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# Long-term responses to selection for parameters of the allometric model in the rat

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Rats (*Rattus domesticus*) were used in an experiment where selection was practised for the 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)]. Both upward and downward selection was practised for $ln\ (a)$ and $b$, for 23 generations and 32 generations, respectively. Selection for $ln\ (a)$ primarily resulted in positive reponses in correlated characteristics during the first post-weaning growth phase, while selection for $b$ primarily resulted in positive responses in correlated characteristics during the second post-weaning growth phase. Selection for $ln\ (a)$ and $b$ both resulted in a change in efficiency (negative for $ln\ (a)$ and positive for $b$), while the 60-day body mass and feed intake were not changed significantly. This result is of practical importance in the pig and poultry industry.

Rotte (*Rattus domesticus*) is in 'n seleksie-eksperiment gebruik waar onderskeidelik vir die helling ($b$) en afsnit ($ln\ (a)$) van die allometriese funksie $w = ln\ (a) + bv$ [waar $w = ln$ (liggaamsmassa) en $v = ln$ (kumulatiewe voerinname)], geselekteer is. Opwaartse en afwaartse seleksie is vir $ln\ (a)$ en $b$ toegepas, waarin 23 generasies van seleksie vir $ln\ (a)$ en 32 generasies van seleksie vir $b$ afgehandel is. Seleksle vir $ln\ (a)$ het hoofsaaklik positiewe responsies in gekorreleerde eienskappe tydens die eerste naspeense groeifase tot gevolg gehad, terwyl seleksie vir $b$ hoofsaaklik positiewe responsies in gekorreleerde eienskappe tydens die tweede naspeense groeifase tot gevolg gehad het. Seleksie vir $ln\ (a)$ en $b$ het beide 'n responsie in doeltreffendheid in die tweede naspeense groeifase tot gevolg gehad (negatief vir $ln\ (a)$ en positief vir $b$), sonder dat 60-dae liggaamsmassa betekenisvol verander het. Hierdie resultaat is veral van praktiese belang in die vark- en pluimveebedryf.

**Keywords**: Allometric model, correlated response, direct response, intercept, slope.

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## Introduction

A knowledge of growth curves is important to all animal scientists who are concerned with production efficiency, since these growth curves reflect the lifetime interrelationships between an animal's inherent ability to grow and the feed it consumes (Fitzhugh, 1976).

The most important advantage of using a growth function, such as the allometric-autoregressive model, is that a more accurate description and evaluation of animal growth can be obtained (Meissner, 1977). Manipulation of the growth curve can be advantageous for the following reasons:

1. The antagonism between the fast and efficient early growth rate of slaughter animals and the low maintenance costs of breeding animals, can be minimized.
2. By increasing the rate of maturity, internal efficiency can be increased.
3. The incidence of distocia can be minimized by restricting the birth mass as a percentage of the mass of the dam.
4. Age at first mating can be lowered by reducing the time needed to reach puberty.
5. By increasing the time to reach physiological maturity, the grade of fatness of the carcass at a fixed slaughter age can be reduced.

Manipulation of the growth curve therefore depends on the degree of genetic flexibility of the curve or parts of the curve. Thus, the possibility of manipulation depends on the heritability of the parameters of the growth curve on the one hand, and the degree of independency (genetic correlations) between these parameters, on the other hand (Schoeman, 1988).

The allometric-autoregressive model (Roux, 1974; 1976), which not only takes feed intake into account, but also considers the basic allometric nature of growth (Roux, 1974; 1976; Meissner & Roux, 1979; Roux, 1980), seems to be of value in genetic studies and some of its parameters exhibit significant heritabilities (Scholtz *et al.*, 1990a). According to Meissner (1977), the allometric-autoregressive model satisfies, on the whole, the specified prerequisites of a model for the functional description of animal growth. Thus, the model can be used in the characterization of growth responses of breeds and feeds in nutritional studies (Scholtz *et al.*, 1990b). A selection experiment was carried out on some of the parameters of the allometric model to investigate the potential of the model for selection purposes, using the rat as a model. The short-term (Scholtz *et al.*, 1990b) and medium-term (Scholtz *et al.*, 1990c) responses to selection for the parameters of the allometric-autoregressive model, have already been reported. In this study the results of long-term selection for the parameters of the allometric model, will be discussed.

## Materials and Methods

For details regarding the materials and methods, Scholtz *et al.* (1990b) should be consulted.

## The model

The well-known allometric function to describe growth efficiency can be expressed by the equation:

$$w = \ln(a) + bv \qquad \text{(Roux, 1976)}$$

where $w$ = *ln* (body mass) and
$v$ = *ln* (cumulative feed intake).

A two-way selection experiment was carried out for the intercept (*ln* (*a*)) and slope (*b*) of the allometric function. No replicates were made. Thus, both upward (*ln* (*a*)H and *b*H) and downward (*ln* (*a*)L and *b*L) selection were practised for *ln* (*a*) and *b* and the high lines (H) could be used as the control for the low lines (L) and *vice versa*.

An unselected control population is an obvious way to eliminate environmental fluctuations when an assessment of the rate of response is made. Assuming that environmental differences affect the selected and control populations alike, the difference between them estimates the genetic improvement made by selection. The use of a control, however, does not always improve the precision with which the response is estimated. Both populations are subject to random drift and to sampling errors and the difference between the two is subject to variance from these causes, i.e. the sum of the variance of the two lines. Furthermore, the scale of an experiment is usually limited by the facilities available, so that the use of a control necessitates a reduced population size of the selected line. If the selected line and control both have half the population size of a single selected line, then the use of a control quadruples the sampling variance of the response, measured as deviations from the control, and so doubles the standard error. This loss of accuracy may counterbalance the gain obtained from eliminating environmental differences. The relative accuracy of the response measured by the use of a control can be improved if the 'control' is not an unselected population, but is selected in the opposite direction (Falconer, 1981). Because this selection experiment was restricted by limited facilities, it was decided to carry out a two-way selection experiment, thereby improving the relative accuracy of the response measured over that of a control line.

Due to serious problems with fitness, selection for *ln* (*a*) was terminated at generation 23. Upward and downward selection for *b*, however, continued up to generation 32, after which it was terminated, also due to problems with fitness.

The response to selection is measured as the percentage difference between the H- (upward) and L- (downward) selection lines:

$$\text{Selection progress} = \{(H - L)/[0.5*(H + L)]\} * 100$$

The *ln* (*a*) and *b* of the allometric model were estimated by linear least square procedures.

## The animals

Rats from the outbred Wistar line were used as models for this selection experiment because of their short generation interval. Each selection group consisted of four families with 10 individual in each (five males and five females).

Litter size was standardized to 12 at three days of age to minimize the influence of maternal effects. To overcome possible infertility, the two best males and females from each family were selected as parents for the next generation. Rotational mating was practised. The best male was first mated to both selected females. After eight days the second best male was mated to the same females.

A number of additional rats were simultaneously mated with the selected rats. When the litter sizes of the selected rats were too small, progeny from the additional rats were used to standardize the litters to 12 pups. At weaning, any additional rats were removed. When the litter sizes of the selected rats were larger than 12, the additional rats were used to foster these pups. These rats were only included in the experiment when necessary.

The rats were kept in standard cages under conventional conditions (not pathogen-free). Room temperature was kept at 21°C ± 2°, 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, up to the age of 60 days, without withholding food and water prior to measurement.

The post-weaning growth of the rat was divided into three growth phases:

1. Phase 1: From 24 to about 36 days of age.
2. Phase 2: From about 37 to 60 days of age.
3. Phase 3: From about 70 days onwards, with a transitional period between 60 and 70 days of age when sexual maturity was reached (Scholtz & Roux, 1981).

## Selection

Inbreeding was kept to a minimum by representing all families in the next generation. Within-family selection was practised, whereby environmental effects, common to litter-mates, and maternal effects were also taken into account (Falconer & Latyszewski, 1952).

With the selection of an equal number from all families and, owing to the exclusion of sib-matings, the effective population size could be determined as:

$$N_e = N + 2 \qquad \text{(Falconer, 1981)}$$
$$= 18$$

Due to the restriction of facilities, selection was practised only during the second growth phase. This phase was preferred for the following reasons:

1. During the first phase the animals could still be subjected to maternal effects which would probably have an influence on the results.
2. The second phase is not very sensitive to errors when calculating $\mu$ (cumulative energy uptake value at the beginning of an experimental phase) (Scholtz & Roux, 1980).
3. Most of the growth takes place during the second phase.

## Results

### Direct responses

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

$$r = i\,\sigma_w\,h^2_w \qquad \text{(Falconer, 1981)}$$

Estimates of $\sigma_w$ (with-in family variance) and $h^2_w$ (with-in family heritability) were calculated from the parental generation (Scholtz *et al.*, 1990a), while the intensity of selection was standardized on 1/5.

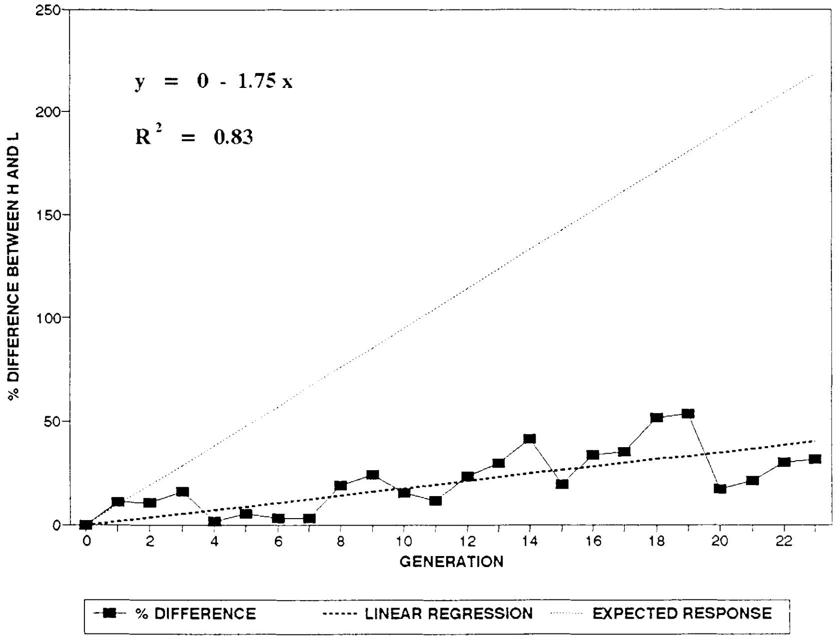

**Figure 1** Observed and expected direct responses, expressed as the percentage difference between the upward (H) and downward (L) selection lines, in *ln* (*a*) (intercept of the allometric growth model: *ln* (body mass) = *ln* (*a*) + *b* * *ln* (cumulative feed intake)).

Regressions were fitted to the responses to predict the attained responses in certain generations, using Systat (1989). In linear regression, the $R^2$ value gives an indication of the accuracy of fit. According to Hill (1976), tests of significance of these $R^2$ values are not valid, because the values of the different generations are 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 to indicate which correlated responses deserve attention (Scholtz *et al.*, 1990a).

A linear regression ($y = c + dx$) fitted the response in *ln* (*a*) the best ($R^2 = 0.83$), while a quadratic regression ($y = c + dx + ex^2$) fitted the response in *b* ($R^2 = 0.78$) best. There was a marked discrepancy between the observed and expected responses in the case of the response in *ln* (*a*). The observed response in *b*, however, tended to approach the expected response up to generation 6. Scholtz *et al.* (1990c) discussed five possible reasons for the discrepancies between the observed and expected responses. These were: poor fit of the model, lack of genetic variance, mutation, genetic drift and natural selection. It was concluded that the presence of natural selection was most likely responsible for these discrepancies.

Long-term selection for *ln* (*a*) resulted in a total response of 40% in 23 generations of selection (Figure 1). After a response of 15% at generation 22 with selection for *b* (Figure 2), the response decreased and a total response of 12% was realized after 32 generations of selection, compared with an expected

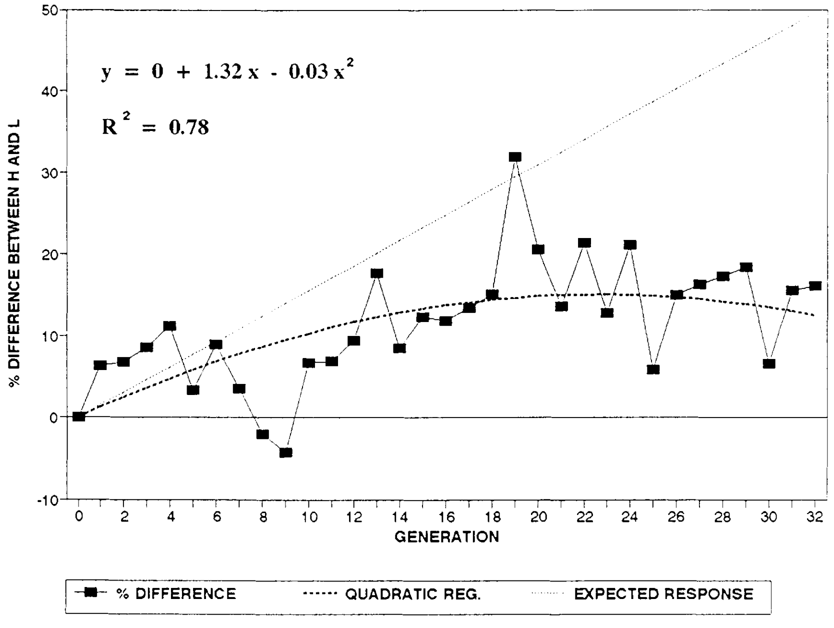

**Figure 2** Observed and expected direct responses, expressed as the percentage difference between the upward (H) and downward (L) selection lines, in *b* (slope of the allometric growth model: *ln* (body mass) = *ln* (*a*) + *b* * *ln* (cumulative feed intake)).

response of 50%. This decline in response was probably due to the deterioration of reproductive capacity, since some individuals were lost and the survivors became a selected group to which the theoretical expectations no longer applied (Falconer, 1981).

The realized genetic correlation between *ln (a)* and *b* of Phase 2 was estimated after 23 generations of selection, using the following formula (Falconer, 1981)

$$r^2_A = CR_x * CR_y / R_x * R_y$$

where:

$CR_x$ = Correlated response in *ln* (*a*) with selection for *b*
$CR_y$ = Correlated response in *b* with selection for *ln* (*a*)
$R_x$ = Direct response in *ln* (*a*)
$R_y$ = Direct response in *b*.

The realized correlation was $r_A = -0.97$, which is in good agreement with the genetic correlation between *ln* (*a*) and *b* of Phase 2 of $r_A = -0.96$, estimated by Scholtz *et al.* (1990a).

## Correlated responses

In Table 1, a comparison is made of the correlated responses as measured only at the generations where the responses in *ln* (*a*) and *b* have peaked (generations 3, 9, 14 and 19 for *ln* (*a*) and generations 4, 13 and 19 for *b*) and as measured for all generations of selection.

**Table 1** A comparison of the direct and correlated responses as measured only at the generations where responses in *ln* (*a*) (column 2) and *b* (column 3) have peaked and as measured for all the generations of selection (columns 4 and 5). Probabilities refer to the significance of the slope of the fitted regression lines

| | Response (%) Peak generations | | Response (%) All generations | |
|---|---|---|---|---|
| Characters | *ln* (*a*) | *b* | *ln* (*a*) | *b* |
| **Direct responses** | | | | |
| Intercept Phase 2 | 54.6*** | – | 40*** | – |
| Slope Phase 2 | – | 30.7*** | – | 12*** |
| **Correlated responses** | | | | |
| Intercept Phase 2 | – | –32.8*** | – | –18.8*** |
| Slope Phase 2 | –24.9 | – | –23.3*** | – |
| ADI Phase 1 | 1.3 | –3.8 | 1.4 | –2.8* |
| ADI Phase 2 | –6 | 5.5 | –10.7*** | 3.8** |
| ADG Phase 1 | 15.7** | –6.7 | 11*** | –0.03 |
| ADG Phase 2 | –27.6*** | 24.9** | –29*** | 28*** |
| Birth mass | 20.5* | –1.4 | 21*** | 1.8 |
| Weaning mass | 18.6*** | 0.2 | 12.5*** | 9.98*** |
| 30-day mass | 21.6*** | –9.3* | 14.4*** | 3.5 |
| 60-day mass | –1.9 | 7.6 | –6.7*** | 10.24*** |
| Efficiency Phase 1 | 11.7** | –5.6 | 12*** | 0.4 |
| Efficiency Phase 2 | –20.8*** | 27.3* | –23*** | 21.1*** |
| Total efficiency at 60 days | –4.37 | 7.51 | –3.6*** | 8.8*** |

* = $P \leq 0.1$
** = $P \leq 0.05$
*** = $P \leq 0.01$

The pattern of long-term responses is diverse and unpredictable (Yoo, 1980) and fluctuates from generation to generation. Part of the variation is caused by errors of estimation, but some will be due to differences in the true generation means, brought about by external environmental causes, by the differences in the size of the selection differential and by genetic sampling (Falconer & King, 1953). Because of these reasons, it was decided to determine the correlated responses at the generations where the direct responses in *ln* (*a*) and *b* have peaked. The effect of gene interactions, delays due to genetic linkage and irregularities due to negative changes in fitness should then also be removed. The rest of this study is therefore based on the correlated responses which are measured in this way.

## Correlated responses with selection for *ln* (*a*)

From Table 1, it is clear that *b* responded strongly and negatively to selection for *ln* (*a*) ($P \leq 0.01$). A response of –25% was realized, which is in accordance with the high negative genetic correlation ($r_G = -0.96$) between *ln* (*a*) and *b* within the same growth phase. All genetic correlations referred to in the text were estimated by Scholtz (1987).

The correlated responses in the other characters that have been investigated are as follows (Table 1):

### *Average daily feed intake (ADI)*

ADI of Phase 1 ($P \geq 0.1$) and 2 ($P \geq 0.1$) was not significantly changed by selection for *ln* (*a*). The response in ADI of Phase 2 was, however, not in accordance with the genetic correlation ($r_G = 0.38$) estimated between *ln* (*a*) and ADI of Phase 2. From this estimated genetic correlation, it was expected that ADI of Phase 2 would respond positively and moderately to selection for *ln* (*a*).

### *Average daily gain (ADG)*

ADG of Phase 1 showed a positive response of 15.7% ($P \leq 0.05$) with selection for *ln* (a). ADG of Phase 2, however, responded strongly and negatively to selection for *ln* (*a*) and a response of –27.6% ($P \leq 0.01$) was realized. This is in accordance with the genetic correlation ($r_G = -0.8$) estimated between *ln* (*a*) and ADG of Phase 2.

### *Body mass*

Birth mass responded positively and strongly to selection for *ln* (*a*) and a response of 20.5% ($P \leq 0.1$) was realized. Weaning mass and 30-day mass also showed strong and positive responses and responses of 18.6% ($P \leq 0.01$) and 21.6% ($P \leq 0.01$) were realized, respectively. Body mass at 60 days, however, did not change significantly ($P \geq 0.1$) with selection for *ln* (*a*). According to the genetic correlation ($r_G = 0.23$) estimated between *ln* (*a*) and 60-day mass, a small positive response in 60-day mass was expected.

### *Feed efficiency*

A positive and moderate response of 11.7% ($P \leq 0.05$) was realized in efficiency during Phase 1. The response in efficiency during Phase 2, however, decreased with –20.8% ($P \leq 0.01$) with selection for *ln* (*a*), which is more than expected from the genetic correlation of –0.29, estimated between *ln* (*a*) and efficiency during Phase 2. Total efficiency at 60 days of age did not change significantly ($P \geq 0.1$) with selection for *ln* (*a*). This is in accordance with the small genetic correlation of –0.1, estimated between *ln* (*a*) and total efficiency at 60 days of age.

### Correlated responses with selection for *b*

From Table 1, it is clear that a strong negative response of –32.7% ($P \leq 0.01$) was realized in *ln* (*a*) with selection for *b*. This response is in accordance with the negative genetic correlation ($r_G = -0.96$) estimated between *b* and *ln* (*a*) within the same growth phase.

*Average daily feed intake (ADI)*

ADI of Phase 1 ($P \geq 0.1$) and Phase 2 ($P \geq 0.1$) were not significantly altered by selection for *b*. According to the small genetic correlation ($r_G = 0.12$) estimated between *b* and ADI of Phase 2, this response in ADI of Phase 2 was expected.

*Average daily gain (ADG)*

ADG of Phase 1 was not significantly changed ($P \geq 0.1$) by selection for *b*. ADG of Phase 2, however, responded strongly and positively to selection for *b* and a response of 24.9% ($P \leq 0.05$) was realized. This is more than expected from the genetic correlation ($r_G = 0.33$) estimated between *b* and ADG of Phase 2.

*Body mass*

Birth mass ($P \geq 0.1$), weaning mass ($P \geq 0.1$) and 60-day mass ($P \geq 0.1$) were not significantly changed by selection for *b*. Mass at 30 days of age, however, showed a moderate negative response of –9.3% ($P \leq 0.1$). The response in 60-day mass is in accordance with the small genetic correlation ($r_G = 0.18$) estimated between *b* and 60-day mass.

*Feed efficiency*

Selection for *b* did not change efficiency during Phase 1 significantly ($P \geq 0.1$). Efficiency during Phase 2, however, responded strongly and positively to selection for *b* and a response of 27.3% ($P \leq 0.1$) was realized. This response is more than expected from the genetic correlation of 0.38, estimated between *b* and efficiency during Phase 2. Total efficiency at 60 days of age did not change significantly ($P \geq 0.1$) with selection for *b*. This response is in accordance with the small genetic correlation of 0.14, estimated between *b* and total efficiency at 60 days of age.

In Table 2 a summary is given of the correlated responses realized with selection for *ln* (*a*) and *b*, the genetic correlations estimated by Scholtz (1987) and, there is an indication of whether the obtained correlated responses were in accordance with expectations regarding the genetic correlations.

**Table 2** Summary of the correlated responses realized with selection for the intercept (*ln* (*a*)) and slope (*b*) of the allometric growth model, the genetic correlations estimated by Scholtz (1987) and an indication of whether the obtained correlated responses were as expected regarding the genetic correlations. Probabilities refer to the significance of the slope of the fitted regression lines

| Character | Selection group | Correlated response (%) | Agreement with estimated $r_G$ | Estimated $r_G$ (Scholtz, 1987) |
|---|---|---|---|---|
| Intercept Phase2 | *ln* (*a*) | – | – | – |
| | *b* | –32.8*** | In accordance | –0.96 |
| Slope Phase 2 | *ln* (*a*) | –25*** | In accordance | –0.96 |
| | *b* | – | – | – |
| ADI Phase 1 | *ln* (*a*) | NS | – | – |
| | *b* | NS | – | – |
| ADI Phase 2 | *ln* (*a*) | NS | Less than expected | 0.38 |
| | *b* | NS | In accordance | 0.12 |
| ADG Phase 1 | *ln* (*a*) | 15.7** | – | – |
| | *b* | NS | – | – |
| ADG Phase 2 | *ln* (*a*) | –27.6*** | In accordance | –0.80 |
| | *b* | 24.9** | More than expected | 0.33 |
| Birth mass | *ln* (*a*) | 20.5* | – | – |
| | *b* | NS | – | – |
| Weaning mass | *ln* (*a*) | 18.6*** | – | – |
| | *b* | NS | – | – |
| 30-day mass | *ln* (*a*) | 21.6*** | – | – |
| | *b* | –9.3* | – | – |
| 60-day mass | *ln* (*a*) | NS | Less than expected | 0.23 |
| | *b* | NS | In accordance | 0.18 |
| Efficiency Phase 1 | *ln* (*a*) | 11.7** | – | – |
| | *b* | NS | – | – |
| Efficiency Phase 2 | *ln* (*a*) | –20.8*** | More than expected | –0.29 |
| | *b* | 27.3* | More than expected | 0.38 |
| Total efficiency at 60 days | *ln* (*a*) | NS | In accordance | –0.10 |
| | *b* | NS | In accordance | 0.14 |

* = $P \leq 0.1$
** = $P \leq 0.05$
*** = $P \leq 0.01$

## Discussion

Selection for *ln* (*a*) primarily resulted in positive responses in correlated characteristics during the first post-weaning growth phase, while selection for *b* primarily resulted in positive responses in correlated characteristics during the second post-weaning growth phase.

Selection for *ln* (*a*) caused an increase in the intercept of the allometric function. This increase can be attributed to a decrease in the slope of the allometric function together with an increase in early body masses and ADG during Phase 1, while ADG and efficiency during Phase 2 decreased. Selection for *b*, on the other hand, caused an increase in the slope of the allometric function. This increase can be attributed to a decrease in the intercept of the allometric function, while early body masses are kept constant or are decreased, and ADG and efficiency during Phase 2 are increased.

It can thus be concluded that the shape of the growth and efficiency curve of an animal, i.e. body mass (g) vs. feed intake (g), can be altered by long-term selection for the parameters of the allometric model.

A response in efficiency in Phase 2 was realized with selection for *ln* (*a*) (efficiency decreased) and *b* (efficiency increased), while, in both cases, 60-day mass was not changed significantly. Since feed intake did not change significantly with selection for both *ln* (*a*) and *b*, the changes obtained in efficiency can be attributed to changes in growth rate. According to Taylor & Murray (1987), as quoted by Roux (1992), an increase in growth rate implies an increase in limit mass. In chickens and pigs, it is general practice to control breeder body mass by restricted feed intake (Thornton, 1978; Siegel & Dunnington, 1988), while the dwarf gene is also employed in chicken breeding (Gous, 1986). Belt *et al.* (1992), who investigated poultry development by following an allometric-autoregressive approach, identified a physiological break at eight weeks of age, when the course of metabolic events of the birds was modified and a new developmental stage initiated. This was assumed to be the onset of puberty. They also thought it safe to assume that a third phase exists during adulthood. Responses to selection for the parameters of the allometric model should therefore be investigated during each particular growth phase of the chicken before final conclusions can be made. From this study it seems that as an alternative to the abovementioned practices, long-term selection for the slope of the allometric model can be considered. Selection for the slope of the allometric model may enable a breeder to restrict early growth rate of poultry, while increasing subsequent growth rate. This would result in lower maintenance requirements during rearing and thus a reduction in rearing costs for breeders. The restriction of early growth rate has two further advantages. Firstly, more efficient mineralization of the skeleton of the birds can take place, which will lead to a reduction in the leg weakness problems in the poultry industry (Pinchasov *et al.*, 1985). Secondly, the incidence of ascites in the broiler industry can be reduced, as rapidly growing broilers are more susceptible to ascites than slower growing broilers (Julian *et al.*, 1987).

The efficient production of lean meat for the consumer is the primary objective of pork production. This objective relies heavily on selection goals related to efficiency, growth and carcass quality and composition. These traits have responded well, either directly or indirectly, to selection, but additional gains are necessary if consumer interest in pork is to be maintained. Feed consumption (appetite) and feed efficiency are traits that impact heavily on the economics of pork production. Both appetite and efficiency have generally be included indirectly in selection programmes. Increased efficiency of gain may, however, reduce appetite and this correlated response could be a limiting factor in future improvement (Rothschild, 1990). From this study, it is clear that selection for the slope of the allometric growth model in the long-term is a way to increase efficiency and growth rate, while feed intake is not changed significantly.

## Conclusion

Based on short-term results (Scholtz *et al.*, 1990a), the possibility for selection progress in the slope of the allometric model (*b*) in rats is limited, since after four generations of gains according to prediction, progress ceased. Furthermore, considerable antagonism between natural and artificial selection sometimes forced the differences between the high and low lines back to the initial level. Although not in accordance with predictions, these long-term results indicate that it is possible to make long-term progress when selecting for *ln* (*a*) and *b*. Selection for *b* resulted in an increase in feed efficiency in Phase 2 without 60-day mass and feed intake being increased. This result may be important in the pig and poultry industry. Improvement in efficiency, without an increase in end mass and feed intake, as can be realized with selection for the slope of the allometric model, may thus be a more acceptable alternative in pig and poultry breeding.

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