

Medium-term responses to and changes in fitness with 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 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 for 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 medium-term, the observed direct responses to selection for parameters of the allometric-autoregressive model were irregular, and there was a marked discrepancy between the observed and expected responses. It was postulated that poor fit of the model in later generations, a lack of genetic variance, mutation, genetic drift and/or natural selection may be causing these discrepancies. The selection responses were accompanied by losses of fitness during certain generations, while in others, the responses disappeared altogether. In certain generations, however, fitness was regained and this was followed by renewed appearance of responses. This pattern of response points to the presence of natural selection, which was corroborated by the differences between the effective and expected selection intensities. It was concluded that the slope of the allometric function seems to be the only parameter worth considering as a selection criterion.

Die allometriese-outoregressiemodel beskryf groei akkuraat en is bruikbaar vir die karakterisering van groei-responsies. Gevolglik is die potensiaal van die model vir seleksiedoeleindes ondersoek. Die rot 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 voerinnam)], sowel as vir ρ , wat die outoregressie-helling van \ln (kumulatiewe voerinnam) is. Fasiliteite vir vyf seleksiegroepe van 40 rotte elk was beskikbaar. Beide opwaartse en afwaartse binne-familieseleksie is vir $\ln a$ en b uitgevoer, terwyl daar slegs vir 'n lae ρ geselekteer is. In die mediumtermyn was die waargenome direkte responsies met seleksie vir parameters van die allometriese-outoregressiemodel onreëlmatig, terwyl 'n aansienlike verskil tussen die waargenome en verwagte responsies gevind is. Daar is gepostuleer dat swakke passing van die model in later generasies, 'n tekort aan genetiese variasie, mutasie, genetiese drywing en/of natuurlike seleksie hiervoor verantwoordelik is. Die seleksievordering gedurende sekere generasies het gepaard gegaan met 'n verlies aan fiksheid, en soms het die vordering verdwyn. Telkens het fiksheid egter herstel waarna hernieude voorkoms van responsies ondervind is. Hierdie responsiepatroon dui op die teenwoordigheid van natuurlike seleksie, wat bevestig word deur die verskille wat tussen die effektiewe en verwagte seleksie-intensiteite voorgekom het. Die gevolgtrekking is gemaak dat die helling van die allometriese funksie die enigste parameter is wat as moontlike seleksiekriterium oorweeg kan word.

Keywords: Allometric-autoregressive model, fitness, genetic drift, natural selection, selection.

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Introduction

The short-term direct and correlated responses to selection for $\ln a$ and b of the allometric function: $w = \ln a + bv$ [where $w = \ln$ (body mass) and $v = \ln$ (cumulative feed intake)], and for ρ , the autoregression slope of \ln (cumulative feed intake) were presented by Scholtz, Roux, de Bruin & Schoeman (1990b).

In general, response to selection cannot be expected to continue indefinitely (Falconer, 1981) and, sooner or later, some deviations from the original response are to be expected. Normally, selection response remains fairly stable as long as selection lasts for only a few generations, although the response may, in some experiments, cease earlier than in others (Pirchner, 1983). Furthermore, extended selection for a trait originally neutral for

fitness may cause a negative relationship between the particular trait and fitness. In this respect, a classic example was discussed by Lerner (1958), where selection was applied to shank length in the fowl. Thus, the results on the medium term of selection are also of importance.

This article will be devoted to the variability in response in the medium term and the problems with fitness which occurred. The results of 12 generations of selection will be discussed.

Material and Methods

The article by Scholtz *et al.* (1990b) should be consulted for details regarding materials and methods. In the current article, the response was measured as the percentage difference between L (downward selection)

and H (upward selection), or as deviation from a control. This made it possible to illustrate graphically in which generations the direct response and fitness were positively or negatively associated, and in which generations these differences or changes occurred.

Results and Discussion

Response in ln a and b

The observed and expected direct responses for ln a and b are illustrated in Figures 1 and 2, respectively. The expected responses were calculated using the equation:

$$r = i\sigma_w h_w^2 \quad (\text{Falconer, 1981}).$$

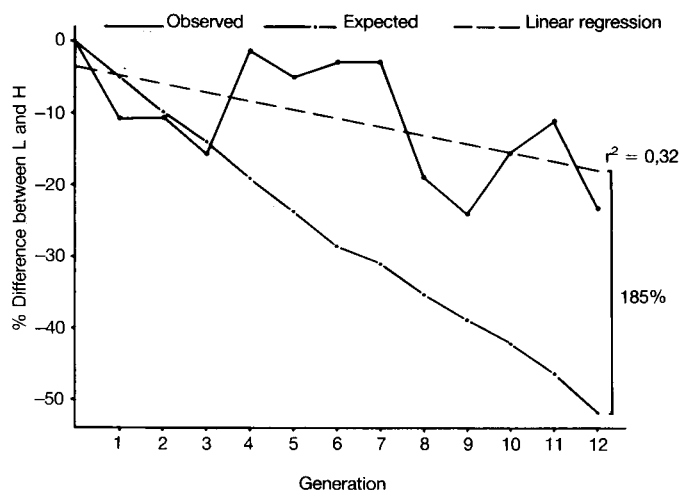


Figure 1 Direct medium-term observed and expected selection response in ln a.

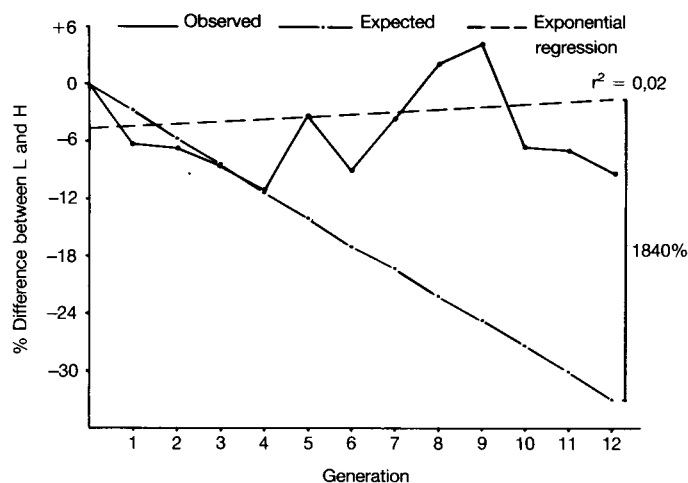


Figure 2 Direct medium-term observed and expected selection response in b.

Estimates of σ_w^2 (within-family variance) and h_w^2 (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. Regressions were also fitted to these responses, and it was found that a linear regression ($y = c + dx$) fits the response in ln a best ($r^2 = 0,32$), while

an exponential regression ($y = ce^{dx}$) fits the response in b best ($r^2 = 0,02$). In both cases, however, the fit was poor.

From Figures 1 and 2, it was clear that the observed responses were irregular, as illustrated by the poor fit of the regressions, especially in the case of b where a response in the wrong direction was also illustrated. Furthermore, there was a marked discrepancy between the observed and expected responses. In the case of ln a, the difference between the observed and expected response was 185%, while the difference in the case of b was 1840%.

Five possible reasons for the discrepancies between the observed and expected responses and the negative response in the case of b were tendered. The reasons were:

1. *Poor fit of the model*

There may be a problem concerning the genetic bases of the parameters of the allometric-autoregressive model when used as criteria of selection. This possibility was investigated by inspecting the accuracy of fit of the model in the initial (generations 0, 1 & 2), middle (generations 5, 6 & 7), and later (generations 10, 11 & 12) stages of selection. The average accuracy of fit (r^2) for the selection groups during the initial, middle or later stages of selection are given in Table 1.

Table 1 Average accuracy of fit (r^2) for the selection groups during the initial (generations 0, 1, 2), middle (generations 5, 6, 7), and later (generations 10, 11, 12) stages of selection

Stage of selection	ln a		b		ρ
	H	L	H	L	
Initial	0,993	0,995	0,992	0,993	0,999
Middle	0,994	0,993	0,993	0,993	0,999
Later	0,990	0,991	0,994	0,992	0,999

From Table 1 it is clear that the accuracy of fit of the model did not change during selection, ruling out, therefore, the possibility of problems with the model during the later generations of selection.

2. *Lack of genetic variance*

The discrepancy between the observed and the expected response may be due to lack of additive genetic variance. This possibility was investigated by estimating the heritabilities of those generations where the discrepancy between the two responses appeared.

When selecting for ln a, the discrepancy appeared after generation 3. However, at this point the heritability estimate of ln a was still 0,25, compared to the initial estimate of 0,31 from the parental generation (Scholtz, Roux, de Bruin & Schoeman, 1990a). Thus, in this experiment, a discrepancy between the observed and expected response of ln a cannot be explained by lack of additive genetic variance.

When selecting for b, the situation was nearly identical. The discrepancy between the observed and expected responses appeared after generation 4. At this point, the heritability estimate was still 0,27, compared to 0,29 of the initial estimate (Scholtz *et al.*, 1990a).

3. Mutation

Mutation may be regarded as a possible reason for the discrepancy between the observed and expected responses. However, where a metric trait is involved, it seems that mutation may be ignored as a possible source of variation during the initial stages of selection (Hill, 1986). Thus, it is unlikely that a mutation was causing the discrepancy between the observed and expected responses.

4. Genetic drift

The magnitude of the expected standard errors of the selection response was investigated to determine whether the variability or discrepancy in the responses encountered here, were within the normal limits of chance (genetic drift). The standard errors were estimated using Hill's (1971) equation for divergent selection for the case where the same proportion of males and females are evaluated. In the case of within-family selection, the variance in response, V(R), is given by:

$$V(R) = 2\sigma_w^2 / Ne th_w^2 [1 - h_w^2 (1 - P)] + (1 - 3/2h_w^4)P$$

where Ne = effective population size

t = generation

P = proportion selected

The standard error of the expected response (R) is $\sqrt{V(R)}$. To get the 95% confidence intervals, the standard error was multiplied by 1,96 and this value was added to, or subtracted from the expected response (R). The expected responses, 95% confidence intervals, and observed responses are illustrated in Figures 3 and 4 for ln a and b, respectively.

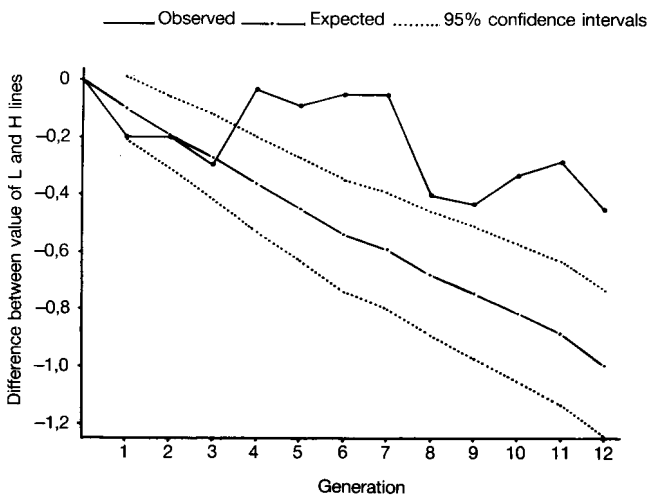


Figure 3 Direct medium-term observed selection response in ln a, expected response, and 95% confidence intervals for the response.

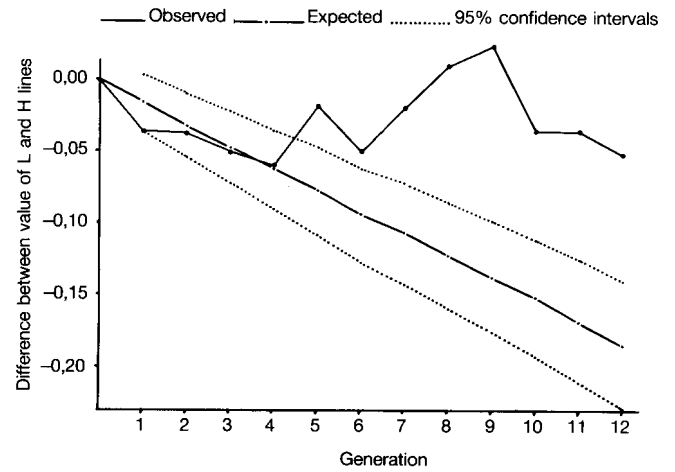


Figure 4 Direct medium-term observed selection response in b, expected response, and 95% confidence intervals for the response.

From these figures, it is clear that the initial responses were within the normal limits of chance. After generation 3 (ln a) and generation 4 (b), however, something happened which caused a failure in response in the selection groups. The observed responses then moved outside the normal limits of genetic drift. Thus, genetic drift did not seem to be the cause of the discrepancies between the observed and expected responses.

5. Natural selection

According to Falconer (1981), a difference between the effective and expected intensity of selection is an indication that natural selection is operating against artificial selection. From Table 2 it can be seen that the effective intensity of selection, expressed as a proportion of the expected intensity of selection, decreased with selection for all the parameters, and in some generations it was less than 50% of that expected. This decrease in the proportion effective/expected intensity of selection, points to the presence of natural selection in this experiment.

Additional evidence on the presence of natural selection will be presented when the correlated responses in fitness are considered.

Fitness

To understand the operation of natural selection, it is necessary to study the correlated responses in fitness. In this study, fitness was defined as the number of mature animals/female mated/100-day period. There were no differences in fitness between the L and H lines; hence their fitnesses were combined, and expressed in absolute terms, and not as a percentage difference between L and H. The fact that there were no differences in fitness between H and L, indicates an optimum value of the metric traits ln a and b associated with maximum fitness, and that any deviation from this optimum, whether it be upwards or downwards, will have an influence on fitness.

Natural selection acts on fitness; thus, the individual with the highest fitness, irrespective of its superiority

Table 2 Effective intensity of selection and the proportion (effective/expected) where the expected intensity of selection is 1,163

Generation	ln a H		ln a L		b H		b L		ρ L	
	Effective	Effective/Expected	Effective	Effective/Expected	Effective	Effective/Expected	Effective	Effective/Expected	Effective	Effective/Expected
	1	1,133	0,974	0,979	0,842	1,146	0,985	0,809	0,696	1,113
2	1,045	0,899	0,771	0,663	0,967	0,831	1,163	1,000	0,996	0,856
3	0,841	0,723	0,930	0,800	0,809	0,696	1,147	0,986	0,959	0,825
4	1,067	0,917	0,909	0,782	1,138	0,979	1,154	0,992	0,937	0,806
5	0,814	0,700	1,066	0,917	1,080	0,929	0,876	0,753	0,921	0,792
6	0,973	0,837	0,966	0,831	1,105	0,950	1,063	0,914	0,809	0,696
7	0,575	0,494	0,400	0,344	0,706	0,607	0,851	0,732	0,711	0,611
8	0,694	0,597	1,106	0,951	1,142	0,982	0,856	0,736	0,612	0,526
9	0,658	0,566	0,717	0,617	1,059	0,911	0,802	0,690	1,041	0,895
10	0,658	0,566	0,710	0,610	1,072	0,922	0,792	0,681	0,867	0,745
11	0,881	0,758	0,738	0,635	1,130	0,971	0,986	0,848	0,859	0,739
12	1,128	0,970	1,076	0,925	1,080	0,929	1,021	0,878	0,826	0,710
Average	0,872	0,750	0,864	0,743	1,036	0,891	0,960	0,826	0,888	0,763

or value for a metric trait, will be represented by the largest number of progeny in the next generation. Artificial selection on the other hand, is selection practised by man and is usually for a metric trait (growth, body mass, efficiency, etc.). In this case, individuals with the highest superiority for the desired value of the metric trait will be favoured as parents for the next generation (Falconer, 1981).

If the desired value of a metric trait becomes negatively associated with fitness, natural and artificial selection will oppose each other. The animals most favoured for a particular metric trait may die before they could reproduce or become less fertile, and contribute only a small proportion of the progeny of the next generation. The animals less favoured for the metric trait will therefore contribute to a larger proportion of the progeny. If natural and artificial selection is in equilibrium, both fitness and the mean of the metric trait will be kept at the level attained. If natural selection becomes more powerful than artificial selection, the fitness of the progeny will rise, whereas the mean of the metric trait moves in the direction contrary to that of artificial selection.

Selection response versus fitness

To simplify the discussion for this particular experiment, the response is divided into different parts according to pattern. The divisions were made at generations where the pattern of the direct response changed, the direction of the correlated response in fitness changed, and/or where the sign or magnitude of the relationship between the direct response and fitness changed.

Selection for ln a

The medium-term response in ln a and the correlated change of fitness are illustrated in Figure 5. There was a favourable response to selection for ln a during the first

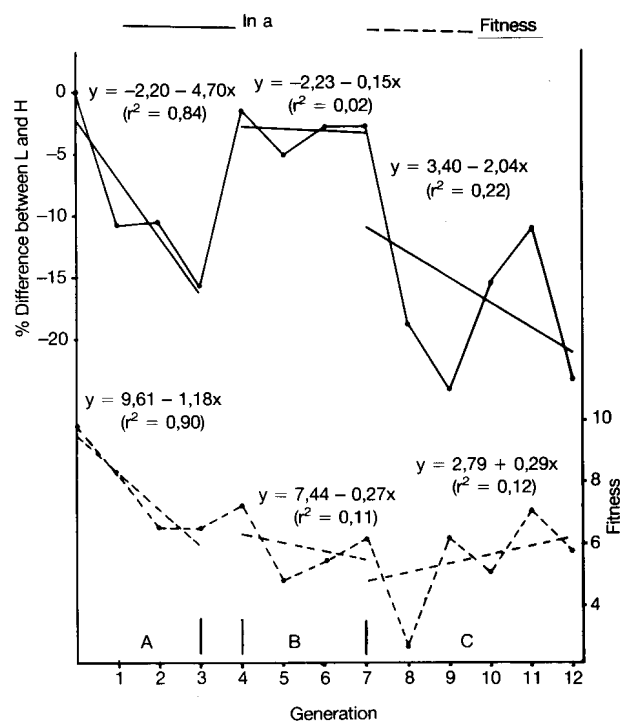


Figure 5 Medium-term response in ln a, the accompanied change of fitness, and equations of responses.

three generations of selection, but at the cost of fitness (part A). However, from the third to the fourth generation, the attained response nearly disappeared. This level of no response lasted until generation 7 (part B). In Part B, natural selection seemed more powerful than artificial selection, and only a slight decrease in fitness was encountered. It is in this part that natural selection seemed to cause movement of the mean of the metric trait in the direction contrary to that of artificial selection, so that the selection response is forced outside the normal limits of chance (Figure 3).

Linear regression ($y = c + dx$) was fitted to both the response in $\ln a$ and fitness, with generation as the x -variable in the different parts. The schematic presentation hereof, in Figure 5, illustrates the points more clearly. For instance, in part A the slope (d) for fitness is $-1,18$ and in part B $-0,27$, indicating a much larger drop in fitness in part A. In case of the direct response, the slope in part A is $-4,70$ versus $-0,15$ in part B, which illustrates practically no response in part B.

Generation 8 (part C) witnessed renewed response to artificial selection, probably due to new genetic combinations formed in part B. Although the response is fluctuating to a large extent, a rather large response is encountered in the first generation (Figure 5). Fitness is also fluctuating, but it seems to increase slowly with a slope of $0,29$.

The response in $\ln a$ is correlated with fitness, with correlation coefficients of $0,89$, $0,91$ and $0,28$ for parts A, B and C respectively. It is interesting to note that fitness and the response in $\ln a$ is strongly correlated in parts A and B, whilst the correlation is much lower in part C. This indicates that the effect of natural selection may be overcome by new genetic combinations formed through recombination, the occurrence of crossing-over between chromosome segments, etc.

Selection for b

The medium-term response in b and the correlated change of fitness are illustrated in Figure 6.

When selecting for b , a remarkable response was found during the first four generations of selection, which is in accordance with the expected response. During this part (A) there was no effect on fitness, which is illustrated by a slope of zero in Figure 6.

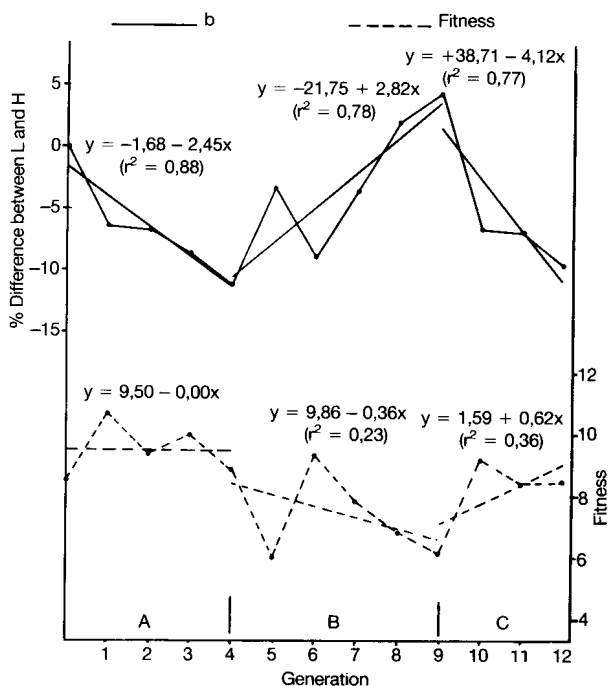


Figure 6 Medium-term response in b , the accompanied change of fitness, and equations of responses.

With further selection there was a sharp decline in the attained response until generation 8 (part B). During part B, natural and artificial selection seem to be in conflict. From generation 6, natural selection seems to be more powerful than artificial selection and a negative response in b was found with a slope of $2,82$ (Figure 6). At this point, the observed response moved outside the normal limits of chance (Figure 4).

As was the case with selection for $\ln a$, part C witnessed renewed response in b to artificial selection ($d = -4,13$) accompanied by a remarkable recovery in fitness ($d = 0,62$).

In part A, the response in b is unrelated to fitness ($r^2 = 0,30$). In parts B and C, however, there is a significant correlation between the response in b and fitness with correlation coefficients of $0,83$ and $0,91$, respectively.

Selection for ρ

Despite a negligible heritability, selection for ρ resulted in a moderate initial response (Figure 7), together with a decline in fitness (part A). Hereafter, natural selection seems to become more powerful than artificial selection, and a negative response in ρ occurred from generation 3 to 4. In part B, an equilibrium between natural and artificial selection seems to exist, with no change in the value of ρ . In part B(1) fitness is fluctuating with no perceptible pattern (generations 4-7). From generation 7 onwards, fitness has stabilized, with a slow but steady recovery in fitness.

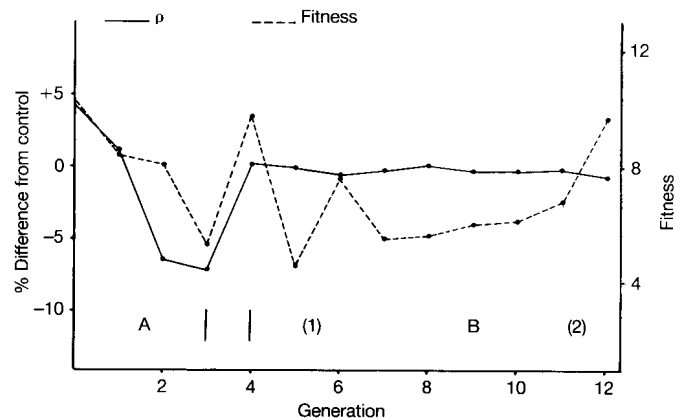


Figure 7 Medium-term response in ρ and the accompanied change of fitness.

Conclusion

In the short term, the direct response to selection for parameters of the allometric-autoregressive model was in accordance with expectation based on genetic theory. In the medium term, however, irregular responses occurred. It seems that these irregular responses can be explained biologically.

Balch and Reid (1976) maintained that feed intake and, therefore, also growth rate are under control of the homeostatic mechanisms of the body. The inherent capacities for growth, and thus also ρ , which is a function of the rate constant of relative growth, must therefore be kept within certain limits to maintain

homeostasis (Balch, 1973). Balch & Reid (1976) believed that deviations from the homeostatic limits may result in metabolic disorders and even death. Hence, the need for the canalization of ρ is evident.

In the medium term, ln a and b showed irregular responses with selection, together with a marked discrepancy between the observed and expected responses. These discrepancies might have been caused by poor fit of the model during later generations, lack of genetic variance, mutation, genetic drift and/or natural selection. All these aspects were investigated, and it was concluded that natural selection seems to be the most acceptable explanation for the observed discrepancies.

Fitness is very important in any production system. It is, therefore, important to investigate whether the problems with fitness encountered in this experiment are common to all selection experiments. A thorough literature survey is therefore needed.

The parameter b seems to be the only parameter of the allometric-autoregressive model which can be used as a selection criterion. Selection for b resulted in an increase in efficiency, while intake tended to decrease (Scholtz *et al.*, 1990b). This is in contrast to selection for a conventional criterion such as growth rate, which increases intake (Hetzl & Nicholas, 1978). Furthermore, selection for b seems to be successful in altering the shape of the efficiency curve (Scholtz *et al.*, 1990b). Unfortunately, selection for b seems to have an adverse effect on fertility in the medium term, and thus necessitates concurrent selection for fertility. This seems to be true for most selection criteria (Roux & Scholtz, 1984).

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