

Comparison of Growth Curves of Mice Selected and Unselected for Postweaning Gain*

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Summary. Mice were sampled from a line selected for increased postweaning weight gain from three to six weeks and from a randombred control line originating from the same base population. Body weights were recorded at each of 14 ages from day 5 to day 98. The Richards and logistic growth functions were fitted to the growth trajectories of each individual mouse by a generalized non-linear least squares procedure. Estimated growth parameters (asymptotic weight, rate, shape of curve, age and weight at inflection, mean absolute growth rate and mean relative growth rate) were computed for each individual. The effects of line, litter within line, sex and line \times sex interactions on these estimated parameters were then studied.

Both the Richards and logistic functions fitted the data equally well and the plotted trajectories coincided over most of the growth curve. There was excellent agreement between the estimates of asymptotic weight and both age and weight at inflection based on the different functions. However, both functions apparently underestimated the asymptotic weight.

Analyses of the line differences showed that selection for postweaning gain increased the mean absolute growth rate over the entire curve but had no effect on the relative growth rate or the shape of the growth curve. Full-sib analyses suggested the presence of considerable genetic variation and some high genetic correlations among the estimated growth parameters.

Introduction

Direct response to selection for body weight at a fixed age invariably results in a correlated growth response at other points on the growth curve. ROBERTS (1961) reported that the difference in mean body weight between lines of mice selected for high and low six-week weight increased with age, but the proportionate difference remained unchanged. ROBERTS (1961) also noted a marked difference in the age at which final weight was reached (26 vs. 52 wks.) between two lines selected for large six-week weight, although both lines attained a similar final weight. In contrast, GALL and KYLE (1968) found similar body weights at all ages in two lines selected for large 42- and 60-day body weight, respectively. These observations suggest the need for further study of the genetic basis for the shape of the growth curve.

Three growth functions which have been used to describe growth patterns in mice are the Gompertz (LAIRD, TYLER and BARTON, 1965), Bertalanffy (GALL and KYLE, 1968) and logistic (MONTEIRO and FALCONER, 1966; TIMON, 1968). EISEN, LANG and LEGATES (1969) compared the suitability of these three functions in describing differences in growth patterns between lines of mice developed by selection for large and small six-week body weight, and concluded that the logistic provided the best fit to their

data. RICHARDS (1959) showed that the three functions are all special cases of a more generalized function, each assuming a different fixed weight, relative to mature size, at which the point of inflection occurs.

The objective of the present study was to describe the changes in the growth pattern of mice which have resulted from selection for increased postweaning weight gain. The logistic and Richards growth functions were compared to determine which function fitted the data best.

Materials and Methods

Source of data: Mice were sampled from a line selected for increased postweaning weight gain from three to six weeks (High) for nine generations and from an unselected randombred control line (Control) originating from the same base population (TIMON and EISEN, 1970). All litters were fostered five days postpartum on Control dams which had given birth within the same 12-hour period as the fostered litter. Litters were standardized to eight mice at five days of age. At weaning (21 days), male and female mice were caged separately in random groups of four per cage and given feed (Purina Laboratory Chow) and water ad libitum. Individual mice were weighed at 5, 12 and 21 days of age, and weekly thereafter to 14 weeks of age. The laboratory was maintained at approximately 22 °C and 50% relative humidity.

Growth functions: Both the generalized (RICHARDS, 1959) and logistic functions were fitted to the growth data of each individual mouse. The Richards function for the n^{th} individual is represented by

$$Y_n(t) = A_n(1 - b_n e^{-k_n t})^{1/(1-m_n)} + E_n,$$

where $Y_n(t)$ = body weight (grams) at time t (days), b_n = integration constant, k_n = rate at which a logarithmic function of weight changes linearly per unit of time, A_n = asymptotic weight, m_n = shape parameter and

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E_n = error term assumed to be $N(0, \sigma^2)$. Substituting $m_n = 2$ in the above equation yields the logistic function

$$Y_n(t) = A_n (1 - b_n e^{-k_n t})^{-1} + E_n.$$

Other traits derived from these functions were the age (t_n^*) and weight (y_n^*) at the point of inflection. In addition the weighted mean absolute growth rate [$A_n k_n / 2(1 + m_n)$] and weighted mean relative growth rate (k_n / m_n) were estimated for the Richards curve (RICHARDS, 1959). The former parameter measures the average weight of the plot of absolute growth rate with respect to time (dy/dt) against weight (y). The weighting factor used is the derivative of body weight with respect to time. The latter parameter may be interpreted as the actual relative growth rate at the point of inflection on the growth curve, where, the absolute rate is maximal.

A generalized least squares non-linear estimation procedure (MARQUARDT, 1963) was used to fit the observed individual growth curves to each function.

Four related criteria were used by EISEN et al. (1969) to compare alternate growth functions having the same number of parameters: (1) residual variances and unbiasedness due to fitting the functions, (2) individual variation (coefficients of variation) of the estimated parameters, (3) intraclass correlations or heritabilities of the estimated parameters of each function and (4) genetic and phenotypic correlations between the estimated parameters derived from each function. These criteria have been modified slightly for the present situation which involves a comparison of growth functions with different numbers of parameters.

Statistical analysis: A comparison of the goodness of fit of each function was based on an approximation of the F distribution to the normal distribution (ABRAMOWITZ and STEGUM, 1964) given by

$$z = \frac{\sigma_L^2 / \sigma_R^2 - v_R / (v_R - 2)}{v_R / (v_R - 2) [2(v_L + v_R - 2) / v_L (v_R - 4)]^{1/2}},$$

where σ_L^2 and σ_R^2 are the residual variances and v_L and v_R are the degrees of freedom of the logistic and Richards functions, respectively. This test involves the assumption that σ_L^2 and σ_R^2 are independent. They will not be independent in this case since the same set of data is being used to fit both functions. In addition, the residual variance from fitting the Richards model must always be equal to or less than the residual variance from fitting the logistic (if the true minimum is attained in each case) since the Richards model contains one more parameter than the logistic. Therefore, a more appropriate criterion for testing the need for the more complex model was used. This criterion involved testing the null hypothesis, $m = 2$, against the alternative hypothesis, $m \neq 2$.

The coefficients of variation (C.V. %) for the estimated parameters of the alternate functions were computed within line-sex subgroups. Coefficients of variation reflect relative variability among individuals of a character, independent of the unit of scale. Approximate tests of significance for the difference between coefficients of variation of the analogous parameters (e. g., asymptote) estimated from the two functions were based on the method of LEWONTIN (1966). Again, the two coefficients of variation will be correlated since they are estimated from the same data.

Each of the estimated parameters of the growth functions was analyzed separately using a generalized least squares procedure (HARVEY, 1960). The following statistical model was assumed

$$Y_{ijkl} = \mu + L_i + S_j + (L S)_{ij} + F_{k(i)} + e_{ijkl},$$

where Y_{ijkl} = an observation on the l^{th} mouse in the $i j k^{\text{th}}$ subclass, μ = population mean, L_i = effect of the i^{th} genetic line ($i = 1, 2$), S_j = effect of the j^{th} sex ($j = 1, 2$), $(L S)_{ij}$ = interaction effect of the i^{th} line and j^{th} sex,

$F_{k(i)}$ = effect of the k^{th} full-sib family (litter) within the i^{th} line and e_{ijkl} = random error term. The effects μ , L_i and S_j were assumed fixed, whereas $F_{k(i)}$ and e_{ijkl} were assumed NID with zero means and variances σ_f^2 and σ_w^2 , respectively. The expected mean squares (based on equal subclass numbers) for this mixed model indicate that the genetic line mean square should be tested against the among full-sib family mean square. The remaining effects were tested by the within full-sib family mean square. Note that these statistical tests are approximate since unequal subclass numbers exist in the present data. Preliminary analyses within each line indicated the absence of sex \times full-sib family interactions, and consequently this term was pooled with the residual variance.

Among full-sib family (σ_f^2) and within full-sib family (σ_w^2) variance components were estimated from the litters within lines and error mean squares. The expectations of these components in terms of direct additive (σ_A^2), direct dominance (σ_D^2), maternal additive (σ_{Am}^2) and maternal dominance (σ_{Dm}^2) genetic variances, direct-maternal additive genetic covariance (σ_{AAm}), together with maternal (σ_C^2) and random (σ_E^2) environmental variances are (EISEN, 1967)

$$\sigma_f^2 = \frac{1}{2} \sigma_A^2 + \frac{1}{4} \sigma_D^2 + \sigma_{Am}^2 + \sigma_{Dm}^2 + \sigma_{AAm} + \sigma_C^2,$$

$$\sigma_w^2 = \frac{1}{2} \sigma_A^2 + \frac{3}{4} \sigma_D^2 + \sigma_E^2.$$

The degree of dominance and maternal variances in these expectations indicate that computed intraclass correlations [$r_j = \sigma_f^2 / (\sigma_f^2 + \sigma_w^2)$] or heritabilities ($h^2 = 2 r_j$) must only be interpreted as providing upper limits on the proportions of additive genetic variance or covariance in the traits studied.

Results and Discussions

Variation in body weight: The total variances in body weight for each of the four line-sex subgroups are plotted against age in Figure 1. The line-sex subgroups showed a marked increase in variance from day 5 to days 28 to 35, followed by a steep decline to day 49. Thereafter the variances began to increase slightly in all groups except perhaps High males. This age pattern in the variance of body weight in the preweaning and early postweaning stages of growth was not a simple function of scaling effects since the coefficients of variation (Figure 1) showed a similar pattern over this period. After day 56 the coefficients of variation remained relatively constant and were similar in the four subgroups.

The age patterns in the variance of body weight (Figure 1) are apparently characteristic of mouse growth (MONTEIRO and FALCONER, 1966; GALL and KYLE, 1968). MONTEIRO and FALCONER (1966) showed that much of the postweaning increase in variance, was due to an increase in the environmental variance particularly in the environmental component common to litter-mates. TAYLOR (1962) has pointed out that this pattern of change in the variance of body weight may be associated with compensatory growth and is inevitable if animals grow at different rates to the same mature size.

Fit of growth functions: Both the logistic and Richards growth functions fitted the observed growth

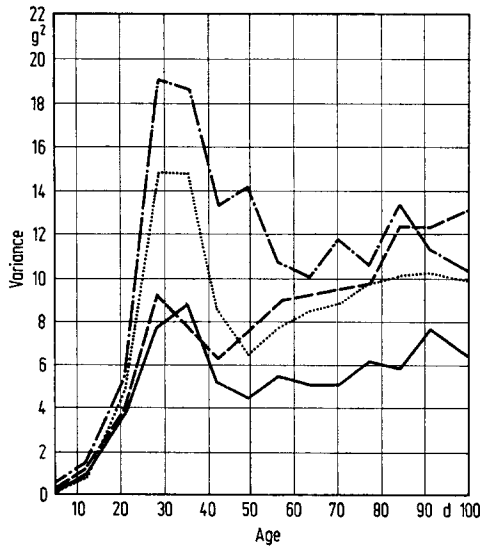


Fig. 1. Total variances and coefficients of variation in body weight of each line-sex subgroup

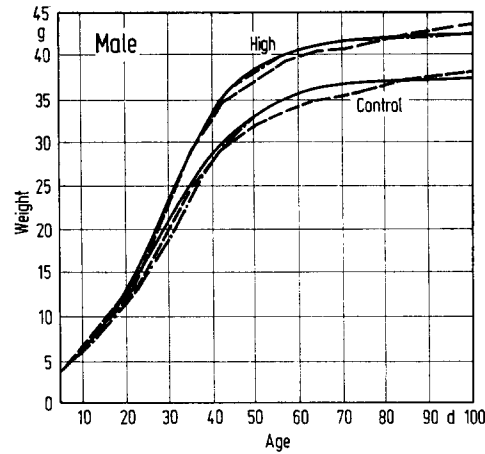
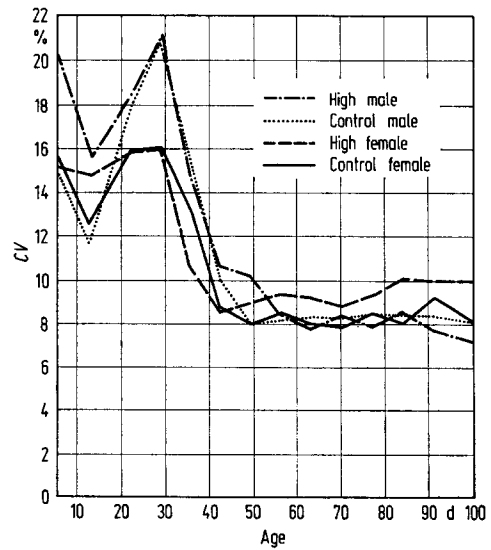
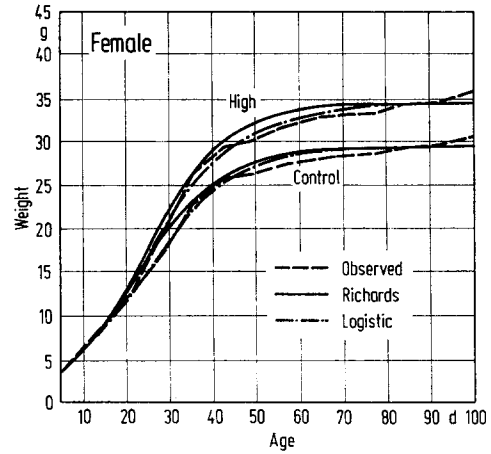


Fig. 2. Observed mean growth trajectories and fitted logistic and Richards functions for male and female mice of each line



trajectories well (Figure 2). Prior to six weeks the agreement between observed weights and both fitted curves was excellent. However, there was a similarity between the two fitted curves in overestimating body weight between six and ten weeks of age and subsequently underestimating weight at 14 weeks.

The residual variances for the Richards and logistic functions, calculated for each individual and averaged within line-sex subclasses, are shown in Table 1. As expected, the average residual variance for the Richards function was smaller than that of the logistic, but the differences between the residual variances of the two functions were not statistically significant ($P > .05$) in any of the four subgroups. However, it has already been pointed out that the test statistic is biased in this case, and is therefore not appropriate

for purposes of testing the need for the more complex model.

The major difference between the Richards and logistic functions concerns the shape parameter (m) of the curve which is fixed at $m = 2$ in the logistic equation, but is an estimable parameter in the Richards equation. The average values of m estimated from the Richards function are shown in Table 2 for each of the line-sex subgroups. The estimates of the shape parameter were not significantly different from $m = 2$ in any of the subgroups, which implies

Table 1. Residual variances of Richards and logistic curves calculated for each individual and averaged within line-sex subclass

Function	Control Males	High Males	Control Females	High Females
Logistic	1.547 (836)*	2.131 (396)	1.529 (693)	2.092 (630)
Richards	1.394 (760)	2.111 (360)	1.448 (451)	2.053 (410)
Normal deviate	1.51 ^{NS}	0.04 ^{NS}	0.67 ^{NS}	0.15 ^{NS}

* Values in parentheses are degrees of freedom. — ^{NS}Not significant ($P > .05$)

Table 2. Student's *t* test of null hypothesis, $m = 2$, against the alternate hypothesis, $m \neq 2$, calculated within line-sex subclasses

Line	Sex	Number of Observations	Shape Parameter (<i>m</i>)	C.V. %	Standard Error	<i>t</i> -Test
Control	Males	76	1.836	45.37	.095	1.72 ^{NS}
High	Males	36	1.928	27.05	.087	0.83 ^{NS}
Control	Females	63	2.129	53.84	.144	0.90 ^{NS}
High	Females	41	2.043	48.44	.155	0.28 ^{NS}

^{NS}Not significant ($P > .05$)

remain a moot question until they are evaluated in mice grown to their final weight.

The coefficients of variation of the estimated parameters (k , t^* and y^*) of the Richards curve were significantly larger than those of the logistic in every case (Table 3). However, the more general model (Richards) will usually lead to larger variances for any one of the estimators simply because of the interrelationships of the parameters. The individual variation in asymptotic weight (A) of the two functions did not differ significantly. In general, there was good agreement between subclass means estimated by

Table 3. Means and coefficients of variation of estimated parameters in the logistic and Richards functions: asymptote (A), rate (k), age (t^*) and weight (y^*) at inflection

Subclass	Function	A		k		t^*		y^*	
		Mean	C. V. %	Mean	C. V. %	Mean	C. V. %	Mean	C. V. %
High-Males	Logistic	42.26	7.61 ^{NS}	.1042	10.13 ^{***}	28.38	10.60 ^{**}	21.07	7.55 [*]
	Richards	42.41	8.03	.1025	21.59	27.68	16.64	20.47	12.31
Control-Males	Logistic	37.14	8.86 ^{NS}	.0945	12.01 ^{***}	28.15	14.61 ^{***}	18.60	8.93 ^{***}
	Richards	37.41	9.03	.0903	32.26	26.38	27.91	17.34	19.79
High-Females	Logistic	34.11	9.66 ^{NS}	.1061	11.83 ^{***}	25.37	10.19 ^{***}	17.06	9.66 [*]
	Richards	34.33	10.72	.1114	43.53	24.41	19.24	16.39	14.83
Control-Females	Logistic	29.23	8.06 ^{NS}	.1017	12.37 ^{***}	23.75	12.54 ^{***}	14.62	8.20 ^{***}
	Richards	29.34	8.72	.1102	45.09	23.02	25.05	14.17	17.83

^{NS}Not significant ($P > .05$), ^{*} $P < .05$, ^{**} $P < .01$, ^{***} $P < .001$. These significance levels refer to the differences in the coefficients of variation of the respective estimated parameters of the Richards and logistic functions.

that the Richards and logistic functions were not significantly different in describing the growth patterns in these mice.

The growth curves of the selected and unselected mice in this study have a mean point of inflection at approximately one-half the asymptotic weight ($A/2$). This result conflicts with some views (BRODY, 1945; TAYLOR, 1965) that the point of inflection occurs at one-third of the asymptotic weight ($A/3$). A possible explanation for this contradiction concern the probable underestimation of asymptotic weight by both functions in the present study. Thus, the usefulness of these equations in estimating mature weight must

the two functions, though the Richards function consistently estimated a higher asymptotic weight and an earlier age of inflection than the logistic.

Least squares differences between lines and sexes in the estimated growth parameters are presented in Table 4 and the corresponding analyses of variance are given in Table 5. The analyses of variance for the logistic and Richards curves yielded similar results for asymptotic weight and age and weight at inflection, respectively. High line mice were significantly ($P < .001$) larger than Controls at the asymptote and at the point of inflection, but the difference in age at inflection was not significant ($P > .05$).

EISEN et al. (1969) reported that selection for high six-week weight resulted in an increase in both the age and weight at which the point of inflection in growth occurs. These authors also found that the change in age at inflection was more pronounced in females than in males. In the present study males were significantly older and larger at the point of inflection than females (Table 4), which is in agreement with previous studies (TIMON, 1968; EISEN et al., 1969).

Table 4. Least squares differences between lines and sexes in the estimated growth parameters [A , k , t^* , y^* , m , k/m and $Ak/2(1+m)$] of the logistic and Richards functions

Estimated Parameter	High-Control		Male-Female	
	Logistic	Richards	Logistic	Richards
A	4.59 ^{***}	4.56 ^{***}	7.74 ^{***}	7.86 ^{***}
k	0.007 ^{***}	0.007 ^{NS}	-0.003 [*]	-0.017 ^{**}
t^*	1.04 ^{NS}	1.64 ^{NS}	2.99 ^{***}	2.12 ^{***}
y^*	2.29 ^{***}	2.64 ^{***}	3.87 ^{***}	3.12 ^{***}
m	—	0.019 ^{NS}	—	-0.316 ^{**}
k/m	—	0.0009 ^{NS}	—	-0.0004 ^{NS}
$Ak/2(1+m)$	—	0.1180 ^{***}	—	0.1106 ^{***}

^{NS}Not significant ($P > .05$), ^{*} $P < .05$, ^{**} $P < .01$, ^{***} $P < .001$

The sex difference for the rate parameter (k) was significant ($P < .05$) for both the Richards and logistic estimates, whereas the line difference was highly significant ($P < .001$) for the logistic function and non-significant for the Richards function. Since the line difference in the rate parameter was similar in both cases the non-significance of the Richards value could be due to the greater variation in this parameter estimated from the Richards function.

There was a significant difference between the sexes in the shape parameter but no difference between the High and Control lines (Tables 4 and 5). Thus, nine generations of selection for postweaning gain did not change the shape of the growth curve in this population. Further evidence for this conclusion can be seen in Figure 3, where body weight as a percentage of final (asymptotic) weight is plotted against age for each of the four line-sex subgroups. On this basis, the curves for the High and Control lines were nearly identical. In concurrence with this observation was the absence of any statistically significant difference in mean relative growth rate (k/m) between the High and Control lines (Tables 4 and 5).

It is clear from Table 4 and Figure 2 that selection for increased postweaning gain from three to six weeks has resulted in an increase in the mean absolute growth rate [$A k/2 (1 + m)$] over the whole curve. This result is similar to that found by EISEN et al. (1969) in their comparison of a line selected for high six-week body weight with a randombred control. It implies a strong genetic correlation between rate of gain in the different stages of growth; i. e., high inter-age genetic correlations in body weight. This interpretation is also consistent with the lack of significant differences between the High and Control lines in either the shape of the growth curve or the mean relative growth rate. The fact that selection for postweaning gain did not change the shape of the growth curve must not be interpreted as evidence that this trait does not have a genetic basis.

Another aspect involved in comparing growth functions which needs further evaluation is the possibility of function x treatment (e. g., line and sex) interactions (EISEN et al., 1969). There was little evidence of any function x treatment interactions (Table 4) in either this study or in the recent study by EISEN et al. (1969).

Estimates of genetic parameters: Phenotypic and genetic correlations among the different parameters of the logistic and Richards curves are shown in Table 6. Also included are the heritability estimates based on full-sib analyses. Bearing in mind the limitations of these estimates, the consistent trends in the relative magnitudes of the heritabilities and the signs of the correlation coefficients are of interest.

The high estimates of heritability must be interpreted with caution, since maternal effects or some degree of dominance may influence the estimated

Table 5. Analyses of variance of the estimated parameters of the logistic and Richards growth functions

Source	df	Mean Squares													
		A		k		i*		y*		m		k/m		Ak/2 (1+m)	
		Logistic	Richards	Logistic	Richards	Logistic	Richards	Logistic	Richards	Logistic	Richards	Logistic	Richards	Logistic	Richards
Line (L)	1	917.27***	903.32***	0.0025***	0.0023	47.11	118.20	213.02***	302.80***	0.016	0.00003	0.6062***			
Sex (S)	1	2538.60***	2610.59***	0.0004*	0.0123**	378.58***	192.60***	610.01***	412.23***	4.231**	0.00001	0.5177***			
L x S	1	4.72	2.06	0.0001	0.0008	6.96	1.50	1.49	9.74	0.363	0.00000	0.0167**			
Litters/Line	51	20.06***	21.04***	0.0003***	0.0022**	34.63***	103.13**	4.99***	19.53***	1.555***	0.00026***	0.0096***			
Within Litters	161	5.78	7.06	0.00009	0.0013	3.96	15.49	1.47	4.62	0.639	0.00005	0.0025			

* $P < .05$, ** $P < .01$, *** $P < .001$

Table 6. Full sib estimates of heritabilities (on diagonal), and phenotypic (above diagonal) and genetic (below diagonal) correlations among parameters of the Richards (R) and logistic (L) growth functions*

	A_R	k_R	m_R	γ_R^*	t_R^*	k_R/m_R	$A_R k_R/2(1+m_R)$	A_L	k_L	t_L^*
A_R	.66 (.15)	-.41	-.33	.14	-.10	.07	.31	.98	-.42	.27
k_R	-.29 (.30)	.30 (.14)	.95	.66	.60	-.42	.28	-.29	.49	.07
m_R	-.11 (.23)	.91 (.04)	.53 (.15)	.78	.79	-.64	.08	-.18	.18	.33
γ_R^*	.39 (.18)	.74 (.13)	.86 (.06)	.86 (.15)	.85	-.79	.26	.32	.04	.50
t_R^*	.49 (.19)	.77 (.13)	.93 (.05)	.85 (.05)	1.17 (.13)	-.86	-.15	.07	-.17	.77
k_R/m_R	-.58 (.19)	-.74 (.29)	-.94 (.23)	-.88 (.20)	-.93 (.18)	1.01 (.14)	.31	-.08	.29	-.62
$A_R k_R/2(1 \times m_R)$.42 (.17)	-.14 (.25)	-.39 (.20)	-.03 (.19)	-.39 (.17)	.49 (.15)	.82 (.15)	.34	.69	-.39
A_L	.99 (.01)	-.13 (.27)	.06 (.22)	.54 (.15)	.21 (.18)	-.22 (.18)	.38 (.17)	.76 (.15)	-.40	.35
k_L	-.28 (.22)	.00 (.27)	-.40 (.19)	-.39 (.18)	-.51 (.17)	.63 (.13)	.74 (.09)	-.34 (.21)	.76 (.15)	-.63
t_L^*	.15 (.18)	.53 (.21)	.77 (.12)	.72 (.09)	.94 (.03)	-.82 (.16)	-.46 (.17)	.28 (.16)	-.63 (.19)	1.32 (.11)

* Values in parentheses are standard errors of heritabilities or genetic correlations (TALLIS, 1959)

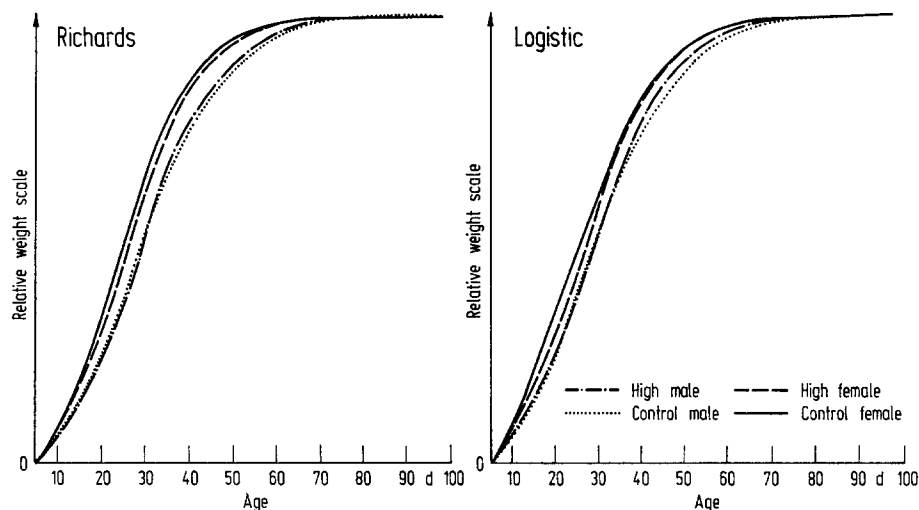


Fig. 3. Body weight as a percentage of final weight plotted against age for each line-sex subgroup

parameters of the growth curve. The heritability estimates of asymptotic weight (A), rate (k) and age at inflection (t^*) based on the logistic function are greater than the corresponding Richards values, which may be a reflection of the increased individual variation in the parameters of the Richards curve. However, the difference is so great in the case of the rate parameter estimates (0.30 and 0.76 for Richards and logistic, respectively) as to suggest that these are different traits. The zero estimate of the genetic correlation between the different estimates of this trait (k_L , k_R) supports this possibility. This result is

particularly noticeable in view of the very high genetic correlations between the analogous estimates of asymptotic weight (0.98) and age at inflection (0.94). There is further evidence in Table 6 to suggest that the rate parameters of the two functions may be different traits. The high genetic (0.91) and phenotypic (0.95) correlations between the rate (k) and shape (m) parameter estimates suggest a near constant relationship between these parameters of the Richards curve. Since the shape parameter (m) is variable in the Richards function but a constant for the logistic ($m = 2$), the possible values for the rate parameter

(k) in the logistic model are highly restricted compared to what would be possible if m is general.

The magnitude of the heritability estimates for the shape parameter ($h^2 = 0.53 \pm .15$) suggests that there may be some additive genetic variation in this trait, even though no correlated response in the shape parameter was observed in the present study. However, it has already been stressed that the estimates of heritability based on full-sib correlations are biased upward in the presence of maternal and dominance effects.

Few general conclusions can be based on the genetic parameter estimates in Table 6 other than that the possibility exists for additive genetic variance and covariance among the different traits. Of particular interest is the possibility that direct selection for a change in the shape of the growth curve would be at least moderately successful. However, it is apparent that unbiased estimates of additive genetic variance will have to be obtained before definitive conclusions can be reached.

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