Short-term responses to selection for parameters of the allometric-autoregressive model

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The allometric-autoregressive model describes growth accurately and is useful in the characterization of growth responses. Hence, the potential of the model for selection purposes was investigated. Rats were used in a selection experiment, where selection was practised for slope (b) and intercept (ln a) of the allometric function: w = ln a + bv [where w = ln (body mass) and v = ln (cumulative feed intake)], and ρ, the autoregression slope of ln (cumulative feed intake). Facilities for five selection groups of 40 rats each were available. Both upward and downward within-family selections were practised for ln a and b, and only downward selection for ρ. In the short term, selection for ln a and b resulted in good direct responses, and it appears that the model can be used to alter the shape of the growth and efficiency curve by selection. The realized heritabilities correspond to the heritabilities of previous studies. Although the heritability estimate of ρ is low, a moderate selection response was realized in the short term. Only the correlated responses to selection for b seem to be of any significance during the four generations of selection. Efficiency during the growth phase in which selection was practised increased markedly (17%), while total efficiency, which includes the estimated efficiency from conception, also increased (13%). Furthermore, selection for b led to an increased growth rate (15%) and a slight increase in body mass (8%), whilst intake tended to decrease (–5%). Normally intake tends to increase as growth rate and mass increase.

Die allometriese-outoregressiemodel beskryf groei akkuraat en is bruikbaar vir die karakterisering van groeiresponsies. Gevolglik is die potensiaal van die model vir seleksiedoeleindes ondersoek. Rotte is gebruik in 'n seleksie-eksperiment waarin daar geselekteer is vir helling (b) en afsnit (ln a) van die allometriese funksie: w = ln a + bv [waar w = ln (liggaamsmassa) en v = ln (kumulatiewe voerinname)], sowel as vir ρ, wat die outoregressiehelling van ln (kumulatiewe voerinname) is. Met die beskikbare fasiliteite kon vyf seleksiegroepe van 40 rotte elk geakkommodeer word. Beide opwaartse en afwaartse binne-familieseleksie is vir ln a en b uitgevoer, terwyl daar slegs vir 'n lae ρ geselekteer is. In die korttermyn het seleksie vir ln a en b tot goeie direkte responsies gelei, en dit wil voorkom asof die model gebruik kan word om die vorm van die groei- en doeltreffendheidskurwe deur seleksie te wysig. Die gerealiseerde oorerflikhede stem ooreen met die oorerflikhede van vorige studies. Alhoewel die oorerflikheidsberaming vir ρ laag is, is 'n matige seleksieresponsie oor die korttermyn gerealiseer. Slegs die gekorreleerde responsie van seleksie vir b was van betekenis gedurende seleksie oor vier generasies. Doeltreffendheid in die groeifase waarin geselekteer is het merkbaar verbeter (17%), terwyl totale doeltreffendheid, wat beraamde doeltreffendheid vanaf konsepsie insluit, ook verbeter het (13%). Verder het seleksie vir b gelei tot 'n verhoging in groeitempo (15%) en 'n geringe verhoging in liggaamsmassa (8%), terwyl inname geneig het om af te neem (–5%). Normaalweg neem inname toe met 'n toename in groeitempo en massa.

Keywords: Allometric-autoregressive model, correlated response, efficiency, growth, realized heritability, selection.

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Introduction

The most important advantage of using growth functions in the description of animal growth, is that animal growth can be described and evaluated more accurately. Most growth functions are limited to the description of growth in terms of output (body mass) only, while input (feed intake) is not taken into account. The allometric-autoregressive model not only takes feed intake into account but also considers the basic allometric nature of growth and describes growth accurately (Roux, 1974; 1976; Meissner & Roux, 1979; Roux, 1980). The model has proved to be useful in the characterization of growth responses of breeds and feeds in many nutrition studies (Meissner, Roux & Hofmeyr, 1975; Meissner, 1977; Meissner, Hofmeyr & Roux, 1977; Siebrits, 1979; Roux & Kemm, 1981; Greeff, Meissner, Roux & Janse van Rensburg, 1986a; 1986b).

The allometric-autoregressive model also seems to be of value in genetic studies and some of its parameters exhibit significant heritabilities (Scholtz & Roux, 1981a; 1981b; Scholtz, Roux, de Bruin & Schoeman, 1990).

Scholtz *et al.* (1990) found positive correlations between some of the common growth and efficiency traits (efficiency, growth rate, body mass) and b, whereas daily intake appeared to be negatively correlated with b. Should these correlations reflect the true situation, it would be advantageous to increase growth rate via b without an increase in feed intake. In order to test this hypothesis, a selection experiment was carried out on some of the parameters of the model to investigate the nature of the direct and correlated responses, using the rat as model.

Material and Methods

Model

The allometric function to describe growth can be expressed by the equation:

$$y = ax^b$$

or

$$w = \ln a + bv$$

where y = body mass, x = cumulative feed intake, w = ln y and v = ln x (Roux, 1976). Slope (b) and intercept (ln a) can be estimated by linear least-square procedures. According to Roux (1976; 1980), the equation for cumulative feed intake (autoregression) is:

$$[x(t) - \alpha_x] = \rho[x(t-1) - \alpha_x] + \varepsilon(t)$$

or

$$x(t) = [\alpha_x - x(o)]\rho^t + \sum_{j=0}^{t-1} \rho^j \varepsilon(t-j)$$

where $x(t)$ = ln (cumulative feed intake) at time t,
$x(o)$ = ln (cumulative feed intake) at time o,
α_x = ln (cumulative feed intake) with $t \rightarrow \infty$
ρ = slope of autoregression,
$\varepsilon(t)$ = error term,
autoregression = linear regression of $x(t)$ as dependent variable on $x(t-1)$ as independent variable.

Both upward (H) and downward (L) selections were applied to the parameters slope (b) and intercept (ln a) of the allometric function, while only downward selection was practised for ρ, the autoregression slope of ln (cumulative feed intake).

Animals

It was decided to use the rat as a model for these selection experiments, because of the short generation interval and the general acceptance of the biological resemblance between laboratory and farm animals. Rat growth may be divided into three growth phases (Scholtz, 1979; Scholtz & Roux, 1981a). Selection, however, was limited to the second growth phase, which is from approximately 37 to 60 days of age.

Rats from the outbred Wistar line were used. In an attempt to minimize the influence of maternal effects, the litter sizes were standardized to 12 pups at three days of age. The animals were kept in standard cages under conventional conditions (not pathogen-free), and remained perfectly healthy. Room temperature was kept at 21 ± 2°C, with a relative humidity of 35—50%. Artificial lighting simulated a diurnal cycle of 12 h daylight and 12 h darkness. After weaning at 21 days of age, the rats were kept in individual cages. Body masses and cumulative feed intake were measured every second day without withholding food and water prior to measurement. This protocol was followed up to the age of 60 days.

Feed was in the form of a ground powder (Epol mixture 4710), and was offered in specially designed hoppers to minimize waste.

Selection

The need to keep inbreeding to a minimum, made it necessary to keep all families represented in subsequent generations. Neither individual (mass) selection nor family selection satisfy this prerequisite. All the families can only be represented if within-family selection is practised (Scholtz, 1987). Within-family selection has the further advantage that environmental effects common to litter-mates and maternal effects are taken into account (Falconer & Latyszewski, 1952).

Matings of least relationships were made according to the system suggested by Alan Robertson (Falconer, 1973), as shown below:

Family no. in current generation ♀ ♂	Family no. in next generation
1 × 2	1
3 × 4	2
2 × 1	3
4 × 3	4

Whereas this system does not reduce the average rate of inbreeding, it has three advantages over the conventional cyclical system. The practical advantage lies in the mating schedule, which is the same in every generation, while the theoretical advantages derive from the fact that inbreeding coefficients are the same for all families in a generation, and that the rate of inbreeding is the same for all generations (Falconer, 1973).

The number of animals used in the experiment was limited by restricted facilities and labour to 200 rats. It was, therefore, decided to use 4 families with 10 individuals (5♂, 5♀) each for each of the five selection groups (bH, bL, ln aH, ln aL, ρ, L). Selection of an equal number from all families resulted in an effective population size (Ne) of 16, and a theoretical rate of inbreeding of 1/32 (ΔF = ½Ne) or 3,125% per generation (Falconer, 1981).

Other researchers (MacArthur, 1949; Falconer, 1953; Falconer & King, 1953; Falconer, 1960) have also used selection groups of this magnitude (Ne = 16, with upward and downward selection). Eisen (1974) concluded that an effective population size of 20 is sufficient for most selection experiments.

The two best (highest values for H and lowest values for L) males and females from each family were selected. The best male was first mated to both selected females. After eight days, the second-best male was mated to the same females in order to maintain the essential family structure. At the same time, the problem of insufficient litter size was overcome. Where the litter size of the best female was insufficient (not 5 ♂ and 5 ♀), it was supplemented with progeny from the second-best female.

It was further decided to use the third-best male and female from each family for additional matings to foster the excess pups, or to provide additional pups to standardize litter size. In a few cases where both the best and second-best female did not produce any pups, the pups of the third-best parents were used to maintain the family and selection structure.

In the selection groups ln a and b, the selection responses were expressed as the difference between H and L. The percentage difference was calculated as follows:

$$[2(H - L)/(L + H)] \times 100$$

In the case of selection group ρ L, no direct control was available. A control value was thus established by adding the values of the ln aH, ln aL, bH and bL groups and dividing the sum by four.

Common growth and efficiency traits

Efficiency of feed utilization may be calculated as feed consumed divided by gain produced, or as its inverse. The two ratios differ only in sign, but not in magnitude of their relationships to other traits, and would rank a group of animals in the same way (Lasley, Sellers & Anderson, 1979; Nielsen, 1979). Consequently, the ratio gain per unit of feed was preferred, since a large value indicated a good performance and a small value a poor performance.

The correlated response (difference between H and L) in three types of efficiencies were investigated. They are:

(1) efficiency between two ages, e.g. in the second growth phase of the rat (± 37—60 days);
(2) efficiency at a specific point, e.g. at 60 days of age. According to Scholtz (1979), efficiency at a specific point (local efficiency) is described by $dy/dx = y/x(b)$, where y = body mass and x = cumulative feed intake;
(3) total efficiency from conception to 60 days of age. The method of estimating preweaning intake has previously been described (Scholtz & Roux, 1980).

To estimate the efficiency between two ages, initial and final mass are needed. In cases where animals were not fasted prior to measurement, as in this experiment, cumulative feed intake can usually be measured with greater accuracy than actual body mass (Roux, 1980), due to a variable content of the digestive tract. This effect on body mass may be smoothed out by using cumulative feed intake to estimate the initial and final mass, with the aid of the allometric function. Growth rate, expressed as average daily gain (ADG), was calculated in the same manner.

Correlated responses

Correlated responses obtained for the different traits tend to vary over generations. It was, therefore, decided to fit a linear regression to these responses to predict the attained response in a certain generation, using the following equation:

$$y = c + dx$$

where y = response; x = generation number; d = slope; c = intercept.

The response estimated from the linear regression, is referred to as the realized correlated response. In linear regression, the r^2 value gives an indication of the accuracy of fit. Hill (1976) indicated that tests of significance on these r^2 values were not valid, since the values of the different generations were not independent. Such tests of significance may be too lenient. However, since no other suitable procedure exists, it was decided to use r^2 merely as an index of which correlated responses deserve attention.

In cases of selection for ln a and ρ, the data of the parental generation and three generations of selection were considered, where an r^2 of 0,81 was needed for significance at the 10 % level. In the case of selection for b, the data of the parental generation and four generations of selection were considered, in which case an r^2 of 0,65 was needed for significance at the 10 % level.

Results

Direct responses

Actual responses to selection for ln a, b and ρ are presented graphically in Figure 1. The observed percentage difference between H and L in the case of ln a and b, and the percentage deviation from the control in the case of ρ, are presented in Figure 2.

The expected responses to within-family selection were calculated using the following equation:

$R = i\sigma_w h^2_w$ (Falconer, 1981).

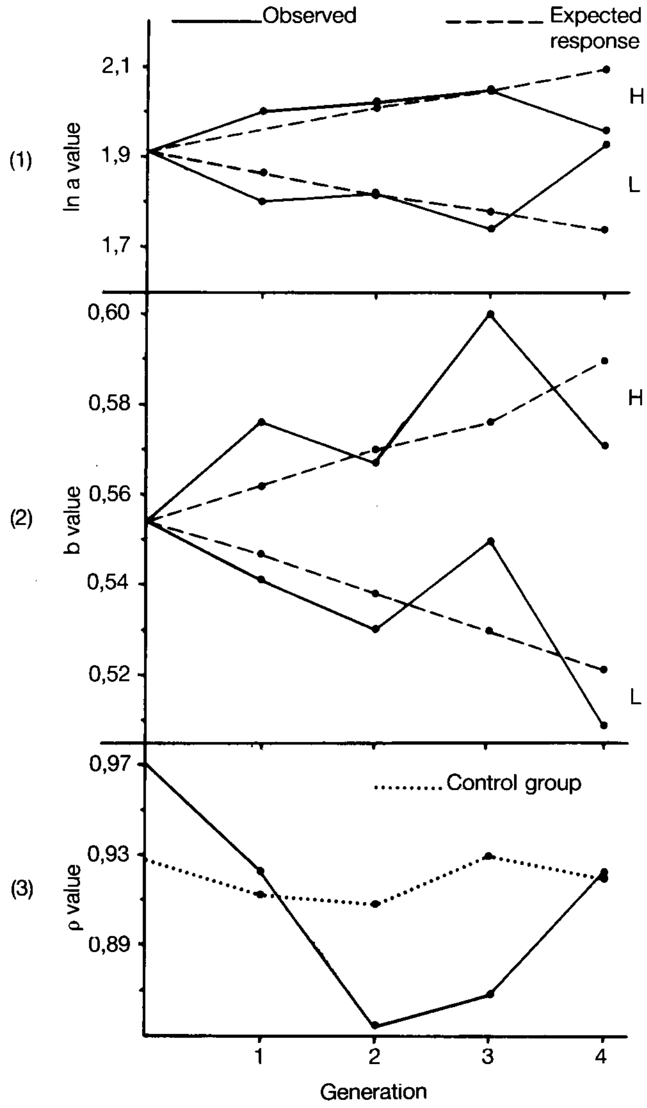

Figure 1 Observed and expected direct responses in (1) ln a, (2) b, and (3) ρ.

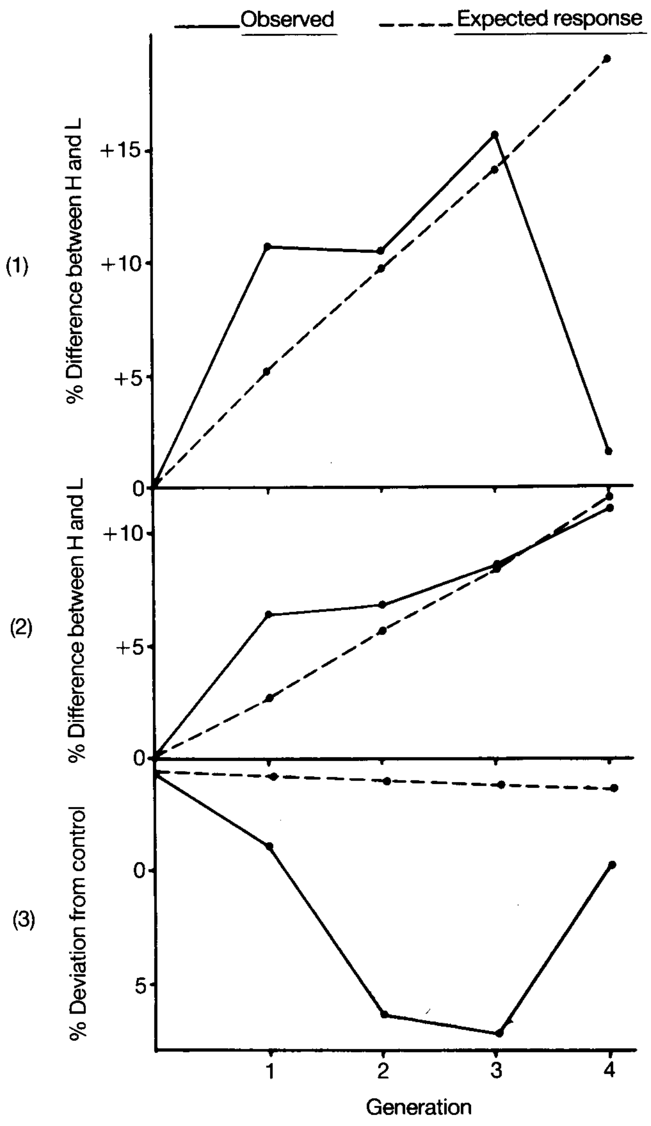

Figure 2 Observed and expected direct responses in (1) ln a, (2) b_2, and (3) ρ, expressed as % difference or deviation.

Estimates of σ^2_w (within-family variance) and h^2_w (within-family heritability) were calculated from the parental generation, while the specific effective intensity of selection (i) was used for each generation and selection group. The expected responses are shown in Figures 1 and 2.

From Figure 2, it can be seen that the expected and observed responses in ln a were in good agreement during the first three generations, whereafter the realized response disappeared. During the first four generations, the expected and observed responses in b were in agreement. Although the heritability estimate for ρ was so small (0,13) that practically no response was expected, Figure 2 shows that a mild selection response was realized during the first three generations of selection.

Realized heritabilities

Response to selection may be used to estimate the heritabilities in the parental population. Heritabilities estimated in this way are known as realized heritabilities (Falconer, 1981). Because within-family selection was applied in this experiment, the within-family heritability (h^2_w) was estimated using the following equation (Falconer, 1981):

$$h^2_w = R/S$$

where R = total response (difference between H and L lines) and S = cumulative selection differential.

To convert the h^2_w to ordinary heritability (h^2), the following equation was used (adapted from Falconer, 1981):

$$h^2 = h^2_w \left(\frac{1-t}{1-r}\right)$$

where r = correlation of breeding values (0,5 for full sibs),
t = intra-class correlation for the trait concerned.

When selecting for ln a, the realized heritability was estimated at generation three of selection. The realized values for h^2_w and h^2 were found to be 0,20 and 0,34, respectively. When selecting for b the realized heritabilities at generation four of selection were found to be 0,16 (h^2_w) and 0,27 (h^2), respectively.

Correlated responses with selection for b

The correlated response in: (1) efficiency in the second phase, (2) local efficiency at 60 days of age and (3) total efficiency up to 60 days of age is given in Figures 3, 4 and 5, respectively. Linear regression was fitted to these

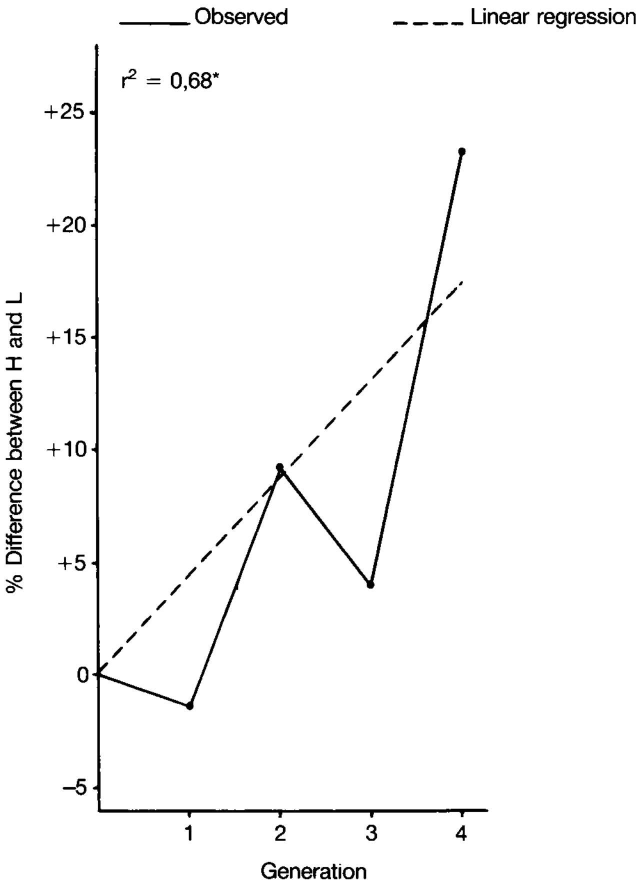

Figure 3 Correlated response in efficiency in phase 2 with selection for b.

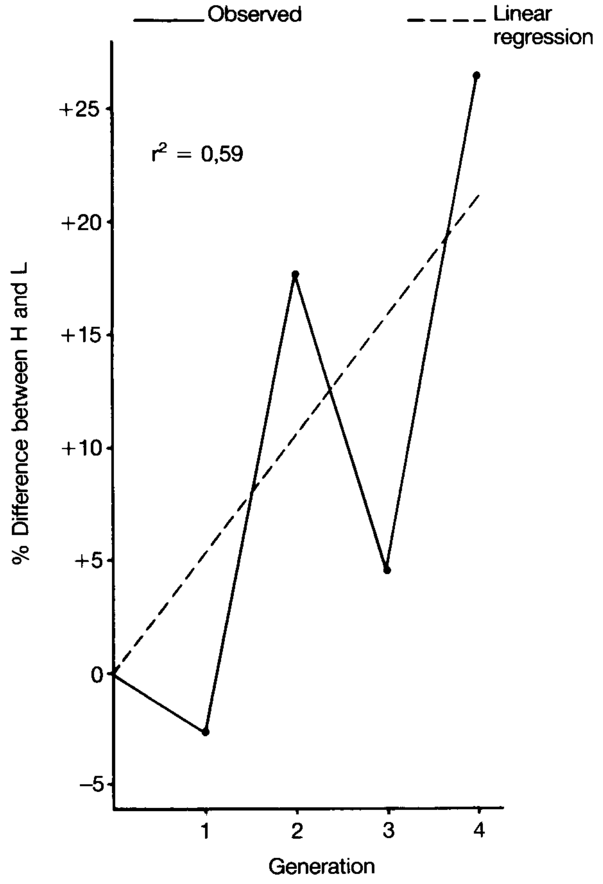

Figure 4 Correlated response in local efficiency at 60 days with selection for b.

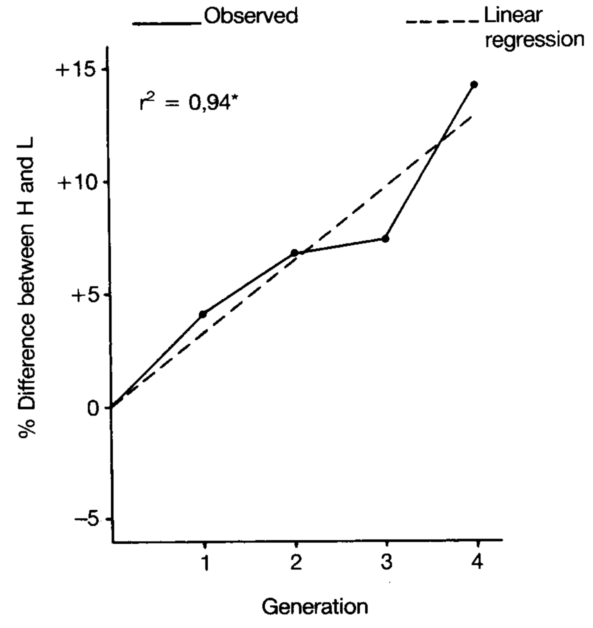

Figure 5 Correlated response in total efficiency at 60 days with selection for b.

correlated responses to estimate the realized correlated responses and the derived data are presented, together with the correlated responses at generation four and the accuracy of fit of the linear regression (r^2), in Table 1.

Table 1 Correlated responses (%) in efficiency with selection for b

Type of efficiency	Observed response	Linear regression	r^2
(1)[a]	23,3	17,4	0,68*
(2)	26,6	21,3	0,59
(3)	14,2	12,9	0,94*

[a] See text for explanation.

* Significant at the 10 % level.

From Figures 3, 4 and 5 and Table 1 it is clear that efficiency responded exceptionally well to selection for b, with the highest response in local efficiency at 60 days of age. The relatively lower response of total efficiency up to 60 days of age is understandable, since this parameter includes efficiency from conception to 60 days of age. These correlated responses are in agreement with the correlations presented by Scholtz *et al.* (1990).

It is also important to report on the correlated effects on body mass, growth rate (ADG) and intake (ADI) with changes in b and efficiency. From Figure 6 it can be seen that ADG responded relatively strongly and positively to selection for b. Body mass at 60 days of age also showed a positive response to selection for b, but this was less marked than for ADG (Figure 7). ADI was not

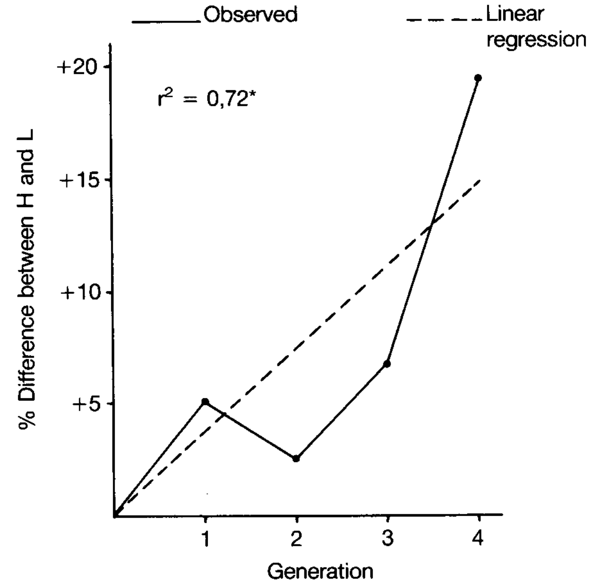

Figure 6 Correlated response in ADG with selection for b.

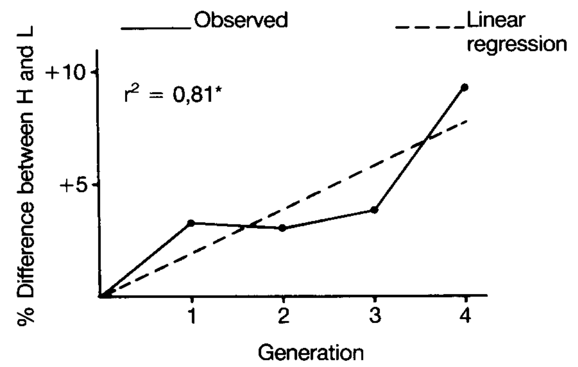

Figure 7 Correlated response in 60-day mass with selection for b.

significantly altered, although it tended to decline with selection for a high value of b (Figure 8), which may be expected from the results of Scholtz *et al.* (1990). Normally, intake tends to increase as ADG increases. The value of the observed correlated responses and realized correlated responses in generation four, as well as the accuracy of fit (r^2) of linear regression, are given in Table 2.

The age at the start of the second growth phase of the rat (onset of puberty) did not change with selection for b (Figure 9). This age seems to be very stable, with changes varying between + 0,30% and − 1,14%.

No noteworthy correlated responses in common growth and efficiency traits of the first growth phase of the rat were found with selection for b of the second phase.

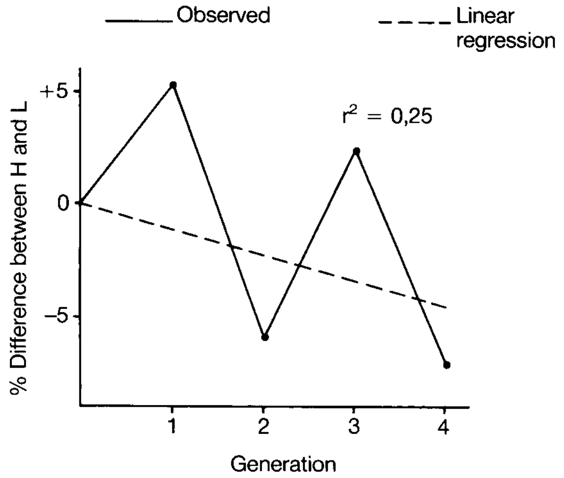

Figure 8 Correlated response in ADI with selection for b.

Table 2 Correlated responses (%) in ADG, body mass and ADI with selection for b

Trait	Observed response	Linear regression	r^2
ADG	19,4	14,8	0,82*
Body mass	9,3	7,7	0,81*
Intake	−7,1	−4,5	0,26

* Significant at the 10% level.

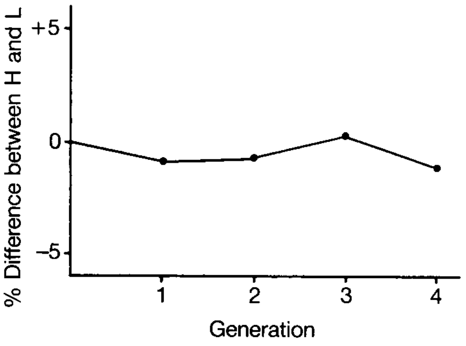

Figure 9 Correlated response in age at first break point with selection for b.

Correlated responses to selection for ln a

Selection for ln a did not seem to have any effect on efficiency, although ln a is mathematically directly proportional to efficiency and moderate genetic correlations between efficiency and ln a exists (Scholtz *et al.*, 1990). From Table 3, it can be seen that selection for ln a had no clear cut effect on: (1) efficiency during phase 2, (2) local efficiency at 60 days of age, or (3) total efficiency at 60 days of age.

The same appeared to be true for ADG during phase 2 and body mass at 60 days (Table 3). The correlated response in ADI with selection for ln a was more variable, but no definite trend in response was observed. Furthermore, there was no effect on traits of phase 1.

Table 3 Correlated responses (%) in common growth and efficiency traits to selection for ln a

Trait	Observed response	Linear regression	r^2
Efficiency (1)[a]	−1,2	−3,3	0,19
Efficiency (2)	−2,3	−5,3	0,22
Efficiency (3)	0,3	−0,1	0,00
ADG	−1,9	−1,8	0,00
Body mass	−1,8	−1,9	0,12
Intake	−1,0	1,0	0,05

[a] See text for explanation.

Correlated responses to selection for ρ

The correlated responses in common growth and efficiency traits are given in Table 4. Most of the traits in Table 4 showed no noteworthy trends of correlated response to selection for ρ . Note especially that ADG in phase 2 showed no definite trend. Total efficiency at 60 days of age showed a very small but steady and significant increase (2%). There was no effect on traits of phase 1.

Table 4 Correlated responses (%) in common growth and efficiency traits to selection for ρ

	Generation				
	0	1	2	3	r^2
Efficiency (1)[a]	−4,1	3,9	2,9	−7,4	0,07
Efficiency (2)	−2,1	4,6	2,9	−5,2	0,10
Efficiency (3)	−0,8	−0,3	−0,2	1,5	0,82*
ADG in phase 2	5,2	7,5	4,0	−2,1	0,64
60-day mass	−4,3	5,6	2,2	−2,1	0,01
Intake in phase 2	−0,6	3,0	2,2	2,3	0,43

[a] See text for explanation.

* Significant at the 10% level.

Discussion

In the case of ln a and b, the expected and observed responses (Figure 2) compared well during the initial stages of selection (three and four generations respectively). In the short term, the direct responses to selection for ln a and b accorded with genetic theory. The value of these parameters may be changed by selection. Thus, it seems that the model may be used to alter the shape of the growth and efficiency curve by selection during the initial stages of selection.

This is in contrast to Eisen's (1976) view that, since heritabilities of the growth functions of body mass *vs.* time were low, changes in growth curves may be more readily achieved by the application of selection indices to actual body mass rather than to parameters of a growth curve.

The realized heritabilities correspond well with the heritability estimates of Scholtz *et al.* (1990) of 0,31 and 0,29 for ln a and b, respectively. The difference between the realized heritabilities and these estimates was less than 10%. These small differences were anticipated from Figure 2, where expected and observed responses were in good agreement. Thus, this selection experiment confirmed that the heritability estimates of Scholtz *et al.* (1990) appear to be fair estimates of the heritabilities of ln a and b.

Selection for ρ resulted in a moderate response during the first three generations of selection. This response was much larger than the expected response considering the magnitude of the heritability estimates. Thus, the heritability estimates for ρ may not be very reliable as they predict very little response. Furthermore, it may appear that ρ is not canalized to the extent previously thought (Scholtz & Roux, 1981b).

Selection for b resulted in strikingly large, correlated responses in the three types of efficiency, with the highest response being more than 20% in local efficiency at 60 days of age in four generations of selection. The relatively lower response in total efficiency at 60 days of age may be explained by the fact that this parameter includes estimated efficiency from conception to 60 days of age. Efficiency in the first phase was not altered by selection, thus there was a dilution effect on this type of efficiency. Therefore, it seems possible to change efficiency in the short term by selecting for the exponent of the allometric equation. Selection for ln a on the other hand, did not significantly affect efficiency. This is quite surprising, since ln a and b are highly correlated (Scholtz & Roux, 1981b).

Growth rate and body mass increased by approximately 15% and 8%, respectively, with selection for b. Responses of this kind are normally expected to be associated with an increase in efficiency. Intake tended to decrease, which is in contrast to results from the literature which suggests that intake tends to increase as growth rate and body mass increase (Fowler, 1962; Stanier & Mount, 1972; Hayes & McCarthy, 1976; Hetzel & Nicholas, 1978; Eisen & Durrant, 1980; Kownacki & Jezierski, 1980; Wang & Dickerson, 1980). It appears to be advantageous to increase efficiency, growth rate and body mass, while intake is decreased or kept constant. Selection for ln a had no effect on any of these traits.

Although some of these correlated responses are so strikingly large (the efficiencies), or in contrast to those reported in the literature (daily intake), they closely correspond to the direction and ranking of the ordinary correlations between b and the common growth and efficiency traits estimated by Scholtz *et al.* (1990). This is illustrated in Table 5 where there is a very good relationship between the realized correlated responses and the ordinary correlation of b with the different growth and efficiency traits estimated by Scholtz *et al.* (1990). A correlation of 0,98 was found between the two columns of Table 5.

Table 5 Realized correlated responses and correlation with b of the different growth and efficiency traits

Trait	Realized correlated response (X)	Correlation with b[a] (Y)
Efficiency (1)[b]	17,4%	0,71
Efficiency (2)	21,3%	0,82
Efficiency (3)	12,9%	0,37
ADG	14,8%	0,31
Body mass	7,7%	0,15
Intake	–4,5%	–0,38
	Ordinary correlation between X and Y = 0,98	

[a] Scholtz *et al.*, 1990.

[b] See text for explanation.

Another interesting feature of this selection experiment is the stability of age at the start of the second growth phase. This point is associated with the onset of puberty and its physiological processes in the rat (Scholtz & Roux, 1981a). Selection for parameters of the allometric-autoregressive model, therefore, does not seem to change the physiological processes of the rat associated with the onset of puberty during the early stages of selection.

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