive ability is concerned nd has also the effect of lowering the variance of its cage mates. y contrast, the JU and C_{57} strains which, when caged together, show a arked reduction in the mean gain of both strains, also show a large ncrease in the within variance of both strains when caged together, as compared with the variance in pure-strain cages. Therefore, where a strain of low competitive ability stabilizes the growth of its cage mates, mice of two strains which interfere with each other have their variances increased.

It seems that mice of a dominant strain do not always behave in a dominant way, sometimes allowing their cage mates to achieve optimum growth whereas sometimes growth is severely affected by competition. This would increase the variance of the submissive strain, as happens with females of the RIII strain when caged with any other strain. Also if the mice caged together belong to equally high competitive strains, the dominant role is not always fulfilled by the same strain. So when mice of one strain behave in a dominant way their growth is optimum and their cage mates of the other strain have their growth depressed. The reverse would happen when the second strain behaves as the dominant one. This would account for the increase of variance observed in the females of both C_{57} and JU strains when caged together. However, in plants an increase in variance is observed when the best and the worst competitors

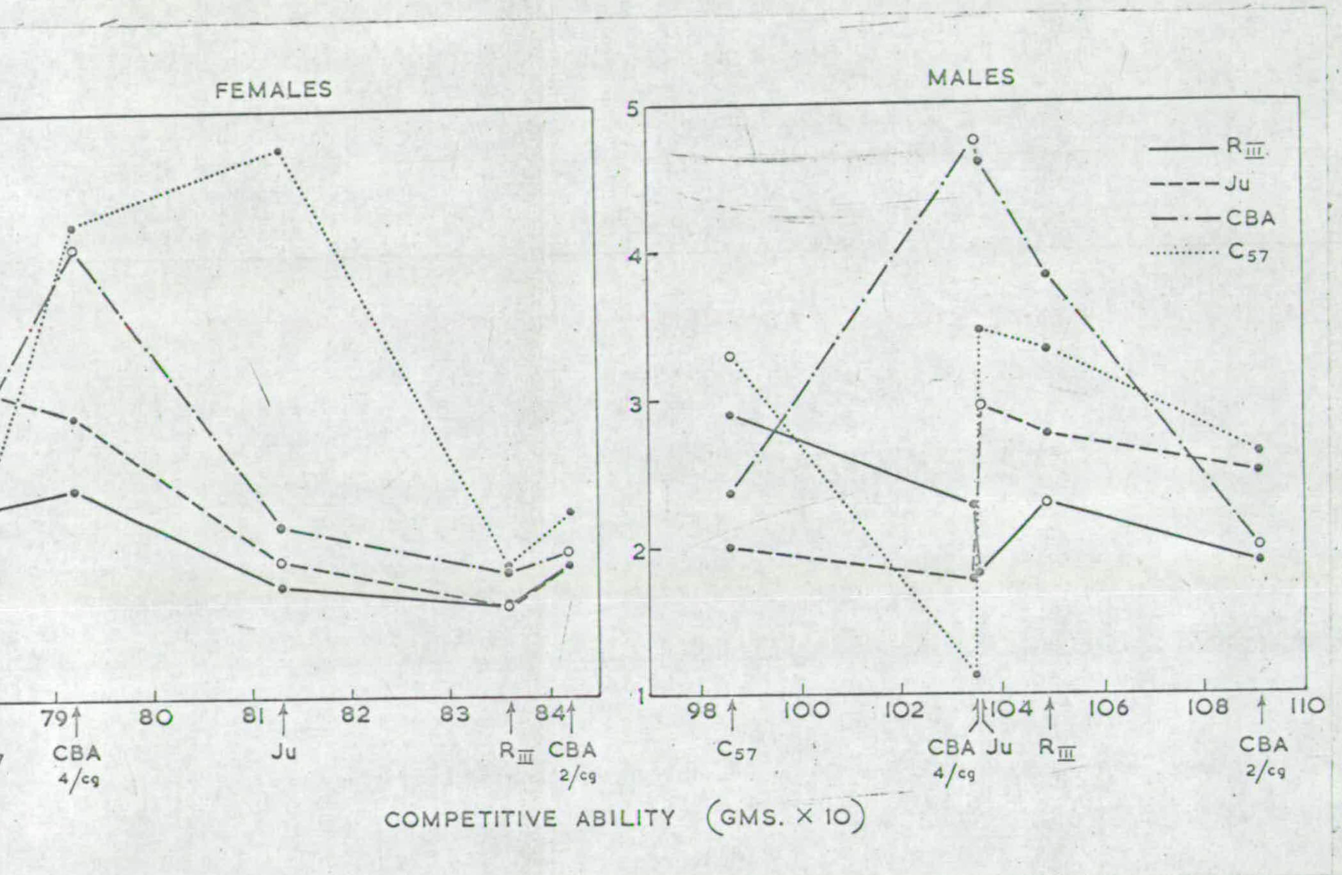

FIG. 2 Relationship between the competitive ability of a strain and the effect on the within-strain variance of its cage-mates. The competitive ability of a strain evaluated by the gain it induces in its cage-mates is plotted against the within-strain variance of each of its cage-mates. Pure cages are represented by open circles, mixed cages by closed circles. Separate values for two and four per cage are given for the CBA strain acting as competitor.

are grown together (Sakai, 1953).

The large variance observed in females of the CBA strain when in pure-strain cages and the C_{57} strain when caged with CBA's requires a different explanation. As the CBA strain is of low competitive ability, it would be expected, following the above argument, to induce low variance in their cage mates. However, as can be seen in Fig. 2, both the mean gain and the variance which the females of the CBA strain induce in their cage mates depends on the number caged together. Also the variance of the CBA strain is itself affected by the number per cage. Where the cage mates of the CBA females when two per cage seem to show a stabilizing effect similar to that induced by the RIII strain, the same combinations, when in groups of four, have their within strain variance strongly increased. Therefore, it seems that the particular behaviour of the females of the CBA strain, when in groups of four mice per cage, is responsible for the variances obtained.

The variance of males of the CBA strain is also affected by the number per cage, as can be seen from the difference in variance between groups of CBA males in two and four per cage. However, by contrast with the effect observed in females, this does not affect the within strain variance of their cage mates. In the same way, the variance of males does not seem to be affected by the competitive ability of their cage mates and no relationship can be found between the variances of males and females when in comparable competitive conditions.

III. COMPENSATORY GROWTH

1. Material and Methods

It has been stated earlier that compensatory growth can be described through the effect of age on the component of variance due to the environmental factor under study. This was the approach used here to determine the influence on post-weaning growth of maternal factors affecting body weight of mice. The measure of growth used was the body weight at successive ages from birth to 8 weeks.

The partition of the phenotypic variance V_P, into additive variance V_A, dominance variance V_D, and environmental variance V_E, is described by Falconer (1960). It is shown that when a number of sires are each mated to several dams from which a number of offspring are measured, the sire component of variance is $\sigma_S^2 = \frac{1}{4} V_A$, the dam component of variance is $\sigma_D^2 = \frac{1}{4} V_A + \frac{1}{4} V_D$, and the progeny component of variance is $\sigma_W^2 = \frac{1}{2} V_A + \frac{3}{4} V_D + V_E$.

The advantage of the use of a sib analysis in the case of mice is the possibility of dividing the environmental variance in variance due to common environment, V_{EC} and variance due to individual environment, V_{EW}. The variance due to common environment arises from the fact that members of a family may sometimes share the same environment for a period of their lives. This contributes to the variance between family means but not to the variance within families. In the case of mice full sib groups reared by their own mother share before birth and during the pre-weaning period a common environment which is going to affect the between full sib or dam component of variance. If there is no other cause of common environment for full sib groups the component of variance due to common environment V_{EC}

equivalent to the variance due to maternal factors. When common vironment between full sib groups exists the dam component of variance comes $\sigma_D^2 = \frac{1}{4} V_A + \frac{1}{4} V_D + V_{EC}$ and the progeny component of variance comes $\sigma_W^2 = \frac{1}{4} V_A + \frac{3}{4} V_D + V_{EW}$. As the sire component estimates $\frac{1}{4} V_A$, joint estimation of $\frac{1}{4} V_D + V_{EC}$ can be obtained by difference between the m and the sire component and an estimation of $\frac{3}{4} V_D + V_{EW}$ can be obtained the difference between the progeny component and twice the sire component. ssuming the non-additive genetic variance to be negligible in amount, these lues in mice can be used as estimates, respectively, of the variance due maternal factors and variance due to environmental effects other than aternal factors. By comparing the estimates of V_{EC} of body weight at ifferent ages, it is therefore possible to study the relationship between rowth and the changes in variance due to maternal factors.

The experiment consisted in a half sib analysis where each ire was mated to three dams and, when possible, four offspring of each ex were measured. The mice used were of the same strain as in the election experiment described before. Mice were identified and weighed at irth and weighed every week until 8 weeks of age. In females age and eight at opening of vagina were also recorded. Although a maximum of four ice of each sex, chosen at random, were measured, the complete litter was eared by the mother until weaning at 3 weeks of age. The other details of anagement were similar to those of the selection experiment, with the xception that, in this case, the choice of the parents was random.

A total of 71 sires was used in two generations. In order to orrect for effects of the different environment for the generations, alculations were made on deviations from the generation means. Calcul- tions were made separately for each sex.

Although sib analyses can be used to estimate maternal effects,
ey are commonly used to estimate heritability. If the heritability is
be estimated from the sire component, the most efficient design for the
cilities available is obtained when all the progeny of a sire have
fferent dams. This is particularly true when the dam component includes
riance due to maternal effects (Robertson, 1959). However, if equal
formation is required from the dam as from the sire component,
bertson recommends the use of three or four dams per sire. As the main
rpose of the experiment was to estimate the dam component accurately,
is last design was used. The number of offspring per dam of each sex
asured was larger than that recommended for the most efficient design.
wever, there were two reasons for increasing the dam family size. It
s desirable to obtain an accurate value of progeny component of variance
order to estimate the individual environmental variance. The other
ason is related to the determination of opening of vagina. Such deter-
nation is subject to a large experimental error. Females were checked
ery day from 3 weeks of age until their vagina opened. This procedure
d to a maximum delay on the determination of opening of vagina of one
y. As at this time growth is maximum the weight at opening of vagina
s the most affected by the experimental error. For the reasons given
an earliersection, it was desirable to determine the mean weight of the
tter at opening of vagina as accurately as possible. Therefore within
e time and space available the maximum number of females should be kept.

Results

(i) Changes of variance with increasing age.

From the data of the half sib experiment the phenotypic variance f weight at different ages and, in the females, the age and weight at opening f vagina, was partitioned in its components of additive variance, V_A, variance ue to common environment, V_{EC}, and variance due to individual environment, V_{EW}. hese values were computed separately for each sex. Negative components of riance were assumed to be zero. The standard errors of the estimates were lculated by the method suggested by Dr. B. Woolf. The results are presented n Table 15 and the changes of variance with increasing age are illustrated raphically in Fig. 3. It is obvious from the partition of phenotypic ariance that the changes with age in the additive genetic variance and ariance due to common environment have a different pattern. The variance ue to common environment starts by increasing until a peak is attained at weeks of age. After that age there is a slight decline at 5 weeks ollowed by a sharp decrease at 6 weeks. The decrease in variance continues n a lesser degree at later ages.

By contrast, the additive variance shows no change or very slight ncrease from birth to 4 weeks of age. After that there is a sharp increase n additive variance which continues until 8 weeks of age. The increase in dditive variance coincides with the decrease in variance due to common nvironment. This implies the existence of an inverse relationship between he two variances. The large differences between the values estimated for he additive variances of males and females seem to be connected with the arger variance due to common environment existing in males. However, the ize of the standard error of the estimates do not allow any conclusion in his respect.

					CHARACTER						
Components of phenotypic variance	Birth weight	1st week weight	2nd week	3rd week	4th week	5th week	6th week	7th week	8th week	Age at opening of vagina	Weight at opening of vagina
					Females						
V_A df = 70	0.000 ±0.008	0.256 ±0.244	0.128 ±0.608	0.912 ±1.500	0.724 ±1.944	1.100 ±1.880	2.080 ±1.528	2.604 ±1.612	3.600 ±1.796	2.484 ±3.564	0.000 ±0.556
V_{EC} df = 131	0.019 ±0.004	0.577 ±0.125	1.746 ±0.336	3.926 ±0.807	5.195 ±1.078	4.448 ±1.019	2.721 ±0.753	2.603 ±0.766	2.331 ±0.806	7.649 ±1.914	1.099 ±0.331
V_{EW} df = 483	0.012 ±0.005	0.000 ±0.299	0.148 ±0.299	0.235 ±0.752	1.279 ±0.979	2.052 ±0.954	1.275 ±0.779	1.036 ±0.820	0.963 ±0.915	5.462 ±1.832	2.334 ±0.315
V_P df = 684	0.031 ±0.003	0.794 ±0.043	2.022 ± 0.109	5.073 ± 0.274	7.198 ±0.389	7.600 ±0.411	6.076 ±0.328	2.43 6.234 ±0.337	6.894 ±0.372	15.595 ±0.843	3.432 ±0.185
Mean and standard deviation.	1.56 ±0.18 gr	4.47 ±0.89 gr	6.75 ±1.42 gr	9.24 ± 2.25 gr	13.92 ± 2.68 gr	18.79 ± 2.75 gr	21.69 ± 2.46 gr	22.97 ±2.50 gr	24.12 ±2.62 gr	31.46 ± 3.95 days	16.30 ± 1.85 gr

TABLE 15. Components of phenotypic variance.

	CHARACTER								
Components of phenotypic variance	Birth weight	1st week weight	2nd week weight	3rd week weight	4th week weight	5th week weight	6th week weight	7th week weight	8th week weight
					Males				
V_A df = 70	0.000 ±0.007	0.206 ±0.224	0.000 ±0.544	0.078 ±1.492	0.000 ±3.408	0.563 ±3.863	2.734 ±2.940	3.795 ±2.688	3.986 ±2.648
V_{EC} df = 130	0.019 ±0.004	0.541 ±0.037	1.703 ±0.322	4.513 ±0.866	10.528 ±2.053	10.452 ±2.208	6.042 ±1.547	4.400 ±1.328	4.034 ±1.293
V_{EW} df = 500	0.014 ±0.005	0.007 ±0.112	0.236 ±0.272	0.760 ±0.749	2.930 ±1.716	4.921 ±1.945	3.919 ±1.509	3.572 ±1.387	3.824 ±1.373
V_P df = 700	0.032 ±0.002	0.754 ±0.041	1.939 ±0.103	5.351 ±0.286	13.458 ±0.707	15.936 ±0.852	12.694 ±0.671	11.767 ±0.629	11.845 ±0.633
Mean and standard deviation	1.60 ±0.18 gr	4.50 ±0.87 gr	6.75 ±1.38 gr	9.23 ±2.31 gr	15.33 ±3.63 gr	21.95 ±3.99 gr	25.63 ±3.56 gr	27.89 ±3.43 gr	29.60 ±3.43 gr

TABLE 15 Components of phenotypic variance
continued

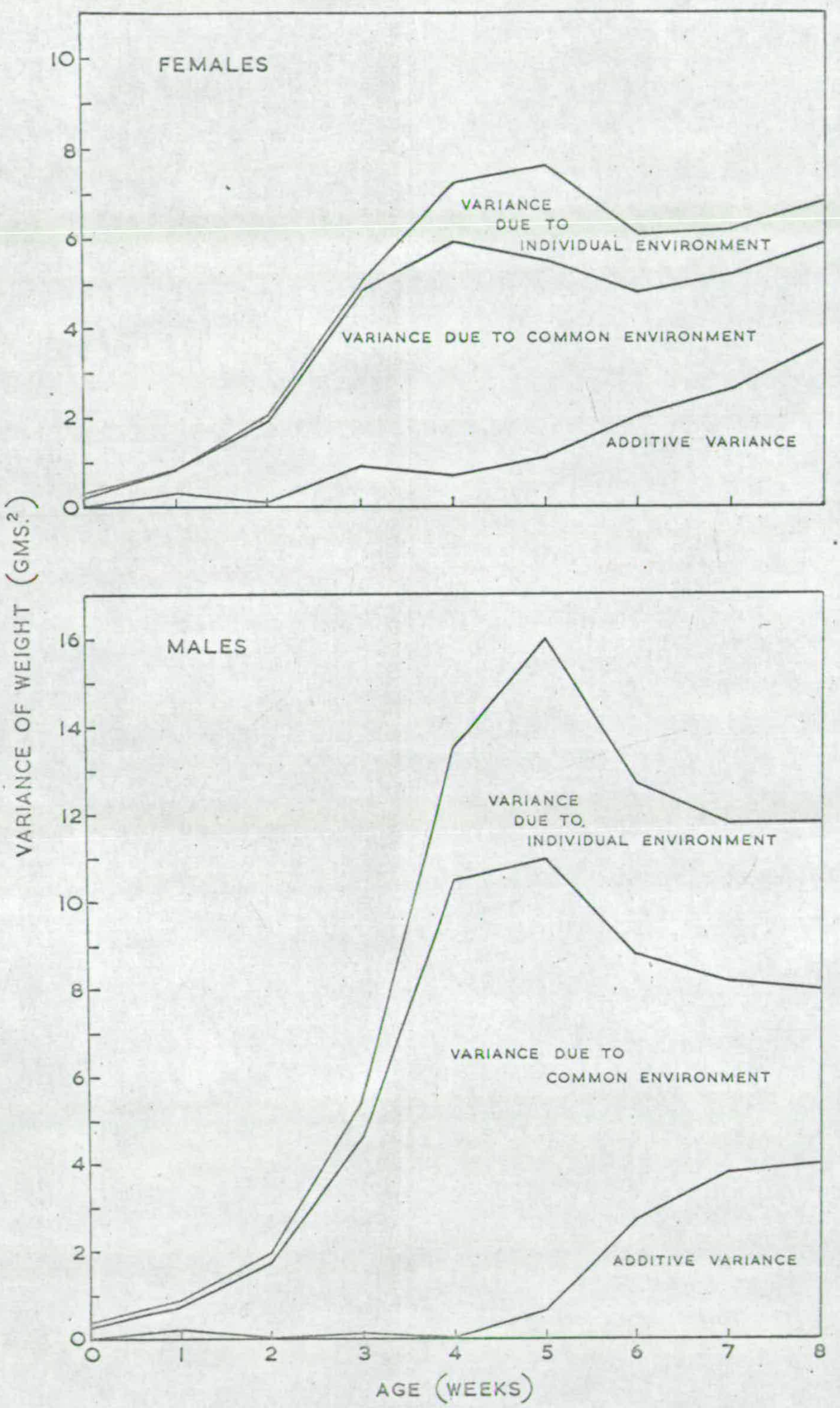

FIG. 3 Partition of the phenotypic variance with increasing age.

An increase of variance with age was expected during the ponential phase of growth. This increase is due to the proportionality tween the variance and the square of the mean weight existing during is phase. The observed increases in total environmental variance from rth to 4 weeks of age are, therefore, a consequence of the scale effect. males, after weaning, are, on average, heavier than females at the same e, variance is correspondingly increased.

The reduction of the variance due to common environment was the pected consequence of compensatory growth acting on maternal effects. was expected, the reduction in variance was not observed immediately fter the maternal factors ceased to act, i.e. at 3 weeks of age. There is further increase in the variance at 4 weeks due to the scale effect of he exponential phase of growth and only after that age the reduction in ariance is apparent.

The variance due to common environment at 8 weeks of age is pproximately 40% of the same variance at 4 weeks, thus showing that ompensatory growth has an appreciable effect in reducing variation. rom 4 to 6 weeks of age this variance is reduced by 50%, thus suggesting hat compensatory growth occurs almost exclusively during this period. t is also worth mentioning that the mean age at opening of vagina, hich is 4.5 weeks, is well within the period in which maximum compensation occurs.

The variance due to individual environment shows some reduction after the fifth week, thus indicating that compensatory growth also occurs, as would be expected for environmental factors other than maternal effects.

The changes observed in phenotypic variance are largely due to corresponding changes in the variance due to common environment.

The weight at opening of vagina shows a very small amount of ariance due to common environment, much smaller than that of the weight t any fixed age, which suggests that vaginal opening occurs at a fairly onstant weight. By contrast, the variance due to individual environment ariance is very large, being 68% of the phenotypic variance. This is bviously due to the experimental error in determination of the weight at pening of the vagina. This does not happen with age at opening of vagina n which the variance due to individual environment is only 35% of the henotypic variance.

The weight of an individual at any age can be divided into two omponents, the weight of the individual at an earlier age and the gain ccurring during the period between the two weights considered, i.e.

$$W_t = W_{t-1} + G_{(t-1)\text{ to }t}$$

$_t$ being the final weight, W_{t-1} the earlier weight and $G_{(t-1)\text{ to }t}$ the ain between the earlier and the final weight. The variance of W_t can lso be expressed in terms of the previous weight and the gain. From the eneral expression for the variance of a sum:

$$\text{Var }(A+B) = \text{Var }(A) + \text{Var }(B) + 2\text{ cov }(AB)$$

he partitioning of variance of weight becomes:

$$\text{Var }(W_t) = \text{Var }(W_{(t-1)}) + \text{Var}(G) + 2\text{ cov }(W_{t-1} \cdot G)$$

f the variance due to common environment is partitioned in this way, a etter understanding of the changes with increasing age can be obtained, nd the way in which the scale effect of the exponential phase of growth nd the compensatory growth of the subsequent phase contribute to the hanges of variance can be elucidated.

The variance of weight at any week was accordingly partitioned nto the variance of the weight at the previous week, the weekly gain, and he covariance between gain and previous weight. The between dam component f variance was used here as the measure of the variance due to maternal ffects. The results are presented in Table 16. From the results it is pparent that the main source of change in the variance of weight is the ovariance between previous weight and gain. From the first to the fourth eeks of age the covariance between gain and previous weight is positive. uring this period there is an increase of both this covariance and the ariance of weight. Therefore the scale effect of the exponential phase f growth is the result of the relationship between weight and subsequent ain. The type of this relationship can be visualised if it is assumed hat an individual is composed of growing units. As during the exponential hase there are no limitations of growth, all the units reproduce. herefore the gain during this phase is dependent on the number of units lready existing.

After 4 weeks of age the covariance between gain and previous eight becomes negative. The largest negative value was found for the ovariance between 5 week weight and gain from 5 to 6 weeks. After that he covariance decreases and becomes very small. The negative covariances ound imply that the reduction of variance, determined by compensatory rowth, is achieved by reducing the growth of previously heavier individuals nd increasing the growth of the lighter ones. This is the reverse of the cale effect. Also where the scale effect increases gradually throughout he exponential phase of growth, compensatory growth seems to act mainly n growth from 4 to 6 weeks of age. This is evident in females. In males he compensatory growth seems to occur slightly later, having an appreciable ffect between 6 and 7 weeks. The small negative covariance of 4 weeks weight nd gain from 4 to 5 weeks is probably the result of a positive covariance

TABLE 16. Decomposition of variance of weight in terms of previous weight and weekly gain.

Age = t	Var W_t	Var $W_{(t-1)}$	Var $G_{(t-1)}$ to t	2xcov $W_{(t-1)}G_{(t-1)}$ to t
		Females		
1st week	0.641	0.019	0.495	+0.128
2nd week	1.778	0.641	0.471	+0.666
3rd week	4.154	1.778	0.765	+1.612
4th week	5.376	4.154	0.316	+0.904
5th week	4.723	5.376	0.274	-0.900 ?
6th week	3.241	4.723	0.462	-1.944
7th week	3.254	3.241	0.088	-0.076
8th week	3.231	3.254	0.124	-0.147
		Males		
1st week	0.593	0.019	0.465	+0.109
2nd week	1.704	0.593	0.467	+0.644
3rd week	4.532	1.704	0.914	+1.914
4th week	10.528	4.532	1.647	+4.349
5th week	10.593	10.528	0.366	-0.301
6th week	6.725	10.593	0.512	-4.380
7th week	5.349	6.725	0.308	-1.684
8th week	5.030	5.349	0.185	-0.504

ue to the scale effect acting in the first part of this period and a egative covariance due to compensatory growth acting in the last part of he same period.

The variance of weekly gain, although not changing very much ith age, shows some relationship with the absolute value of the covariance etween weight and subsequent gain. This relationship is due to the fact hat the variance of weekly gain is increased by a proportion equal to the quare of the correlation of weight and subsequent gain. However, these hanges in the variance of gain have very small effects on the variance of final weight.

(ii) Relationship between sexual maturity and the inflexion oint of the growth curve.

The results of the half sib analysis indicate that compensatory growth succeeds immediately the exponential phase of growth. In the ypothesis described in an earlier section, compensatory growth was related to a shift of the inflexion point of the growth curve determined by the weight at an earlier age. A possible relationship between sexual maturity and the inflexion point of the growth curve was also suggested. The existence of such a relationship would allow the inflexion point of the growth curve to be estimated in each individual by an easily scored character. The next step is, therefore, to relate the opening of vagina, which is an indication of sexual maturity, with the inflexion point of the growth curve.

The inflexion point was estimated from growth curves fitted to the mean weight of the females of each litter of a sample of 71 litters drawn from the half sib experiment. The curve fitted was the logistic urve of growth of the form:

$$Y_t = \frac{k}{1+be^{-at}}$$

here Y_t is the weight at age t and a, b and k parameters to be estimated rom the data. It can be shown that this curve has a lower asymptote t $Y=o$ and an upper one at $Y=k$. Therefore k estimates the final adult eight. The inflexion point of the curve is attained when $Y_i = \frac{k}{2}$. The eight at the inflexion point is at mid-way between the two asymptotes. he age at the inflexion point is obtained by the expression $t_i = \frac{1}{a} \log_e b$.

The parameters a and k and the weight at the inflexion point ere estimated by Fisher's method and the parameter b and the age at the nflexion point were estimated by Rhodes' method (Nair, 1954).

The values obtained for weight and age at the inflexion point f the growth curve fitted to the litter mean weights of the females ere compared with the values obtained for mean weight and age of aginal opening of the females of the same litters.

The correlation between age at the inflexion point and age at pening of vagina estimated from this sample was:

$$r_{Ai.AV} = +0.761 \quad (P < 0.01).$$

he correlation between the weight at the inflexion point and weight at pening of vagina was:

$$r_{Wi.WV} = +0.082 \quad (P > 0.05).$$

here is a very close relationship between age at the inflexion of the rowth curve and age at sexual maturity but no relationship between the eight at the inflexion point and weight at sexual maturity. The pparent contradiction of the two correlations estimated is closely related o the problem of whether age or weight is the main determinant of sexual maturity. If weight is the principal determinant of sexual maturity, this means that sexual maturity, and hence vaginal opening, are attained as soon as the females reach a certain weight regardless of the age they have when that weight is attained. Therefore the opening of the vagina would occur at a constant weight, and the variation in weight at opening of the vagina would be the result of random deviations from the expected weight. This, of course, would lead to a zero correlation between weight at opening of the vagina and the inflexion point. If the inflexion point also occurred at a constant weight, the correlation of age at inflexion point and age at opening of vagina should be close to unity. The high positive correlation estimated for these two characters is a good indication that this is the case.

A method which gives an approximate idea of the relative importance of weight and age in determining the opening of the vagina consists in comparing the variance of these two characters. If weight is the only determinant the expected variance of weight at opening of the vagina would be zero and the variance in age at that weight would depend on the differences in growth rate existing between females. Therefore, comparing the two variances, the character with the lowest variance would be the main determinant of opening of the vagina. In order to be compared, the variances have to be expressed in the same units. The age at opening of vagina was therefore transformed into the expected weight and the variance computed from this transformation. The transformation of age at opening of vagina into expected weight was obtained by fitting a growth curve to the mean weights of the females of the half sib experiment, and from the equation of the curve the factor which transformed the variance of age into variance of expected weight was calculated. As individual measurements of age at pening of vagina were used, it was possible to fit the growth curve to he mean weights which, otherwise, would be incorrect (Yates, 1950).

The curve used was a asymptotic curve fitted to the female ean weekly weights from 3 to 8 weeks of age. The method of Patterson 1956) was used for fitting the growth curve.

The equation of the growth curve for the weight W at the time is:

$$W_t = 27.84 - 18.74\ (0.71)^t.$$

he factor to transform the variance of age into variance of expected eight, derived from the equation of the growth curve, is:

$$\text{Var } W = 14.84 \text{ Var } t.$$

he variances compared were the between dam components of variance obtained rom the half sib analysis. These components evaluate the environmental ariation due to maternal effects. The observed variance of weight is 1.10 grams^2 and the variance of age is 8.27 days^2 or 0.169 weeks^2. The transformed variance of age is 2.51 grams^2. Comparing the two variances:

$$F = \frac{2.51}{1.10} = 2.28 \quad (P < 0.01).$$

Therefore the variance of weight is significantly lower than the transformed variance of age. Hence, weight can be considered to be the main determinant of sexual maturity.

The relationship between age and weight at opening of the vagina further supports the hypothesis that the vagina opens when all females reach the same weight. The between dam regression of weight on age at opening of vagina is:

$$b_{WV.AV} = 0.007 \pm 0.032 \text{ grams/day } (P > 0.05).$$

This regression is not significantly different from zero. The weight at which a female opens the vagina is not affected by the age she is at that weight. As during growth the weight attained depends on age, if there is no relationship between the two characters, this indicates that one of them is constant, in this case, obviously, the weight.

However, if the conversion of variance of age of opening of vagina into expected weight and the regression of weight on age at opening of vagina are computed from individual deviations from litter means, i.e. within dams, the results are quite different. The observed variance of weight at opening the vagina is 2.03 grams^2 and the transformed variance of age is 2.33 grams^2. These variances are not significantly different from each other. Also the regression of weight on ages at opening of vagina computed within dams is:

$$b_{WV.AV} = 0.326 \pm 0.022 \text{ grams/day } (P < 0.01).$$

Therefore the individuals of the same litters show differences in weight at opening of vagina which are dependent on age at opening of vagina. If a female's vagina opens at a later age she will be heavier than her full sister.

The most likely explanation of these differences is the experimental error in scoring the opening of the vagina. This would lead to an increase of the within dam variance of weight but it would have very little effect on the variance of age. Also if the opening of the vagina was scored at a heavier or lighter weight than its real value, it would also be scored at, respectively, earlier or later age, which would result in the positive regression obtained. However, genetic factors affecting the weight at opening of the vagina could have the same effect on both the variances and regression. As the additive variance of weight at opening of the vagina is very small, these effects would be likely to be determined by large dominance variances.

(iii) The inflexion point and compensatory growth.

The next step in the analysis of compensatory growth consists in relating the maternal effects with the change in time of occurrence of the inflexion point of the growth curve. The maternal effects were evaluated by the mean litter weight at 3 weeks of age. These values were related to the mean litter weight and age at opening of the vagina, in order to determine which of these is affected by the maternal effects. The relationship between the same characters computed within dams is also presented.

The regression of weight at opening of the vagina on 3 week weight computed between dams is:

$$b_{WV.3w} = 0.16 \pm 0.04 \text{ grams/grams} \quad (P < 0.01).$$

The small effect of 3 week weight on weight at opening of the vagina is better expressed by the percentage of the variance removed by this regression which is the square of the correlation coefficient:

$$r^2_{WV.3w} = 0.09.$$

Therefore only 9% of the between dam component of variance of weight at opening of vagina can be accounted for by the variance of 3 week weight. It can be concluded that the weight at opening of the vagina is very little affected by the maternal environment.

By contrast, the regression of age at opening of the vagina on 3 week weight also computed between dams is:

$$b_{AV.3w} = -1.28 \pm 0.05 \text{ days/grams} \quad (P < 0.01)$$

and the square of the correlation coefficient is:

$$r^2_{AV.3w} = 0.83.$$

In this case nearly all the variance in age at opening of vagina can be accounted for by the variation in 3 week weight.

In terms of compensatory growth these results mean that those mice who had a poor maternal environment have sexual maturity delayed in order to achieve the same weight as individuals which had a better maternal environment. The close relationship between sexual maturity and the inflexion point of the growth curve implies that those females which had a slow early growth have their exponential phase of growth prolonged, whereas those who had a fast early growth have their exponential phase of growth shortened. If growth during the asymptotic phase does not depend on the duration of the exponential phase, this would obviously lead to greater similarity between the adult weights of individuals as compared with their weights at any age when the maternal effects were acting, and would therefore account for the observed decline in the variance due to common environment.

Very similar results were obtained for the relationship of 3 week weight with weight and age at opening of the vagina computed within dams. The within dam regression of weight at opening of the vagina on 3 week weight is:

$$b_{VW.3w} = 0.30 \pm 0.08 \qquad (P < 0.01),$$

and the percentage of variance of weight at opening of the vagina removed is approximately 3%.

The regression of age at opening of the vagina on 3 week weight also within dams is:

$$b_{AV.3w} = -1.23 \pm 0.13 \qquad (P < 0.01),$$

and the percentage of the variance removed is approximately 16%.

The same effect of 3 week weight on age at opening of the vagina is observed between and within dams. Therefore compensatory growth also acts on environmental effects other than maternal factors. However, the proportion of the within dam variance of age at opening of the vagina removed by 3 week weight suggests that other factors have a large influence on that variance. These are probably environmental effects occurring after weaning.

The effect of growth on sexual maturity can be further studied from the correlation of the weekly gain with the age and with the weight at opening of the vagina. As before, the between dam correlations, referring mainly to the maternal effects, and the within dam correlations, referring to individual environment, were estimated. The results are presented in Table 17. The between dam correlation coefficients of weekly gain and age at opening of the vagina are negative, until 4 weeks of age, becoming, after that, positive. This indicates that those females which had a poor maternal environment have their sexual maturity delayed whereas those with better maternal environment have their sexual maturity advanced. The fact that the largest negative correlation coefficients are obtained during the preweaning period stresses the dependence of age at sexual maturity on maternal environment. The positive correlation coefficient estimated for gain after 4 weeks of age is the consequence of the change in the inflexion point of the growth curve by compensatory growth. Those females which had the vaginal opening later are still in the exponential phase of growth when the gain was measured, whereas those which had the vaginal opening earlier are already in the asymptotic phase. Therefore larger gain would be expected from the former females and hence the positive correlation obtained. After compensatory growth has finished acting no difference in gain is observed between those females with earlier and later vaginal opening, as is shown by the non-significant correlation of gain from 7 to 8 weeks and age at opening of vagina. Hence subsequent gain is not dependent on the duration of the exponential phase.

TABLE 17. Correlation coefficients of weekly gain with age and with weight at opening of vagina.

Gain from	Between dam correlation of weekly gain with (d.f. = 130)		Within dam correlation of weekly gain with (d.f. = 482)	
	Age at opening of vagina	Weight at opening of vagina	Age at opening of vagina	Weight at opening of vagina
Birth to 1st week	-0.803**	+0.291**	-0.278**	+0.094*
1st to 2nd week	-0.714**	+0.178*	-0.288**	+0.029 NS
2nd to 3rd week	-0.821**	+0.291**	-0.288**	+0.186**
3rd to 4th week	-0.507**	+0.325**	-0.436**	+0.216**
4th to 5th week	+0.379**	+0.059 NS	-0.226**	+0.155**
5th to 6th week	+0.576**	-0.202*	+0.208**	-0.047 NS
6th to 7th week	+0.207*	+0.097 NS	+0.166**	-0.014 NS
7th to 8th week	+0.143 NS	-0.058 NS	+0.003 NS	-0.057 NS

NS (P > 0.05)

* (P < 0.05)

** (P < 0.01)

Compensatory growth is not completely effective in removing the effects of maternal environment. This is shown by the positive correlations of weekly gain and weight at opening of the vagina. However only a maximum of 10% of the variance of weight at opening of the vagina can be attributed to any weekly gain as compared with nearly 70% for age at opening of the vagina.

The within dam correlation coefficients show that compensatory growth acts in a similar way on individual environmental factors. The correlation coefficients are generally smaller than those estimated between dams, showing that compensatory growth is less effective for environmental factors which, unlike maternal effects, do not finish acting at an early age. The analysis of compensatory growth gives support to the hypothesis outlined in an earlier section. The compensation of early occurring environmental factors affecting body size is achieved, not by a change in growth rate, but mainly through changes in the duration of the exponential phase of growth. Thus, if an individual had a poor maternal environment, its exponential phase is prolonged so that the inflexion point of the growth curve will appear at the same size as an individual which had a good maternal environment. This effect is exemplified in Fig. 4 where theoretical growth curves were fitted to the mean weights of two extreme litters chosen from the half sib experiment. The close relationship existing between the inflexion point of the growth curve and sexual maturity implies that the age at sexual maturity changes according to the duration of the exponential phase whereas the weight at sexual maturity remains constant. Therefore the inflexion point of the growth curve can be evaluated by the sexual maturity. As the growth after compensation has occurred is independent of the duration of the exponential phase, it can be concluded that compensatory growth is effective in normalising adult body size.

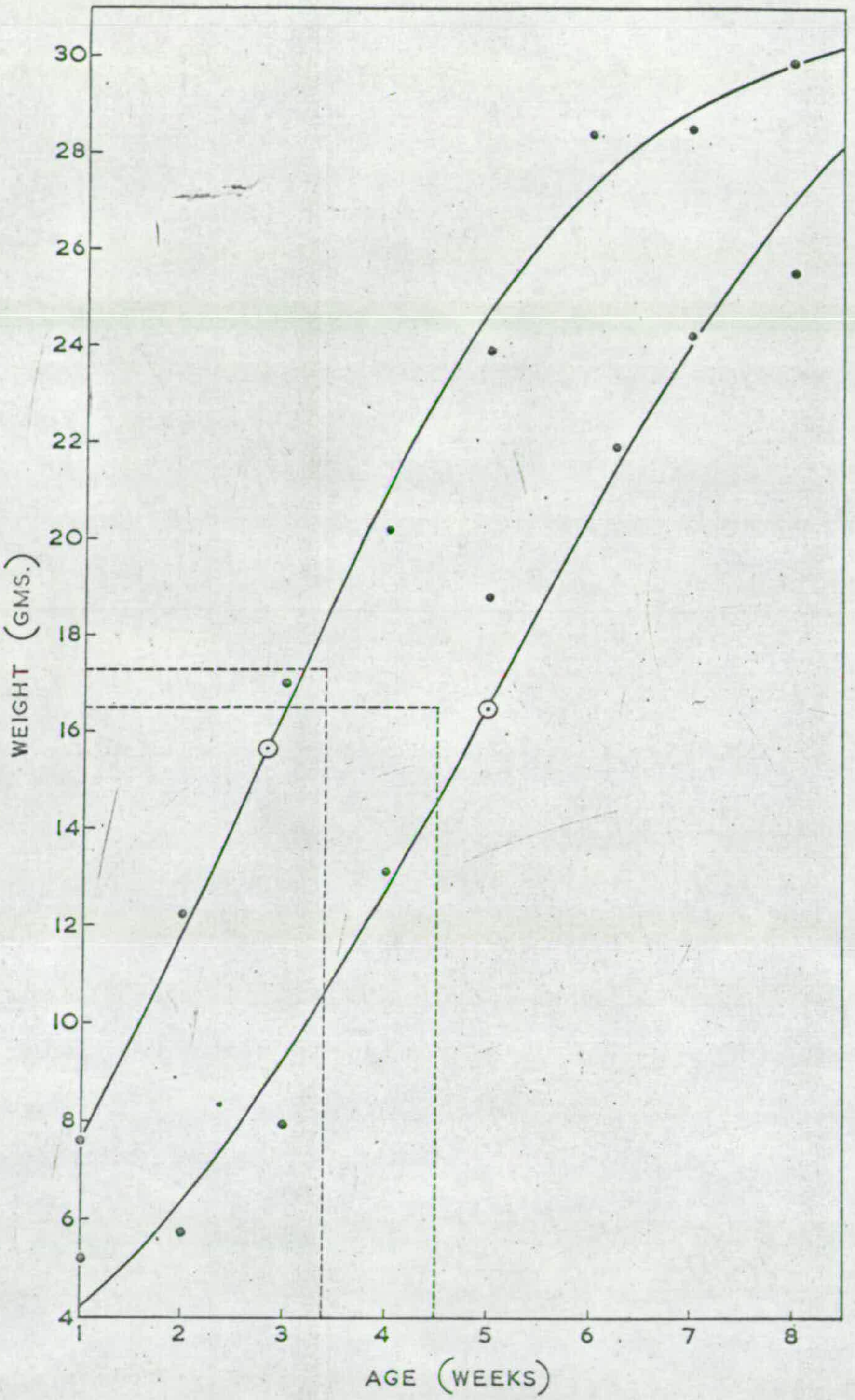

FIG. 4 An example of compensatory growth in mice which had a good and a poor environment. A growth curve was fitted to the mean weights of the females of each litter. Open circles mark the inflexion point of the growth curve. Broken lines indicate the age and weight at opening of the vagina.

IV SELECTION EXPERIMENT

The selection for 3 week weight, which was the source of the different genotypes used in the cross-fostering experiment, was carried out for four generations.

Besides the 3 weeks weight, weekly weight from 3 to 7 weeks of age was measured in both large and small lines. In females the weight and age at opening of the vagina was also measured. The direct and correlated responses to selection were obtained by the differences between the large and small line. These results, with the weights of males and females averaged, are presented in Table 18 and illustrated graphically in Fig. 5.

The differences between the large and small lines show that selection was effective over the four generations of selection. However, during the first three generations there was practically no response to selection in 3 week weight. This lack of response obtained in the first three generations can be accounted for by the correlated changes in litter size which are shown in Fig. 5. The line selected for large 3 week weight has a substantial increase in litter size at weaning whereas the litter size of the line selected for small 3 week weight decreases with selection. Through maternal effects determined by the size of the litter, the response to selection was delayed until there was sufficient genetic differences to overcome the maternal effect. When the responses to selection of 3 week weight and of litter size are considered together and expressed as the total weight of the litter at weaning, a very marked difference between the lines is observed. The changes in litter size between lines result in a negative correlation between genotype and environment.

TABLE 18. Means and standard errors of the difference between the response to selection of the large and small lines.

Character	Generation of selection			
	1st	2nd	3rd	4th
3rd week weight	0.04 ± 0.32	-0.06 ± 0.44	0;27 ± 0.38	0.90 ± 0.36
4th week weight	0.03 ± 0.45	0.28 ± 0.60	0.31 ± 0.57	1.35 ± 0.52
5th week weight	-0.01 ± 0.47	0.60 ± 0.61	0.68 ± 0.59	1.40 ± 0.54
6th week weight	0.04 ± 0.41	0.51 ± 0.54	0.77 ± 0.47	0.94 ± 0.49
7th week weight	-0.05 ± 0.37	0.40 ± 0.52	0.72 ± 0.44	0.87 ± 0.46
Age at opening of vagina	-0.19 ± 1.04	-1.59 ± 0.91	-1.00 ± 0.99	-2.18 ± 0.84
Weight at opening of vagina	0.39 ± 0.29	-0.13 ± 0.43	0.35 ± 0.36	-0.53 ± 0.29

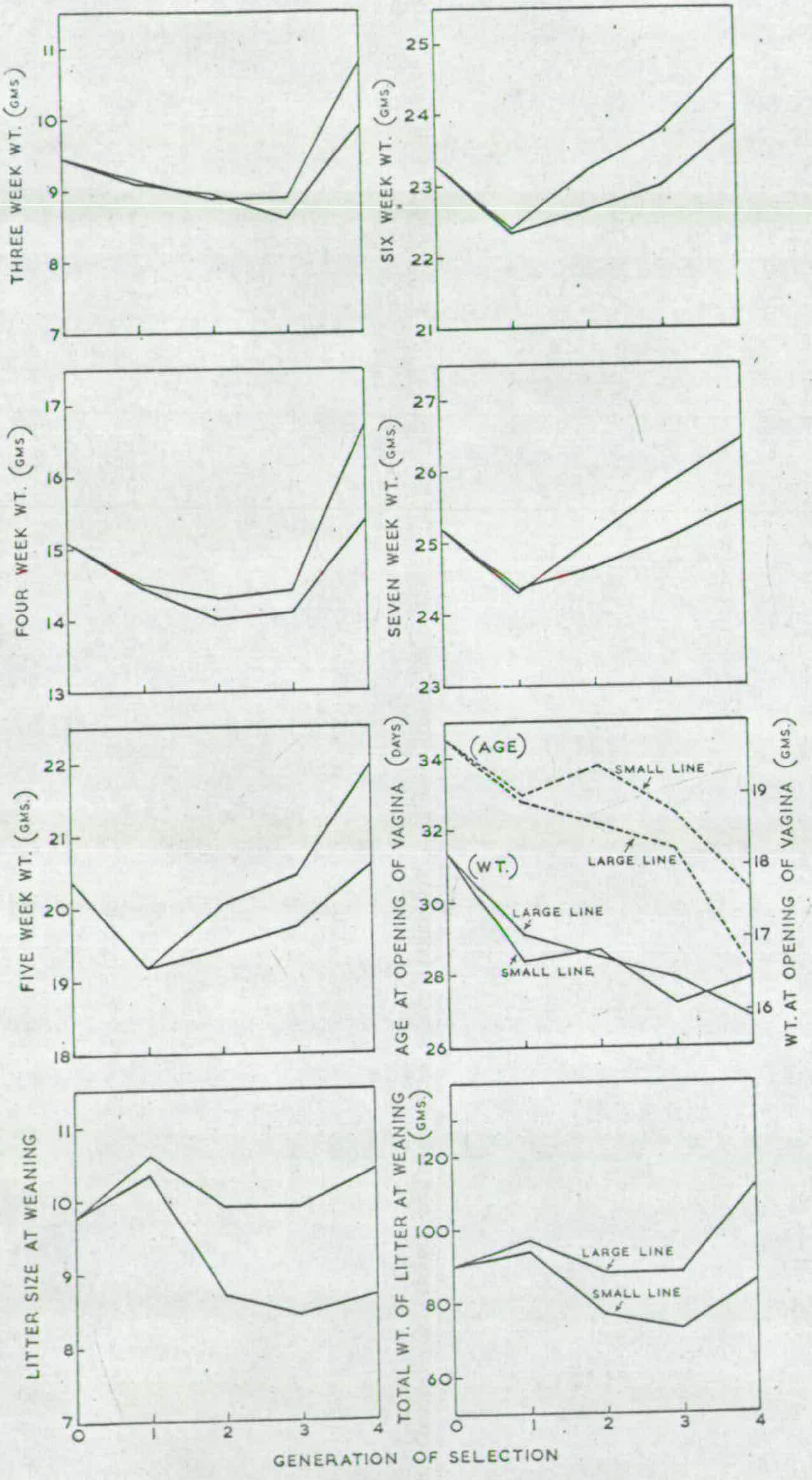

FIG. 5 Direct and correlated responses to selection for 3 week weight.

All the characters measured, with the exception of the weight at the opening of the vagina, show, in the last generation of selection, significant differences between lines, thus indicating the existence of genetic correlations between 3 week weight and these characters. The weight at opening of the vagina, however, does not show a significant response to selection. Also the differences in weight at opening of the vagina do not increase with the generation of selection, being alternatively positive and negative. Therefore this character is genetically independent of 3 week weight. By contrast, the age at opening of the vagina shows a very large difference between lines. The line selected for large 3 week weight has the vagina open earlier than the line selected for small 3 week weight. This is an indication of a negative genetic correlation between 3 week weight and age at opening of the vagina.

Although the estimations of genetic parameters obtained from the half sib analysis are, in the majority, non-significant, these estimations were used to calculate the expected direct and correlated responses to selection for the cumulative selection differential at the fourth generation of selection. As the additive variance of weight at opening of the vagina estimated in the half sib analysis was negative, no value for the genetic correlations was obtained. The results of expected and observed responses at the fourth generation of selection for the remaining characters are presented in Table 19.

The expected direct and correlated responses to selection are, in general, larger than those observed, although they are well within the confidence limits of the estimates. The low responses observed are probably due to the differences in litter size between

TABLE 19. Observed and expected direct and correlated responses after four generations of selection for 3 week weight estimated as differences between the large and small lines.

Character	Responses	
	Observed	Expected
3rd week weight	0.90	1.51
4th week weight	1.35	1.22
5th week weight	1.40	1.43
6th week weight	0.94	1.85
7th week weight	0.87	1.63
Age at opening of vagina	-2.18	-1.77

ines, which reduces the realised heritability and genetic correlations. owever this is not the case with the age at opening of the vagina where he observed response is larger than expected. The differences in litter ize between lines would result in an effect which would be the reverse f that observed.

The responses to selection are in general agreement with the results of the half sib analysis. However, in view of the small number of generations of selection, the quantification of the estimates of genetic parameters has very little meaning and only their general direction can be ascertained. This is the case of the correlations between 3 week weight and opening of the vagina. The negative phenotypic correlation between 3 week weight and age at opening of the vagina, found in the half sib analysis, is due to an environmental negative correlation due to compensatory growth and also to a negative genetic correlation. By contrast, the phenotypic correlation of 0.21 between 3 week weight and weight at opening of the vagina found in the half sib analysis seems to be only due to an environmental correlation or, if partly genetic, it is not due to an additive genetic correlation.

V DISCUSSION

The principal reason for studying competition was to determine its relative contribution to environmentally induced variance and, hence, to assess the expected increase in efficiency following its control in genetical experiments concerning body weight of mice. This information would be expected to be relevant to domestic animals kept in groups in confined spaces.

Competition was found to have a very small effect on pre-weaning growth. However, if individuals with very large differences in growth rate are reared in the same litter, the competitive effect could be increased to an appreciable amount. Attention should also be given to the mother's rearing ability as competition seems to depend to a certain extent on this factor. Therefore, care should be taken in not using as foster mothers females with poor mothering ability.

Although competition has been considered as part of the environmentally induced variation, in certain cases its existence affects the estimation of genetic variance. This is the case when the genotypic value of a strain is measured by the growth performance of individuals in mixed strain cages. If the genotypic value of a strain is measured by its mean growth and its growth is affected by competition, this results in the variance due to competitive ability being included in the genotypic variance, unless growth is also measured in non-competitive conditions. The competitive variance which becomes included in the genotypic variance depends on the genotype of a strain and on the environment, which is itself dependent on the genotype of the cage-mates. Therefore the changes in mean growth due to competition are the result of a genotype-environment interaction. If, however, the competition between strains affects e within-strain variance the genotype-environment interaction ll then be included in the estimate of environmental variance.

Changes in both means and variances of gain were found in the alysis of the effect of competition between inbred strains on post-eaning growth. The effect of competition on mean gain was found to be ery small in both males and females, being approximately 3% of the henotypic variance. Therefore the increase in the estimate of between train variance is negligible.

By contrast, the effect of competition on the within-strain ariance of the females is, in certain cases, very large and would affect o a large extent the estimates of environmental variance. For example, estimates of genotypic and environmental variance of gain from 3 to 6 weeks can be made from females of the JU and C_{57} strains, as shown below.

Variance	Pure cages	Mixed cages
V_G	1.85	1.85
V_E	1.06	2.94
V_P	2.91	4.79

The between-strain component of variance represents twice the genetic variance and the within-strain variance the environmental variance (Falconer, 1960). The estimation of the environmental variance, in this case, would depend largely on whether the strains were kept in separate cages or were mixed with each other, the within strain variance being nearly three times as great when it includes competitive effects in mixed cages. Thus, if estimates of the degree of genetic determination $\frac{V_G}{V_P}$ were made, the value obtained in pure cages would be 64%, whereas in mixed cages it would be only 39%. In this example, the strains which showed the largest competition on within-strain variance were chosen. However, even with smaller effects the estimation of genetic parameters can largely depend on the competitive conditions.

The effect of the number of mice per cage is very small and therefore has very little effect on the estimation of genetic parameters. In the case of the CBA strain, however, the within-strain variance increases considerably with increasing numbers of mice per cage, and estimates of the environmental variance of this strain would be increased when large numbers are caged together.

If competition tends generally to inflate the estimates of environmental variance of body weight, compensatory growth has the opposite effect. Genetic parameters have higher values after compensatory growth has acted than at any earlier age. As the higher values of the heritability are achieved by reduction of the component of variance due to common environment, the existence of compensatory growth might involve the choice between within-litter or individual selection as the most efficient way of selecting for adult body size.

A similar situation to that of compensatory growth in mice was found by F.W. Robertson (1959, 1960a) in Drosophila. There is a marked capacity for regulation of body size of Drosophila in such a way that environmental effects do not change adult body size. When larvae are reared in sub-optimal diets there is a lengthening of the larval period and no decline in final body size. If the nutritional deficiency becomes too severe, body size is then reduced and the larval period proportionately lengthened. This situation is directly comparable with the compensatory growth of mice. Where compensatory growth for Drosophila reared in sub-optimal conditions is attained by lengthening of the larval period, the same effect is achieved in mice reared by poor mothers by a delay in attaining sexual maturity. As mice were reared under normal conditions, no evidence is available which could suggest that the inverse relationship between length of the larval period and body size observed in Drosophila reared in severely deficient diets would lead to an equivalent effect in mice also reared in extremely poor conditions. However, the independence observed between age and weight at opening of the vagina suggests that even when sexual maturity is delayed for long periods the weight at that stage is not changed. The effect observed in Drosophila is explained as being a kind of safety mechanism that ensures that the reproductive adult size is attained sooner than it would be if the homeostasis in body weight was complete (F.W.Robertson, 1960b). The efficiency of the mechanism regulating adult size in different species is probably dependent on the relationship between body size and reproductive fitness. If the reproductive ability of Drosophila is less affected by a smaller body size than by a shorter reproductive period, it is advantageous for the adult size to be attained at an early age. If in mice the reverse is true, then sexual maturity will be delayed until the normal body size can be attained. Therefore the effectiveness of compensatory growth would be determined in any species by the relationship between body size and fitness and also by the severity of the environmental factors.

Homeostasis in age at sexual maturity was studied by Yoon (1955) in relation to time of vaginal opening of inbred and crossbred mice. It was found that crossbred mice had a lower variation in time of vaginal opening than inbreds. Also the variance of time of opening of vagina of females coming from a backcross in which crossbreds were used as female parent was lower than when inbreds were used as female parent. It was concluded that heterozygotes have a superior developmental homeostatic function than homozygotes and that the lack of heterozygosity of a female leads to an unfavourable condition for the homeostatic function of their offspring. However, the same results would be expected if the increased variation in time of vaginal opening in the inbred females was a consequence of increased variability in body size. If also larger variation in maternal ability exists in inbreds than in crossbreds, the weaning size of backcrosses having an inbred mother would be more variable than mice with the same genetic make-up but having crossbred mothers. This difference in variation of weaning size in the two groups would lead, through compensatory growth, to the observed relationship between the inbreeding of the mother and the variance at opening of vagina of her offspring.

The effect of compensatory growth, being responsible for the reduction in variance of adult body size, is related to the phenomenon of canalisation of development. Canalisation is defined by Waddington (1957) as the exhibition of regulatory behaviour in development. When a mass of material is developing, it will tend to return to the normal path of development if it is forced out of it by some experimental means. Maternal effects in mice, in certain cases, force body size out of the normal path of development either by stimulating or depressing growth in the early stages. These deviations from the normal path are later corrected by compensatory growth. Therefore compensatory growth is the means by which canalisation of body size is achieved. As compensatory growth is the result of the constancy in weight at the inflexion point of the growth curve and, consequently, of the constancy of weight at sexual maturity, the homeostatic properties of these two characters is the essence of canalisation of body size.

In relation to the environment provided by their mother, the degree of canalisation of body size in mice is different during the growth before and after sexual maturity is attained. Considering the degree of canalisation of body size at any age to be inversely related to the variance of body size at that age, development is less canalised before sexual maturity than after that stage. Using Waddington's terminology, the creodic profile of body size is narrow after sexual maturity and broad before that stage. These two degrees of canalisation can be related to the variation in environment existing during these two periods. A large part of the growth before sexual maturity is dependent on the maternal ability, and a loose canalisation allows the young to adapt themselves to the existing conditions. After this source of variation in environment ceases, the canalisation becomes steep in order that the normal adult body size can be attained. The effectiveness of these two degrees of canalisation in achieving maximum fitness is probably related to the different contribution of reproductive ability to fitness before and after sexual maturity. Before sexual maturity is attained the main component of fitness would be viability whereas after sexual maturity fertility would become a large component of the fitness of an individual. When only survival is important and environment is variable, the fitness of an individual would depend, to a large extent, on the plasticity of body size, which would allow the animal to cope with a large range of environments. However, when reproductive ability becomes important and a normal body size is desirable for reproduction, the large variation which was favourable in the previous period has to be reduced. This is effected by compensatory growth.

VI SUMMARY

The effect of competition between mice of different genotypes was studied by comparing the growth of mice which have different strains as cage mates. Competitive effects on pre-weaning growth were analysed by rearing in the same litter mice belonging to two lines selected for large and small body weight at 3 weeks of age. Competition had a very small effect on growth and was only apparent when mice were reared by females of poor maternal ability.

The effects of competition and number per cage on post-weaning growth were analysed by comparing the growth from 3 to 6 weeks of age of mice of different strains in pure and mixed-strain cages and in groups of two and four mice per cage. Four inbred strains were used in this experiment - the JU, RIII, CBA and C_{57} strains. It was found that in both males and females the mean gain of a strain was dependent on the strain of the cage-mates. It was possible to rank the strains for competitive ability in the following order: $C_{57} > JU > CBA \geqslant RIII$. There was an indication of an inverse relationship between the mean gain of a strain and its competitive ability.

The number per cage also had an effect on the mean gain of mice, growth being generally better in groups of two mice per cage. The JU strain, however, had better performance in groups of four mice per cage. Altogether the effects of competition and number per cage only account for about 6% of the phenotypic variance.

A direct relationship was found in females between competitive ability of a strain and the within-strain variance of its cage-mates. This effect is independent of the number per cage with the exception of

the CBA females which induce large variance in groups of four and have no effect on groups of two females per cage. No effect on the within strain variance was found in males. It was concluded that changes in the within strain variance due to competition will have large effects on the estimation of the environmental variance, thus affecting the estimates of genetic parameters of body weight.

The effect of early occurring environmental factors on subsequent growth was also studied. It was found that, in a half-sib analysis, the variance of body weight due to common environment, which represents largely the variance induced by maternal factors, after increasing from birth to 4 weeks of age, showed a marked reduction after that age. It was also found that the reduction in environmental variance was the result of an inverse relationship between weekly gain and previous weight. It was suggested that the reduction in environmental variance was the result of a compensation in growth which is achieved by changes in the duration of the exponential phase of growth. A very close relationship was found between the inflexion point of the growth curve and sexual maturity evaluated by the opening of the vagina. It was also possible to show that sexual maturity occurs at a fairly constant weight, the age at opening of the vagina being inversely related to the mean 3 week weight of the litter. As this last measurement is mainly dependent on maternal effects, it was then concluded that a late age sexual maturity represented a prolonged exponential phase of growth and a compensation for the low 3 week weight determined by the maternal environment.

The selection experiment designed to provide the two lines for the analysis of the effect of competition on pre-weaning growth was carried out for four generations of selection. The weekly weights from 3 to 7 weeks and, in females, the age and weight at opening of the vagina, were measured. The results are in general agreement with the findings of the half-sib analysis. However, due to differences in litter size between lines, the expected responses were larger than the observed.

As mechanisms regulating body size, similar to compensatory growth, have been found in species other than mice, it was suggested that such mechanisms belong to the type of phenomenon called canalisation of development.

ACKNOWLEDGEMENTS

I am indebted to Professor C.H. Waddington, C.B.E., F.R.S. for laboratory facilities, the "Comissão Organizadora da Investigação Para a Otan" for financial support, and the Direcção Geral dos Serviços Pecuários for leave of absence.

I am grateful to Dr. D.S. Falconer for his supervision and his continued interest throughout this work. I would like to thank Dr. R.C. Roberts and Mr. R.B. Land for many helpful discussions and Dr. B. Woolf for statistical advice and for providing the computer programme for the half-sib analysis.

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