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The Effects of Selection for Different Combinations of Weights at Two Ages on the Growth Curve of Mice

J.C. McCarthy
Faculty of Agriculture, University College, Dublin (Ireland)

H. Bakker
Department of Animal Science, Agricultural University, Wageningen (the Netherlands)

Summary. The weights of mice in lines selected for different combinations of high and low body weights at 5 and at 10 weeks of age were recorded from 3 to 21 weeks of age. The average growth curve for each line was computed using the Gompertz function. The growth curves of lines selected for high or low weight at a single age (ST lines) showed large differences in estimates of mature size and small differences in estimates of maturing rate, i.e. of the relative rate of growth to maturity. The growth curves of lines selected by independent culling for divergent combinations of deviations of opposite sign in 5- and 10-week weights (ICL lines) showed little difference in estimates of mature size and a large difference in estimates of maturing rate. The growth curves of lines selected by index for divergence in 5-week weight with no change in 10-week-weight or for divergence in 10-week-weight with no change in 5-week weight showed large differences in estimates of mature size and large differences in estimates of the maturing rate. The relationship between mature size and maturing rate was affected in different ways by the three types of selection.

Key words: Mice – Selection – Growth curve

Introduction

The direct and correlated effects of selection for high and low body weight in mice have been studied by several workers (for reviews, see Roberts 1965; Eisen 1974, McCarthy 1977). Almost all the lines involved were selected for weight at a single fixed age (or rate of gain to a fixed age) and the consequent changes in body weight, carcass composition and fertility have been well documented. But there have been relatively few studies of the growth curves of such lines. Roberts (1961) recorded the lifetime growth curves of several Large, Small and Control lines. He found that these lines had vastly different mature weights and that the difference in weight between Large and Small lines selected for 6 week weight increased with age so that the proportional differences remained about the same throughout life. However, he noted one marked difference between the growth curves of two Large lines between 6 and 50 weeks of age; both lines had the same mean weight at 6 weeks but reached similar mature weights at 6 and at 12 months respectively. He concluded that this was 'presumptive evidence that mature weight, and the path whereby it is reached, are to some degree under separate genetic control'. Timon and Eisen (1969) compared the growth curves of a line selected for post-weaning growth rate and its unselected Control using different growth functions. Although there was a large difference between the lines in weight at maturity, differences between estimates of other parameters describing the form of the growth curve were not statistically significant in most cases. However, they obtained high estimates of heritability for these latter parameters from an analysis of full-sib data. As a result, they suggested that selection for a change in the form of the growth curve could be moderately successful.

There has been one selection experiment with mice which gave some indirect support to this statement. Wilson (1973) selected two lines of mice for an increase in the ratio of gain in weight from 6 to 9 weeks relative to that from 3 to 6 weeks of age for 8 generations. He obtained responses in gain from 6 to 9 weeks without affecting gain from 3 to 6 weeks; estimates of the realised heritability of the ratio were 5% and 13%. However, he did not record the growth curves of the two lines.

There have been two experiments with chickens and one with turkeys which showed that it is possible to select for 'antagonistic' combinations of body weights, i.e. for changes opposite to those predicted by the high positive genetic correlations between body weights at different ages. Abplanalp, Ogasawara and Asmundson (1963) selected a line of Broad Breasted turkeys using an index intended to increase 8-week weight and hold 24-week weight constant. For seven generations the mean value of the earlier weight increased in a linear fashion while the later weight was 'restricted' as intended. Merritt (1974) selected a line of broilers for high 7-week weight and low 21-week weight. In the first part of the experiment he increased the earlier weight without changing the later one. However, he subsequently obtained positively correlated responses in the two weights. Unfortunately, the growth curves of these lines of turkeys and broilers were not recorded. However, Ricard (1975) did record the growth curves of lines of poultry selected using independent culling for various combinations of high and low weights at 8 and 36 weeks of age after 12 generations of selection. As expected, the lines selected for high weight or for low weight at both ages diverged markedly at all points in the growth curve, the high line becoming progressively heavier than the low one. However, two lines selected for High-Low and Low-High combinations of weights at the two ages ranked differently in weight before and after about 18 weeks of age. Up to that age, the High-Low line was heavier. The growth curves then crossed and diverged markedly; the line selected for low 8-week and high 36-week weight became progressively heavier at older ages.

The selection experiment reported here is more comprehensive than those outlined above in several ways. The objectives of selection included (1) changing early and later weights in opposite directions, (2) changing early weight without altering later weight and (3) changing later weight without changing early weight. Also, selection was exercised for more generations than in previous studies of this type. An account of the changes in 5- and 10-week weights has already been published (McCarthy and Doolittle 1977). This paper extends that report to changes in the form of the growth curve from 3 to 21 weeks of age.

Materials and Methods

The lines used in this study are listed in Table 1. The details of their breeding have been given by McCarthy and Doolittle (1977). Mice in the ST (single-trait) lines were selected for high or low body weight at 5 or 10 weeks of age. Selection was performed separately for each weight in the I.C.L. (independent culling level) lines and for various indices of the two weights in the R.I. (restricted index) lines. The objective in the I.C.L. lines was to change 5-week weight and 10-week weight in opposite directions and in the R.I. lines, to hold weight at one age fixed while changing the other. When the lines were bred for the periods shown in Table 1, selection was relaxed and lines were bred as the Control by random mating. Then weights from 3 to 21 weeks in each line were recorded. The data from each group of selection lines were collected contemporaneously with a replicated unselected Control line (Q/Fa) from which the lines were originally bred. In all lines, litters were reduced to 12 animals if originally larger than this. All mice were weaned at three weeks. At weaning, not more than 3 mice of each sex from each litter were sampled. These mice were weighed individually at weekly intervals from 3 to 11 weeks of age and at intervals of two weeks from 11 to 21 weeks.

Table 1. Nomenclature and selection history of lines

Type of selection and line	Selection objective	Duration (generations)
(a) Single trait (ST)		
H_5	Increase W_5	15
L_5	Decrease W_5	15
H_{10}	Increase W_{10}	15
L_{10}	Decrease W_{10}	15
QA	No selection	–
(b) Independent culling levels (ICL)		
H_5 L_{10}	Increase W_5, Decrease W_{10}	22
L_5 H_{10}	Decrease W_5, Increase W_{10}	22
QB_1	No selection	–
(c) Restricted index (RI)		
H_5 R_{10}	Increase W_5, Restrict W_{10}	14
L_5 R_{10}	Decrease W_5, Restrict W_{10}	14
R_5 H_{10}	Restrict W_5, Increase W_{10}	14
R_5 L_{10}	Restrict W_5, Decrease W_{10}	14
QB_2	No selection	–

W_5 indicates 5-week weights
W_{10} indicates 10-week weights

The growth curve of each mouse was described in terms of the Gompertz growth function. This function was chosen after preliminary research on data from a small number of mice from each line. The Richards function (Richards 1959, 1969) was fitted to these data as a first step.

The Richards formulae are:

$$W_t^{(1-m)} = A^{(1-m)} (1 - be^{-kt}) \text{ for } m < 1$$

$$W_t^{(1-m)} = A^{(1-m)} (1 + be^{-kt}) \text{ for } m > 1, \text{ where}$$

W_t = body weight at age t,
A = the asymptote of the function; it estimates the adult weight of an animal.
b = an integration constant; it estimates the starting position of the growth curve along the time axis.
k = the rate at which a logarithmic function of weight changes lineary per unit of time; it estimates the rate of maturing of the curve (i.e. the relative rate at which A is reached).
m = a weight exponent constant; it determines the position of the point of inflexion of the curve.

The most used growth functions (Monomolecular, Gompertz, von Bertalanffy and logistic function) can be deduced from the Richards function by substitution of different values for m.
For example:

$m = 0$ is the monomolecular function
$m = 2/3$ is the von Bertalanffy function
$m \rightarrow 1$ is the Gompertz function ($m = 1$ gives no solution)
$m = 2$ is the logistic function

When m is between 0 and 1 the curves are transitional in form between monomolecular and Gompertz; between 1 and 2 the transition is between Gompertz and logistic (Richards 1959). The Richards function proves that there is a strong relationship between these formulae.

In theory, the best function to describe the growth curve is the four parameter Richards function fitted by means of iterative procedure. In practice, however, fitting the Richards function is complicated by the number of parameters in the iteration and lack of convergence of the parameter m (Bakker and Koops 1978). In addition, wrong estimations of m occur when local minima or 'saddle-points' in the residual variance are met during the iteration. We used an alternative method suggested by Bakker and Koops (1978), i.e. fitting the Richards function to a sample of the total data set, using a number of alternative values of m.

The results of that analysis showed that the value of the parameter m close to unity gave the smallest residual variance. Consequently, the Gompertz function was selected as the best function to describe the growth curve of the mice in the different lines. This is in the form of:

$$W_t = Ae^{-be^{-kt}}$$

The Gompertz function was fitted by iteration, resulting in values of A, k and b per mouse giving the smallest residual variance.

Results of the analysis of the total data set are presented by graphical representation of the growth curves and by statistical analysis of the following traits:

- body weight at 3, 5, 10 and 21 weeks of age
- the parameter A
- the parameter k

No attention was given to the parameter b as it has no particular physiological significance (Richards 1969).

The data were analyzed by means of least squares method (Harvey 1960) according to the following model:

$$Y_{ijkl} = u + L_i + W_j(i) + S_k + LS_{ik} + E_{ijkl}$$

Y_{ijkl} = an observation from the l^{th} mouse in the ijk^{th} subclass
u = overall mean
L_i = effect of the i^{th} line (i = 1,..........13)
W_j = effect of the j^{th} litter within the i^{th} line
S_k = effect of the k^{th} sex (k = 1,2)
LS_{ijk} = effect of interaction if i^{th} line and k^{th} sex
E_{ijkl} = random error

Effects L, S and LS were assumed to be fixed, while W_j and e_{ijkl} were assumed to be random with means zero and variances $\sigma^2{}_W$ and $\sigma^2{}_e$, respectively. As a consequence, MS_L was tested against MS_W, while MS_W, MS_S and MS_{LS} were tested against MS_e. In the statistical analysis, the following calculations were made:

- least squares means by line and by sexes,
- analyses of variances according to the model given,
- linear contrasts between diverging lines and between sexes.

Relative body weights (body weights expressed as percentages of A) were plotted against age to get an impression of differences among lines in 'degree of maturity' (i.e. the proportionality of weights at any particular age to mature weight).

In addition, after pooling within-line sums of squares, the heritabilities of W_3, W_5, W_{10}, W_{21}, A, k were calculated using full-sib analysis specified by the model given above. Phenotypic and genotypic correlation among these traits were also calculated. These estimates of heritabilities and genotypic correlations are biased by maternal effects and by non-additive genotypic effects and thus the estimated values of the parameters must be considered as the upper limit of the real values.

Results

The effects of selection in the various lines on weights at 5 and at 10 weeks of age have been described in detail by McCarthy and Doolittle (1977). In the ST lines, selection resulted in rapid changes in body weights in both directions and the realised heritability estimates were between 30% and 40%. In the ICL lines, selection did not cause statistically significant divergences of opposite sign in 5 and in 10-week weights. Selection in the RI lines was effective; the realised heritability estimates for the restricted indexes were about 15% in each of the four lines. However, there were correlated changes in the restricted trait in two of the four lines. There was a very high realised genetic correlation of over 0.9 between weights at 5 and 10 weeks.

Changes in litter size were similar in all lines during selection, i.e. there was no significant change in number born but a small decline in number at weaning (Doolittle, unpublished). There was no significant correlation however, between number at weaning and body weight over the generations of selection. Thus, no adjustments for changes in litter size were made.

The growth curves of the three groups of lines are shown in Figure 1. It is obvious that there were large differences in body size which increased with age between the High and Low ST lines. In contrast, there was little difference in weight at any age between the ICL lines. The RI lines showed a more complex pattern of changes in body weight. The RI lines selected for restriction of 5-week weight showed no divergence up to that age but a large and rapidly increasing divergence in weight occurred at subsequent ages. The RI lines selected for restriction of 10-week weight showed a relatively constant difference in weight from 5 weeks of age onwards.

The estimates of the mean weights at 3, 5, 10 and 21 weeks of age and of the weight at the asymptote (A) and the rate parameter (k) are shown for each line in Table 2. The differences between pairs of lines selected for a divergence in a particular criterion are shown for the same traits in Table 3. The statistical evidence for the effects of selection on A supports the statements made already on the basis of the visual evidence in Figure 1. Selection in the ST lines resulted in large differences in A. Selection in the ICL lines had a very small effect on A. Selection in the RI lines had effects on A which were consistent with the objectives of selection in the lines selected for divergence in 10-week only, i.e. an increasing divergence in weight at later ages but inconsistent with the objectives of selection in the lines selected for divergence in 5-week weight only. In that case, there were divergences of approximately equal magnitude in weights from 5 to 21 weeks of age.

The maturity curves of the three groups of lines are shown in Figure 2. The largest changes in the degree of

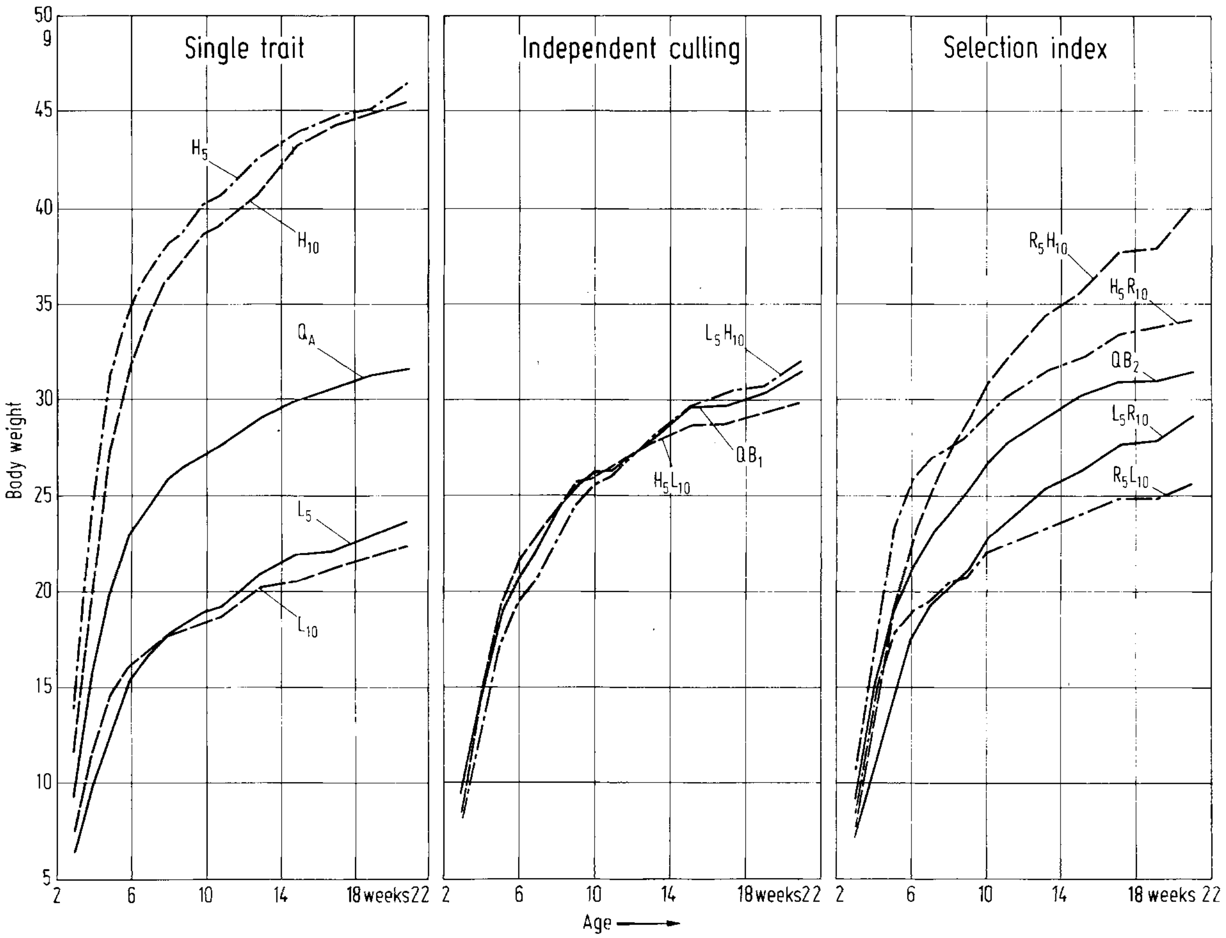

Fig. 1. Growth curves of lines of mice selected by different methods for 5 and 10 weeks of age

maturity took place in the RI lines. The ICL lines showed slightly less divergence in degree of maturity and the ST lines least of all. The H_{10} and L_{10} lines showed almost no divergence in degree of maturity.

These changes are reflected by the estimates of k in Table 2, early maturing lines having higher values of k. The difference in estimates of k between pairs of lines are shown in Table 3 and in all cases except one are statistically significant.

The estimates of phenotypic and genotypic parameters for the same range of traits, based on full-sib analysis, are shown in Table 4. The estimates of heritability for the various weights are extremely high and obviously reflect the environmental covariance which biases upwards estimates based on full-sib data. The fact that the estimate for k is less than 0.5 suggests that an unbiased estimate of heritability may be quite low. The estimates of the genetic correlations between traits appear more realistic. The estimates for pairs of weights at different ages do not deviate alarmingly from estimates realised on selection by McCarthy and Doolittle (1977) in the same population.

Discussion

The objectives and results of the selection experiment which yielded the lines described here were reported in detail by McCarthy and Doolittle (1977). Selection in the ICL lines was an empirical attempt to make changes of opposite sign in 5- and 10-week weights. In practice, little or no selection was applied to 10-week weight and the realised response in 5-week weight was much less than expected (McCarthy and Doolittle 1977). Estimates of realised genetic parameters from early generations of the ST lines were used to compute the restricted indexes used in selecting the RI lines. Selection in those lines, designed to alter weight at one age but not at another, was partially successful. However, the actual responses were much less than those predicted using a value of +0.9 for the genetic correlation – a mean value based on responses in the ST lines. The reasons for this discrepancy and for the failure of the responses in the ICL lines to come anywhere near expectation are not clear. It is possible that the genetic correlation may have been increased over the value of +0.9 during selection in these lines. Rutledge, Eisen and Legates (1973) have reported a case where the realised value of the genetic correlation between two 'antagonistically' correlated traits in mice was apparently inflated in index lines relative to single trait ones. How this might occur is not clear.

When it was decided to assess the impact of the three types of selection on the form of the growth curve, the first problem was to decide which particular growth function to use. As explained above, the Gompertz function was chosen after fitting a Richards function with different values of the 'shape' parameter, m, and finding that a value of m close to unity caused best fitting of the data in all of the lines. Use of the Gompertz equation obviates any consideration of differences between lines in the 'shape' parameter, m, since the point of inflexion is fixed at a constant proportion of mature weight, i.e. at Ae^{-1} which is approximately one-third of A. Differences among lines in the integration constant, b, were trivial and were ignored. Thus, interest was concentrated on variation in just two parameters of the curve, A and k.

Table 2. Least-squares means of body weight traits and growth curve parameters

		Traits					
Lines	n	W_3(g)	W_5(g)	W_{10}(g)	W_{21}(g)	A(g)	100 k
QA	87	9.4	19.8	27.2	31.7	30.8	37.8
H_5	71	13.9	31.2	40.1	46.5	44.4	43.4
L_5	44	6.4	12.7	19.1	23.8	23.0	30.1
H_{10}	63	11.5	27.2	38.6	45.7	44.2	37.8
L_{10}	53	7.4	14.7	18.6	22.7	21.8	34.3
QB_1	95	9.4	18.6	26.2	31.4	30.5	30.8
H_5L_{10}	70	8.5	18.8	25.8	29.8	28.9	40.6
L_5H_{10}	48	8.1	16.9	25.6	32.0	31.3	26.6
QB_2	125	8.8	19.1	26.8	31.4	31.1	33.6
R_5H_{10}	61	7.7	19.1	30.8	40.0	38.6	28.7
R_5L_{10}	101	8.5	17.8	22.2	25.7	24.9	41.3
H_5R_{10}	107	10.5	23.2	29.2	34.2	32.4	46.9
L_5R_{10}	90	7.1	14.5	22.8	29.2	28.5	26.6
Females	464	9.0	18.3	24.9	30.5	29.7	30.1
Males	551	9.1	20.9	29.5	34.8	33.5	40.6
Standard error (n = 70)		.47	.59	.67	.80	.80	2.2

W_i indicates weight at week i, in grams
n indicates the number of animals, in this and following tables

The correlated responses to selection in these two parameters are readily appreciated by perusal of Figures 1 and 2 which portray, in approximate terms, the changes in A and k, respectively. Selection for a single weight predictably changed weights at other ages including A, because of the high positive interage genetic correlations. However, only selection for weight at the younger age, i.e. in the H_5 and L_5 lines, significantly affected k. This presumably reflected the less strong correlation between weight at the younger age and mature size.

The most dramatic correlated changes in the form of the growth curve occurred in the RI lines where A and k changed simultaneously in each of the selection lines. A and k both increased in the H_5R_{10} line and both decreased in the L_5R_{10} line. A and k showed changes of opposite sign in the other two lines. These results indicate that there is genetic variation in k independent of A and although we cannot estimate the strength of the realised genetic correlation between these two parameters from the observed correlated responses, it would seem from the within-line estimate of the correlation between them (–0.5 in Table 4) that only about 25% of the variance in each trait is dependent on differences in the other. Timon and Eisen (1969) obtained estimates of about –0.3 for the genetic correlation between A and k parameters of

Table 3. Linear contrasts of populations for body weight traits and growth curve parameters

Contrasts between:	Difference for trait					
Lines	W_3	W_5	W_{10}	W_{21}	A	100k
$H_5 - L_5$	7.4^a	18.4^a	21.1^a	22.7^a	21.4^a	13.3^a
$H_{10} - L_{10}$	4.1^a	12.6^a	20.1^a	23.0^a	22.4^a	3.5
$H_5L_{10} - L_5H_{10}$	0.4	1.9^b	0.3	-2.1^b	-2.5^b	13.3^a
$R_5H_{10} - R_5L_{10}$	–0.7	1.3	8.7^a	14.3^a	13.7^a	12.6^a
$H_5R_{10} - L_5R_{10}$	3.4^a	8.7^a	6.4^a	5.0^a	3.9^a	19.6^a
♀♀ – ♂♂	–0.1	-2.8^a	-4.6^a	-4.3^a	-3.8^a	-10.5^a

^{a} $p < 0.01$
^{b} $p < 0.05$

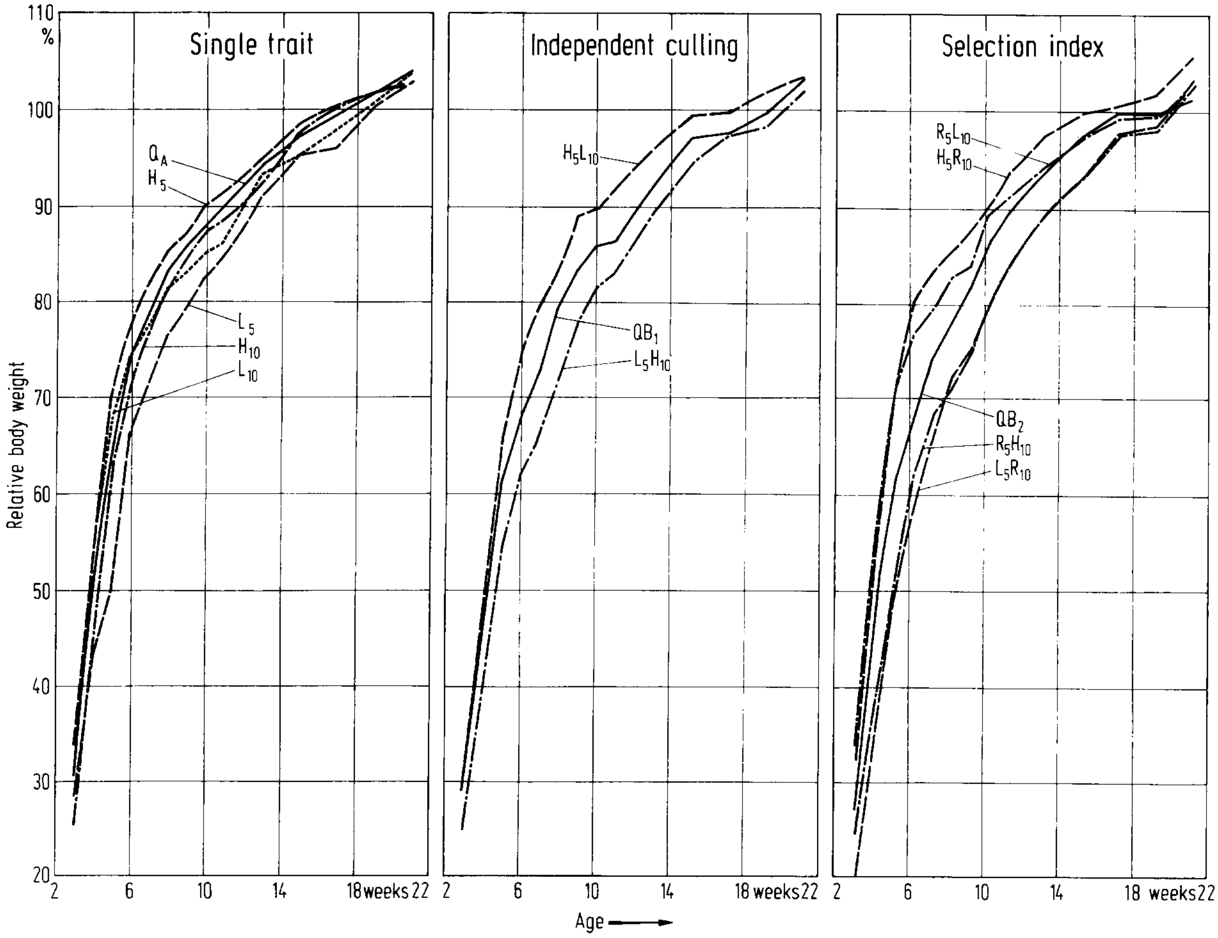

Fig. 2. Maturity curves of different selected lines of mice

Table 4. Phenotypic (above diagonal), genotypic (below diagonal) correlations and heritabilities (diagonal) of body weight traits and growth curve parameters

	W_{03}	W_{05}	W_{10}	W_{21}	A	k
W_{03}	**1.40^a**	0.67^a	0.50^a	0.46^a	0.50^a	−0.15^a
W_{05}	0.74 (0.05')	**0.84^a**	0.74^a	0.59^a	0.56^a	0.20^a
W_{10}	0.57 (0.07)	0.85 (0.03)	**0.90^a**	0.81^a	0.81^a	0.06$^{n.s.}$
W_{21}	0.57 (0.07)	0.79 (0.05)	0.94 (0.02)	**0.81^a**	0.95^a	−0.30^a
A	0.63 (0.06)	0.78 (0.05)	0.93 (0.02)	0.99 (0.00)	**0.87^a**	−0.37^a
k	− 0.40 (0.10)	− 0.08 (0.12)	− 0.17 (0.11)	− 0.41 (0.11)	− 0.49 (0.11)	**0.46^a**

s.e. of genetic correlations given in parenthesis
^{a} $p < 0.01$ respectively

Richards and logistic curves fitted to lines of mice selected for postweaning gain. It would thus appear that selection for an increase in A would be expected to result in later maturing animals, i.e. ones with a lower k value. It also follows that selection for early-maturity (with higher k values) would be expected to result in a reduction in A. As expected, estimates of the genetic correlations between A and weights at various ages were very high positive ones and increased in magnitude at later ages. The estimates of the genetic correlation between k and weights at 5 and 10 weeks of age were very small. They were not consistent in sign with the small correlated responses found in k values in the ST lines. Similar inconsistency was reported between static and realised genetic correlations estimates for k and A values in a pair of lines selected for high and low weight at 6 weeks of age (Eisen, Lang and Legates 1969).

In the vast majority of body weight selection experiments with laboratory animals and in both experimental and practical selection work in poultry, the selection criterion has been weight at a relatively young age, or for gain between two such ages. Roberts (1979) and McCarthy (1977) have recently reviewed the theoretical and practical implications of the correlated responses in efficiency and carcass composition which result during such selection. On the plus side, there is a desirable increase at young ages in the efficiency of food utilisation; on the minus side there are undesirable increase in size and fatness in adulthood. The possibility of diminishing the latter effects while obtaining the benefits of increased growth rate in the younger animal has inspired the relatively small number of experiments reviewed in the Introduction. The problem in theory is relatively simple. If one had unlimited resources one could measure and select animals for any combination of early growth rate and adult weight. The genetic correlation between maturing rate (i.e. the relationship between early growth rate and adult size) and adult weight appears to be low enough not to be an inhibitory factor in mice and, also, from indirect evidence, in poultry. In practice, however, because of exigencies of resources, one is forced to adopt a simpler strategy involving selection for a small number of weights or gains. The success achievable with such an approach – say using an index designed to keep a later weight constant while increasing weight at a young age – depends critically on the value of the genetic correlation between the traits in the index; only a portion $(1\text{-}r_g^2)$ of the additive variance in the unrestricted trait is exploitable. In the lines described in this paper, the correlation was over 0.9 and still moderate but impressive changes were wrought in the shape of the growth curve. Obviously, use of an index involving a later weight would have been more successful.

The relatively more successful results of restricted index selection for two weights in turkeys (Aplanalp et al. 1963), however, suggest a much lower genetic correlation than in mice. McCarthy (1977) computed realised estimates of +0.6 from their data and suggested that the correlation between the two weights selected simultaneously in broilers by Merrit (1974) may be similar in magnitude. The results of Ricard (1975) substantiate this view. The results of his selection for high-low and low-high combinations of weight at 8 and 36 weeks of age in poultry gave a most impressive change in the relationship between juvenile growth rate and adult weight. However, the major contribution to this change resulted from change in adult weight – not growth rate. The average estimate of the genetic correlation between 8 and 16 weeks in the early generations of his experiment was about 0.5 which bears out the point made earlier regarding the critical nature of the magnitude of the correlation.

The difficulty of selecting for earlier maturity in cattle without increasing mature size has been discussed by Taylor (1968) and Fitzhugh and Taylor (1971) suggested that selection for relative growth rate might be useful in this context. The only experiment, with mice, in which this has been tried (Bakker 1974) was singularly unsuccessful in changing the maturing rate. The results of the experiments reported here and of those referred to for comparison suggest that simple index methods of the sort discussed above could be effective in suppressing correlated responses in the mature weight of strains of animals selected for increased juvenile growth rate – but at the cost of slow genetic progress in the primary trait.

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Dr. J.C. McCarthy
Faculty of Agriculture
University College
Belfield
Dublin 4 (Ireland)

Dr. H. Bakker
Department of Animal Science
Agricultural University
Wageningen (the Netherlands)