The effect of long-term selection for the parameters of the allometric model on fitness in the rat

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The long-term effect of selection for the parameters of the allometric model on fitness is investigated to evaluate the allometric model for long-term selection purposes. Fitness is defined as the number of mature animals / female mated / 100-day period, where mature animals are defined as animals at the age of joining (standardized at 90 days). The results of 23 generations of selection for the intercept (ln (a)) and 32 generations of selection for the slope (b) of the allometric function $w = ln$ (a) $+ bv$ [where $w = ln$ (body mass) and $v = ln$ (cumulative feed intake)], are discussed. Fitness decreased as a correlated response to selection for ln (a) and b. The response in fitness with selection for ln (a) and b is best described by a quadratic regression. It was concluded that the parameters of the allometric growth function can be used as selection criteria in long-term selection experiments, but special attention should be given to fertility in the breeding plan. This can be realized by concurrent selection for fertility or, for example, in the poultry industry, by selecting male lines for the parameters of the growth model and female lines for growth and reproductive performance.

Die langtermyn effek van seleksie vir die parameters van die allometriese groeimodel op fiksheid is ondersoek om vas te stel of die allometriese model vir langtermyn seleksie-doeleindes aangewend kan word. Fiksheid is gedefinieer as die hoeveelheid volwasse diere / vroulike dier gepaar / 100-dae periode, waar volwasse diere gedefinieer is as diere op paringsouderdom (gestandaardiseer op 90 dae). Seleksie vir ln (a) sowel as vir b het 'n gekorreleerde afname in fiksheid tot gevolg gehad. Die gekorreleerde responsie in fiksheid met seleksie vir ln (a) en b word die beste deur kwadratiese regressies beskryf. Die gevolgtrekking dat die parameters van die allometriese groeimodel wel as seleksie-kriteria in langtermyn seleksie-eksperimente gebruik kan word, word gemaak, maar die teelprogram sal ook voorsiening moet maak vir die verbetering van vrugbaarheid. Dit kan deur middel van óf gelyktydige seleksie vir vrugbaarheid, óf, soos byvoorbeeld in die pluimvee-bedryf, deur middel van die toepassing van seleksie vir die parameters van die groeimodel slegs in vaderlyne, terwyl moederlyne vir groei en vrugbaarheid geselekteer word, geskied.

Keywords: Allometric model, correlated response, direct response, fitness.

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Introduction

According to Roux (1992a) the profit rate for a meat production enterprise can be broken down into the unit price for meat and herd efficiency. There are three ways of appreciably improving herd efficiency, i.e. (i) by increasing fertility and viability, (ii) by feeder-breeder dimorphism (Roux, 1992b), and (iii) by increasing growth efficiency (Roux, 1986). Mostert *et al.* (1994) concluded that an improvement in growth efficiency without an increase in end mass, can be realized by long-term selection for the slope of the allometric growth model. Scholtz *et al.* (1990c) found that, on the medium-term, selection responses obtained from selection for the slope (b) and intercept (ln (a)) of the allometric model were, however, accompanied by losses of fitness during certain generations, while in others, the responses disappeared altogether. In certain generations fitness was regained and was followed by the renewed appearance of responses. It was concluded that this pattern of response behaviour pointed to the presence of natural selection.

In this study, the long-term effect of selection for the parameters of the allometric model on fitness will be investigated to evaluate the allometric model for long-term selection purposes. The results of 23 generations of selection for the intercept (ln (a))
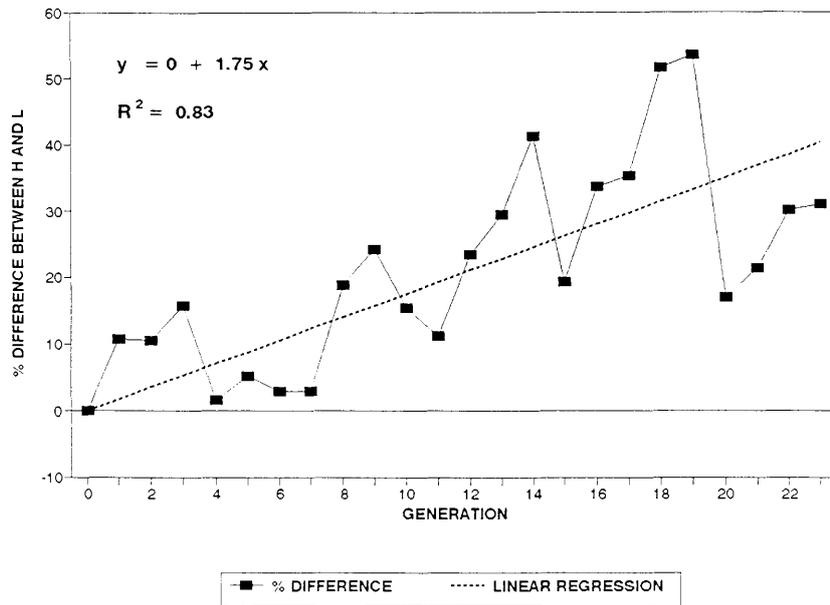
and 32 generations of selection for the slope (b) of the allometric function: $w = ln$ (a) $+ bv$ [where $w = ln$ (body mass) and $v = ln$ (cumulative feed intake)], will be discussed.

Materials and Methods

For details regarding the materials and methods, Scholtz *et al.* (1990b) and Mostert *et al.* (1994) should be consulted.

A two-way selection experiment was carried out for the intercept (ln (a)) and slope (b) of the allometric growth function. No replicates were made. Both upward (ln (a)H and bH) and downward (ln (a)L and bL) selection were practised for ln (a) and b and the high lines (H) could be used as the control of the low lines (L) and *vice versa*. Restricted by the available facilities, it was decided that each selection group should consist of four families with ten individuals in each family; five males and five females, as far as possible.

Since long-term selection was planned, it was important to keep inbreeding to a minimum. This could be done by representation of 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).

$$y = 0 + 1.75\,x$$

$$R^2 = 0.83$$

% DIFFERENCE BETWEEN H AND L (y-axis)

GENERATION (x-axis)

◼ % DIFFERENCE   ⋯⋯ LINEAR REGRESSION

Figure 1 Direct observed response in *ln* (a) (intercept of the allometric growth model), expressed as the percentage difference between the upward (H) and downward (L) selection lines.

Although the initial aim was to keep the intensity of selection constant to one animal out of five, this was not always possible owing to small litter sizes and infertility in later generations. The effective intensity of selection was calculated for each generation and selection group, using the tables of normal order statistics by Beyer (1968). These tables can be used to calculate the intensity of selection, since the variables *ln* (a) and b are normally distributed.
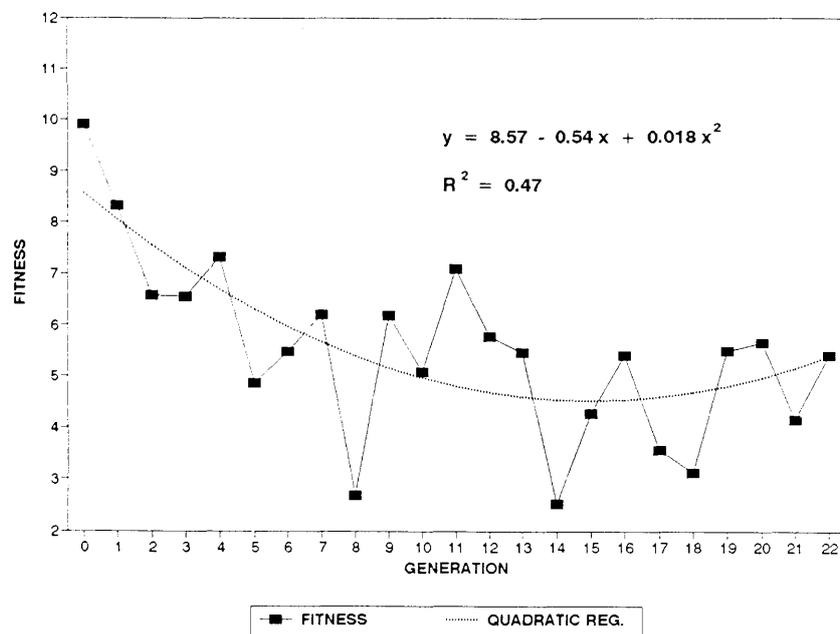
Fitness is defined as:

Fitness = Number of mature animals/female mated/100-day period

'Mature animals' is defined as animals being at the age of joining. In all generations, age at joining was standardized at 90 days. In this way, all possible components of fitness, eg. fertility, litter size, survival (pre-weaning and post-weaning) and days from joining to birth, are included (Scholtz *et al.*, 1990c).

Because there were no differences in fitness between the H (upward) and L (downward) selection lines during the first 12 generations of selection, their fitnesses were combined and expressed in absolute terms.

Regressions were fitted to the responses in fitness, using Systat (1989). According to Falconer & King (1953) the measurements of progress under selection are based on the calculated linear regression line, because little reliance can be placed on the means of individual generations. The calculation of a regression line minimizes the effect of all fluctuations from generation to

$$y = 8.57 - 0.54\,x + 0.018\,x^2$$

$$R^2 = 0.47$$

FITNESS (y-axis)

GENERATION (x-axis)

◼ FITNESS   ⋯⋯ QUADRATIC REG.

Figure 2 Correlated observed response in fitness (fitness of the upward and downward selection lines combined and expressed in absolute terms) with selection for *ln* (a) (intercept of the allometric growth model).
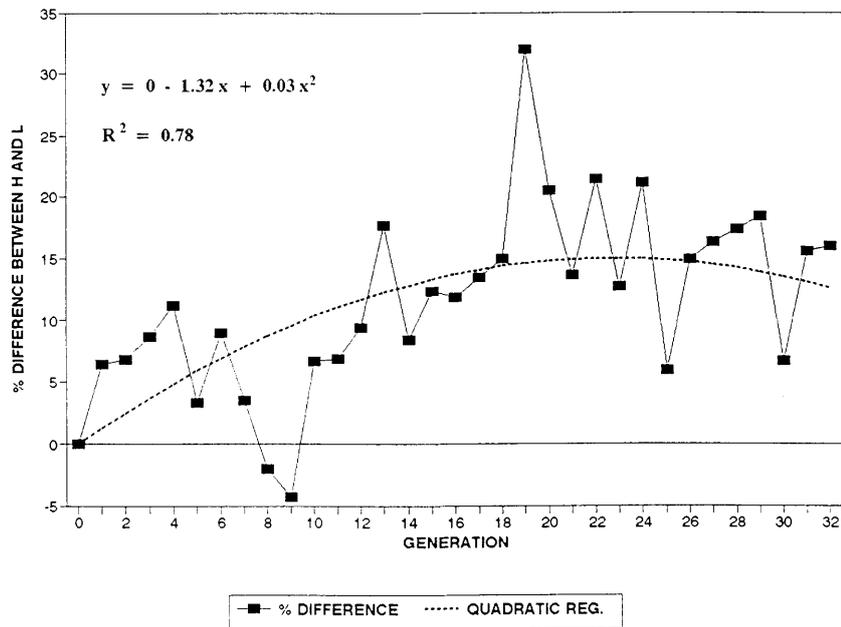
Figure 3 Direct observed response in b (slope of the allometric growth model), expressed as the percentage difference between the upward (H) and downward (L) selection lines.

generation, whatever their cause. Part of the variation will be caused by errors of estimation, but some will be due to differences in the true generation means brought about by external environmental causes, i.e. differences in the size of the selection differential and by genetic sampling. However, unless the selection differential is very variable from generation to generation, and unless the population size is very small and genetic sampling therefore important, the regression line should give a good estimate of the average progress per generation. In linear regressions, the R^2-value gives an indication of the accuracy of fit. Hill (1976) is, however, of the opinion that tests of significance of R^2-values in these situations are not valid, because the values of the different generations are not independent. Such tests of significance may be too lenient. Since no other suitable procedure

exists, it was decided to use R^2 merely as an index of responses which deserve attention (Scholtz et al., 1990a).

Results

From Figure 2 & 4, it is clear that a quadratic regression ($y = c + dx + ex^2$) fitted the correlated response in fitness with selection for $ln (a)$ ($R^2 = 0.47$) and b ($R^2 = 0.25$) best.

The regression estimate for the direct response in $ln (a)$ (Figure 1) was 1.75 ± 0.16 ($P \leq 0.01$). Fitness, however, decreased steadily with selection for $ln (a)$ (Figure 2) until generation 15, whereafter a slight increase was again observed.

The direct response in b (Figure 3) is best described by the quadratic regression $y = 1.32x - 0.03x^2$ ($R^2 = 0.78$). The
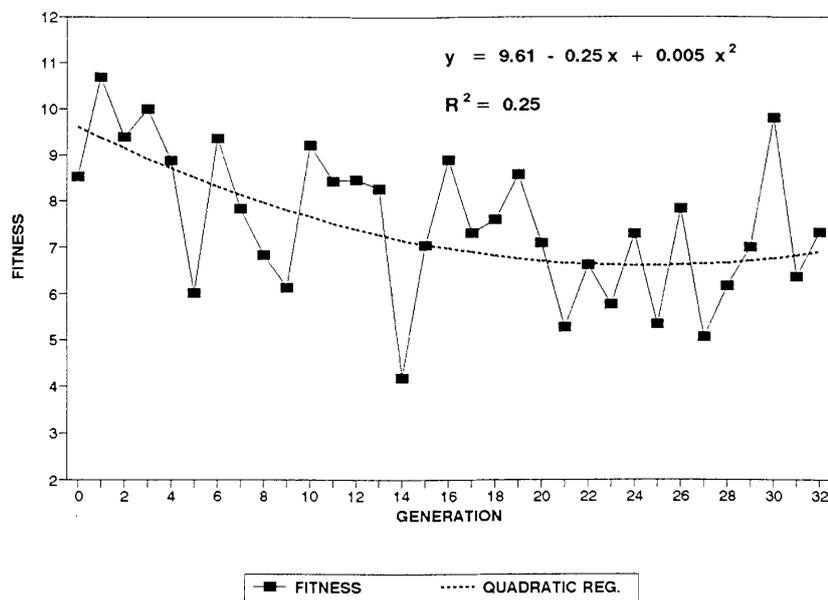
Figure 4 Correlated observed response in fitness (fitness of the upward and downward selection lines combined and expressed in absolute terms) with selection for b (slope of the allometric growth model).

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maximum response in b was obtained in generation 22, while the minimum response in fitness was obtained in generation 25 (Figure 4), showing that the direct response in b and the correlated response in fitness are related.

Discussion

When artificial selection alters the mean of a population in either direction, total reproductive fitness might be expected to decline (Falconer & King, 1953). The results of this study are in accordance with this statement. Long-term selection for the intercept of the allometric growth model resulted in a decline in fitness. At generation 23 selection for $\ln (a)$ was terminated owing to serious problems with fitness, mainly because of litter sizes being too small and too many pre-weaning mortalities.

The correlated response in fitness with long-term selection for the slope of the allometric model and the direct response in b, followed the same pattern, but were mirror images of each other. When a positive direct response was realized in b (generations 0 – 22), fitness decreased as a correlated response (generations 0 – 25). When the direct response in b was delayed (generations 22 – 25), the correlated response in fitness was also delayed (generations 25 – 27) and, when the direct response in b started to decline (generations 26 – 32), the correlated response in fitness started to increase (generations 28 – 32). This is probably the result of natural selection becoming more powerful than artificial selection. There are two stages at which natural selection might operate. Firstly, there might be differential mortality in the young stages, with the result that the superior phenotypes die

Table 1 Effective intensity of selection and the proportion of effective/expected intensity of selection for the $\ln$ (a)H, $\ln(a)$L, bH and bL selection lines, where the expected intensity of selection is 1.163 (one animal out of five)

Generation	$\ln (a)$ H Effective	$\ln (a)$ H Effective/Expected	$\ln (a)$ L Effective	$\ln (a)$ L Effective/Expected	bH Effective	bH Effective/Expected	bL Effective	bL Effective/Expected
1	1.133	0.974	0.979	0.842	1.146	0.985	0.809	0.696
2	1.045	0.899	0.771	0.663	0.967	0.831	1.163	1.000
3	0.841	0.723	0.930	0.800	0.809	0.696	1.147	0.986
4	1.067	0.917	0.909	0.782	1.138	0.979	1.154	0.992
5	0.814	0.700	1.066	0.917	1.080	0.929	0.876	0.753
6	0.973	0.837	0.966	0.831	1.105	0.950	1.063	0.914
7	0.575	0.494	0.400	0.344	0.706	0.607	0.851	0.732
8	0.694	0.597	1.106	0.951	1.142	0.982	0.856	0.736
9	0.658	0.566	0.717	0.617	1.059	0.911	0.802	0.690
10	0.658	0.566	0.710	0.610	1.072	0.922	0.792	0.681
11	0.881	0.758	0.738	0.635	1.130	0.971	0.986	0.848
12	1.128	0.970	1.076	0.925	1.080	0.929	1.021	0.878
13	1.136	0.977	1.001	0.861	1.080	0.929	0.954	0.821
14	0.798	0.686	1.008	0.867	1.033	0.888	1.147	0.986
15	0.916	0.787	1.051	0.903	0.963	0.828	0.983	0.845
16	0.686	0.589	0.725	0.624	0.587	0.505	0.879	0.756
17	0.953	0.819	0.926	0.796	0.909	0.781	0.887	0.762
18	1.038	0.893	0.830	0.714	1.402	0.848	0.980	0.842
19	0.915	0.787	0.546	0.470	0.776	0.667	1.044	0.898
20	0.948	0.812	0.457	0.393	0.731	0.628	0.980	0.842
21	1.056	0.908	1.021	0.878	1.027	0.883	1.000	0.860
22	0.871	0.749	1.058	0.909	1.043	0.897	0.882	0.758
23	0.693	0.596	0.609	0.523	0.622	0.535	0.957	0.823
24	1.032	0.887	0.872	0.750	0.932	0.802	0.855	0.735
25					0.792	0.681	1.092	0.939
26					1.062	0.914	0.732	0.629
27					1.070	0.920	1.108	0.952
28					0.866	0.745	0.942	0.810
29					0.980	0.842	1.024	0.880
30					1.040	0.893	1.029	0.885
31					0.753	0.647	0.966	0.831
32					1.076	0.925	1.113	0.957
Average	0.896	0.770	0.853	0.734	0.974	0.827	0.971	0.835

before the age of measurement. Secondly, there might be differential fertility, when the superior phenotypes leave relatively fewer offspring in the next generation. Both these forms of natural selection would reduce the progress by reducing the selection differential (Falconer & King, 1953). Thus, a difference between the effective and expected intensity of selection is an indication that natural selection is operating against artificial selection (Falconer, 1981). The effective intensity of selection, expressed as a proportion of the expected intensity of selection, was therefore investigated (Table 1) to discover if natural selection was operating against artificial selection. From Table 1, it can be seen that there is no clear pattern in any of the selection lines regarding the proportion effective/expected intensity of selection for all the generations. Great variation exists between these values within each selection line for all the generations (for example from 0.977 (generation 13) to 0.494 (generation 7) or 98% variation in the ln (a)H selection line). Furthermore, in some generations the effective intensity of selection was less than 40% of that expected.

Since no definite decrease occurred in the proportion of the effective/expected intensity of selection for the generations of selection, the presence of natural selection acting against artificial selection can not be detected from the difference between the effective and expected selection intensities in this study. Inbreeding, however, should also play an important role in the responses realized in fitness, since the theoretical inbreeding coefficient was already 41.47% at generation 19.

Roux (1992a) suggested that a fair degree of genetic or physiological canalization for the allometric slope exists. Forcing b beyond its canalized borders by selection, leads to a decline in reproduction and viability. This is supported by the present results in b.

A review by Scholtz et al. (1990) on the consequences of selection for growth, size and efficiency, indicated that selection for increased body mass or growth rate may have an adverse effect on body composition, fertility and survival rate. Selection for increased efficiency, on the other hand, may lead to fewer adverse effects. Siegel & Dunnington (1985) stated that artificial selection for broiler growth created reproductive complications attributable to neuro-endocrine imbalances, disrupted synchrony in gametogenesis, dysfunction in ovulation-oviposition patterns and reduced libido. According to McCarthy & Siegel (1983), these reproductive failures are due to a physiological limit imposed by natural selection, which results in the cessation of response. Because of this, genetically determined limits are seldom reached.

Selection for b and ln (a) have thus an adverse effect on fertility. Using the parameters of the allometric model as selection criteria in selection experiments will, therefore, require that special attention is paid to fertility in the breeding plan. This can be realized by concurrent selection for fertility (Scholtz et al., 1990c), or, for example, in the poultry industry, by selecting the male lines for the parameters of the allometric model and the female lines for growth and reproductive performance. Selection within the female lines has always included the early assessment of growth and conformation, followed by attention to egg production, fertility and hatchability at various levels (Hunton, 1990). The current situation is that for an efficient broiler female line, selection has to be practised for a combination of growth

and fertility with quite a heavy accent being placed on growth rate.

It is known that the pattern for long-term response is diverse and unpredictable (Yoo, 1980) and that the results for a single selection line are disappointingly unreliable (Hill, 1972). The question therefore arises as to how repeatable the results of this study are. According to Eisen (1974), an effective population size of 20 is sufficient for most selection experiments to accommodate drift variance and the variability of selection response. Since the effective population size of this study was 18 (Mostert et al., 1994), it seems sufficient for drawing general conclusions.

Conclusion

The parameter, b, of the allometric model, seems to be a better alternative to conventional breeding objectives in the broiler industry. Selection for b increases efficiency and alters growth rate without increasing final body mass. Selection for the parameters of the allometric model, however, has an adverse effect on fertility, so special attention should be given to fertility in a breeding plan when the parameters of the allometric model are used as selection criteria.

Acknowledgements

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