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THE ALLOMETRIC–AUTOREGRESSIVE MODEL IN GENETIC STUDIES: HERITABILITIES AND CORRELATIONS IN THE RAT*

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(Sleutelwoorde. *Rot, groeimodel, oorerflikhede, korrelasies)*

OPSOMMING: DIE ALLOMETRIESE–OUTOREGRESSIEWE MODEL IN GENETIESE STUDIES: OORERFLIKHEDE EN KORRELASIES BY DIE ROT

Die allometriese-outoregressiewe kwantifisering van groei en doeltreffendheid verdeel rotgroei in 3 verskillende fisiologiese fases. Betekenisvolle verskille tussen families vir sommige van hierdie parameters kom voor. Die oorerflikhede, en fenotipiese en genetiese korrelasies is gevolglik vir die verskillende parameters beraam. Sommige van die parameters toon betekenisvolle oorerflikhede terwyl ander oorerflikhede van nul toon. Die verskillende korrelasies tussen die parameters wissel van sterk negatief of positief tot korrelasies van feitlik nul. Hoewel die aantalle waarop hierdie beramings gebaseer is, relatief klein is, is die verkreë beramings biologies sinvol. Selfs as slegs die onderste grense van die betroubaarheidsintervalle van die betekenisvolle oorerflikheidsberamings geneem word, word redelik hoë oorerflikhede verkry. Die beramings van oorerflikhede van sommige parameters wat na aan nul was, word in die lig van moontlike homeostatiese effekte verklaar, terwyl die betekenis van die ander beramings ook bespreek word.

SUMMARY:

The allometric-autoregressive quantification of growth and efficiency divides rat growth into 3 different physiological phases. Significant differences between families for some of these parameters existed. Consequently, heritabilities and, phenotypic and genetic correlations of the different parameters were estimated. Significant heritabilities were found for some of the parameters, while the heritabilities for others were close to zero. The correlations between the parameters varied from highly positive or negative to correlations of practically zero. Although based on few animals, the heritability estimates appear to be reasonably acceptable, both statistically and in their biological context. The heritability estimates which approach zero for some parameters are discussed in the light of possible homeostatic effects and the implications of the different estimates are evaluated.

The application of an allometric-autoregressive model in the quantification of growth and efficiency of feed utilization for purposes of selection for efficiency and growth has been discussed by Scholtz & Roux (1980). This model is based mainly on the following 2 equations.

(1) The well known allometric function to describe efficiency namely:

$$w = av^b$$

or

$$\ln w = \ln a + b \ln v, \qquad (1)$$

where w = body mass and v = cumulative feed intake (Roux, 1976). Slope (b) and intercept (ln a) can thus be estimated by linear least squares procedures.

(2) The equation for cumulative feed intake is (Roux, 1976; 1980):

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

or

$$x(t) = (\alpha_x - x(0))\,\rho^t + \sum_{j=0}^{t-1} \rho^j \varepsilon(t-j), \qquad (2)$$

where $x(t)$ = ln (cumulative feed intake) at time t,

$x(0)$ = ln (cumulative feed intake) at time O.

Further, if $t \to \infty$ then $x \to \alpha_x$, if $|\rho| < 1$.

A similar equation holds in w (body mass).

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Scholtz & Roux (1980) reported in a previous publication that rat growth and efficiency can be divided into 3 different growth phases by this model, each of which can be described by a straight line in terms of slope and intercept. These different growth phases are associated with the physiological processes of the rat.

Significant differences between families for both slope and intercept in the first 2 phases and for x (O) in all 3 phases were reported by Scholtz & Roux (1980). These significant differences between families are an indication that the allometric-autoregressive quantification of growth and efficiency of feed utilization may be of value in the selection of animals for efficiency of feed utilization, or in changing the growth curves of animals. Genetic parameters such as heritabilities and correlations are therefore reported in this publication.

The numbers on which these heritabilities and correlations were based are in some instances too small to obtain accurate estimates. Preliminary indications of what to expect may, however, serve an important purpose in suggesting further topics for research and methods to be used in such investigations. Several suggestions are made in the Discussion.

Materials and Methods

Animals

Ninety rats, from the outbred Wistar line, consisting of 10 families with 8 to 10 rats each, were used in the experiment. Litter size was standarized and the animals were maintained in standard cages under conventional conditions and controlled environmental conditions. The details have been reported by Scholtz & Roux (1980).

Data

Details of data collection and procedures followed to estimate the different parameters have been described by Scholtz & Roux (1980).

Heritability estimation

In this experiment a male was mated to only one female, so that all families consisted of full sibs (FS) only. The heritability (h^2) can thus be estimated by the following equation (Falconer, 1964):

$$h^2 = 2t_{FS} = \frac{2\sigma_B^2}{\sigma_T^2} \qquad (3)$$

where t_{FS} is the intraclass correlation, σ_B^2 is the between family variance, and σ_T^2 is the total variance. Values of σ_B^2 and σ_T^2, where $\sigma_T^2 = \sigma_B^2 + \sigma_W^2$, and where σ_W^2 is the within family variance, are therefore required for estimation of h^2. For estimation purposes a mixed model was used with sexes as the fixed variable and families and progeny within families as the random variable. Table 1 shows the expected values of the mean squares (MS) in a two-way analysis of variance (Snedecor & Cochran, 1967). σ_B^2 can be calculated from the mean squares for B in Table 1,

Table 1
Expected values of Mean Squares in a two-factor experiment

Mean Squares	Mixed model, A fixed, B random
A	$\sigma_W^2 + k\,\sigma_{AB}^2 + k\,n\,\sigma_A^2$
B	$\sigma_W^2 + ks\,\sigma_B^2$
AB	$\sigma_W^2 + k\,\sigma_{AB}^2$
error	σ_W^2

where s is the number of sexes, n is the number of families, k is the number of individuals per family, A is sexes and B is families.

$$\sigma_B^2 = \frac{MS_B - MS_E}{ks}$$

where $\sigma_W^2 = MS_E$ which is directly available from the analysis of variance table. According to Snedecor & Cochran (1967) varying family sizes can be accommodated by

$$k = \frac{1}{(n-1)}\left(N - \frac{\Sigma\, k_i^2}{N}\right),$$

where N is the total number of animals, and k_i is family size of the i – th family.

The confidence intervals of t_{FS} were calculated according to Graybill (1961), Turner & Young (1969), and Searle (1971) as follows:

$$P\left\{\left[\frac{MS_{error}\, kF_{1-\alpha/2}}{MS_B + MS_{error}(k-1)F_{1-\alpha/2}}\right] \leq \frac{\sigma_W^2}{\sigma_B^2 + \sigma_W^2} \leq \left[\frac{MS_{error}\, kF_{\alpha/2}}{MS_B + MS_{error}(k-1)F_{\alpha/2}}\right]\right\} = 1 - \alpha$$

where, $F_{1-\alpha/2}$ and $F_{\alpha/2}$ are the lower and upper limits corresponding to a confidence level of $(1-\alpha)$ for an F distribution. Bearing in mind that $h^2 = 2t$, the confidence interval for h^2 from Turner & Young (1969) is,

$$P\{2(1-C_1) \geq h^2 > 2(1-C_2)\} = 1-\alpha,$$

where C_1 and C_2 are the upper and lower limits of the interval respectively.

Correlations

The 3 types of correlations, viz., phenotypic (r_P) genetic (r_G) and environmental (r_E) were calculated between the different parameters by the methods given by Becker (1967). The standard errors of the correlations were calculated according to Scheinberg (1966).

Results

The average values and standard deviations of the different parameters were as described by Scholtz & Roux (1980). The values of σ^2_B and σ^2_T for all the parameters were calculated from the analyses of variance tables and are given in Table 2 for purposes of possible future experimental design.

Table 2

Values of σ^2_B and σ^2_T for the parameters in the different phases

	Phase	ℓn a	b	ρ	α_x	α_y	x (O)
	1.	$4{,}508 \times 10^{-3}$	$1{,}190 \times 10^{-4}$	$7{,}000 \times 10^{-4}$	$7{,}760 \times 10^{-4}$	$9{,}682 \times 10^{-4}$	$1{,}800 \times 10^{-3}$
σ^2_B	2.	$7{,}806 \times 10^{-3}$	$2{,}050 \times 10^{-4}$	$3{,}010 \times 10^{-6}$	$3{,}691 \times 10^{-4}$	$-2{,}480 \times 10^{-4}$	$5{,}869 \times 10^{-4}$
	3.	$-4{,}730 \times 10^{-4}$	$-7{,}800 \times 10^{-5}$	$-1{,}000 \times 10^{-5}$	$-9{,}595 \times 10^{-3}$	$4{,}438 \times 10^{-4}$	$1{,}126 \times 10^{-3}$
	1.	$1{,}918 \times 10^{-2}$	$7{,}550 \times 10^{-4}$	$1{,}657 \times 10^{-4}$	$5{,}326 \times 10^{-2}$	$1{,}973 \times 10^{-2}$	$7{,}292 \times 10^{-3}$
σ^2_T	2.	$4{,}136 \times 10^{-2}$	$1{,}111 \times 10^{-3}$	$6{,}600 \times 10^{-5}$	$1{,}032 \times 10^{-1}$	$2{,}989 \times 10^{-2}$	$3{,}118 \times 10^{-3}$
	3.	$3{,}056 \times 10^{-1}$	$6{,}313 \times 10^{-3}$	$3{,}350 \times 10^{-3}$	$8{,}444 \times 10^{-1}$	$2{,}746 \times 10^{-1}$	$3{,}285 \times 10^{-3}$

Table 3

Heritability estimates and confidence limits for the parameters in the different phases

	Phase	ℓ_n a	b	ρ	α_x	α_y	x (O)
h^2	1	0,47	0,32	0,08	0,03	0,10	0,49
		0,33 – 1,41	0,18 – 1,21	–0,05 – 0,73	–	–0,04 – 0,77	–
	2	0,43	0,38	0,08	0,01	–0,02	0,38
		0,30 – 1,37	0,25 – 1,31	–0,06 – 0,71	–	–0,15 – 0,35	–
	3	–0,09	–0,61	–0,06	–0,02	0,69	0,69
		–	–	–0,19 – 0,13	–	–0,13 – 0,44	–

Table 4

r_P, r_G and r_E within and between a and b within and between phase 1 and 2

	r_P	r_G	r_E
a_1 b_1	– 0,97 ± 0,21	– 0,96 ± 0,42	– 0,99 ± 0,26
a_2 b_2	– 0,95 ± 0,21	– 0,96 ± 0,43	– 0,94 ± 0,20
a_1 a_2	0,20 ± 0,19	0,76 ± 1,34	– 0,21 ± 0,21
a_1 b_2	– 0,18 ± 0,18	– 0,67 ± 1,21	0,17 ± 0,18
a_2 b_1	– 0,05 ± 0,16	– 0,67 ± 3,83	0,28 ± 0,98
b_1 b_2	0,06 ± 0,18	0,65 ± 3,15	– 0,24 ± 0,72

Subscript indicates phase

The different heritabilities were estimated using equation 3. Confidence intervals for some of the heritabilities were calculated to illustrate the accuracy of the heritability estimates for the different magnitudes (Table 3).

The different correlations, r_P, r_G and r_E within and between ln a and b within and between phases 1 and 2, where significant differences between families exist, were estimated, and the standard deviations calculated (Table 4).

The phenotypic and genetic correlations between all the parameters involved (ln a, b, ρ, α_x, α_y and x (O)) within and between all the growth phases were estimated and are represented in Table 5. The 95% confidence intervals for some of the phenotypic correlations were estimated from the graphs of Beyer (1968), to illustrate the confidence intervals which can be expected from the numbers involved and for the range of correlation coefficients recorded. The phenotypic correlations are given above the diagonal and the genetic correlations below the diagonal in Table 5.

Discussion

Heritabilities of ln a and b

The significant heritabilities of ln a and b in phases 1 and 2 (Table 3) indicate that progress in selection can be expected for either of the 2 parameters. All these heritabilities are between 0,3 and 0,5. The heritability estimates of ln a and b obtained for the third phase are unrealistic. The numbers on which the estimates are based are too small to provide accurate estimates. As judged by the lower limits of the interval, it would appear that the estimates in phases 1 and 2 indicate heritabilities of considerable magnitude, although the confidence intervals are rather wide.

The magnitude of these heritability estimates is in agreement with the heritability estimates of the conventionally accepted description of efficiency. Johannson & Rendel (1969) quote heritability estimates for efficiency of 0,26 – 0,60 for pigs, 0,36 – 0,42 for cattle and of approximately 0,29 for sheep.

It appears that the allometric part of this allometric-autoregressive model may be of value in selection for efficiency, as both ln a and b are directly proportional to growth efficiency, where growth efficiency can be defined as either $\frac{w}{v} = av^{b-1}$ or $\frac{dw}{dv} = abv^{b-1}$. Since the allometric parameters show significant heritabilities, it is possible to use this model to change the entire efficiency curve of animals in a predictable manner. This would appear to be of value as opposed to the conventional approach with its focus on specific growth intervals.

Other heritabilities

It is of interest to note that the parameters ρ and α_x apparently have heritabilities of close to zero (Table 3). If this is the true situation, it would appear that these values tend to be fixed for certain environments, whatever the genetic constitution of a rat from a particular strain. This is analogous to the way in which, say, a four-chambered heart is a fixed feature of a rat. Thus, heritabilities of zero may be evolutionary in origin with factors involved such as canalization, adaptive norms and stabilizing selection. Further details of these factors have been described by Dobzhansky (1970). Balch & Reid (1976) maintain that feed intake, and therefore also growth rate, are part of the natural mechanisms which control homeostatis in the animal body. The inherent capacities for growth must, therefore, be kept within certain fixed limits to maintain homeostasis (Balch, 1973). According to this author the importance of feed intake as an active controlling agent in the maintenance of homeostasis is also reflected in the fact that certain areas of the hypothalamus appear to have as their prime function the co-ordination of intake behaviour. Balch & Reid (1976) believe that deviations from the homeostatic limits may result in metabolic disorders and even death. Accordingly, if this argument is valid, one would expect the parameters ρ and α_x, which quantify feed intake, to be canalized.

The heritability estimates for limit mass, α_y, is non-significant in the first 2 phases, while it is high (0,69) in the third phase (Table 3). A limit value for body mass in the first 2 phases is not of direct practical importance, since the animals switch to a different phase before the limit is reached. A limit value for body mass in the third phase is, however, directly meaningful, since in this phase α_y is a measure of the mature mass that the animal may reach. Mature mass is highly heritable and Johannson & Rendel (1968) found the heritability to be 0,40 for sheep and cattle.

On ignoring the error terms in equation 2, the following equation for growth rate can be derived:

$$\frac{dw}{dt} = \gamma w \ln \left(\frac{\alpha_w}{w(0)}\right) \exp(-\gamma t) \quad (4),$$

where y (0) is body mass at time t = 0, and $\gamma = -\ln \rho$. From the equation it is therefore evident that the parameters by which growth rate $\left(\frac{dw}{dt}\right)$ can be altered are

γ and α_W. However, γ ($= -\ln \rho$) has a heritability of zero, so that only α_W (mature size) with a sizeable heritability remains. This is in agreement with Eisen's (1976) remark that the parameters analogous to γ, which are proportional to growth rate, of some of the growth functions most widely used in the past have estimated heritabilities of approximately zero. Furthermore, all the equations of these functions include mature or final mass (Eisen, Lang & Legates, 1969), for which Johannson & Rendel (1968) give heritability estimates ranging from 0,4 to 0,8. This conclusion is in agreement with the observation of Webster (1980) that differences in growth rate in cattle are mainly due to differences in size.

The heritability estimates for x (0) (cumulative feed intake at the beginning of a phase) is significant in all 3 phases. This is expected, as the amount of feed consumed up to a particular age should be heritable since it is related to body mass at that point.

Correlations involving ln a and b in phase 1 and 2

Very high negative correlations (approximately –0,96, for r_P, r_G and r_E) exist between ln a and b of the same phase (Table 4). The standard errors of r_P and r_E are reasonably small, in all cases less than a quarter of the correlation. The standard error of r_G, however, is relatively large. The high negative correlations between ln a and b of the same phase are not present between ln a and b of different phases. These high negative correlations between ln a and b of the same phase lead to practical problems, since both are directly proportional to growth efficiency, where growth efficiency can be defined as either $\frac{w}{v} = av^{b-1}$ or $\frac{dw}{dv} = abv^{b-1}$. Hence the negative correlations indicate that efficiency at any point is a compromise between the benefits of a large a and a large b, with a large a probably important for efficiency early in a phase and b important in the long term (Roux, 1980). It thus appears that selection for efficiency at a certain age will probably result in an optimal combination of a and b. A case in point is the comparison of Meissner (1977) between Karakuls and Mutton Merinos. Meissner (1977) found that Mutton Merinos had a larger a and a lower b than Karakuls on a concentrate diet. It is likely that the Mutton Merino was indirectly selected for efficiency as a correlated response to selection for growth rate at an early age, since according to Johannson & Rendel (1968) growth rate and efficiency of feed utilization are positively related.

The high negative correlation between ln a and b of the same phase is probably due to geometric as well as genetic causes. The geometric effect is illustrated by

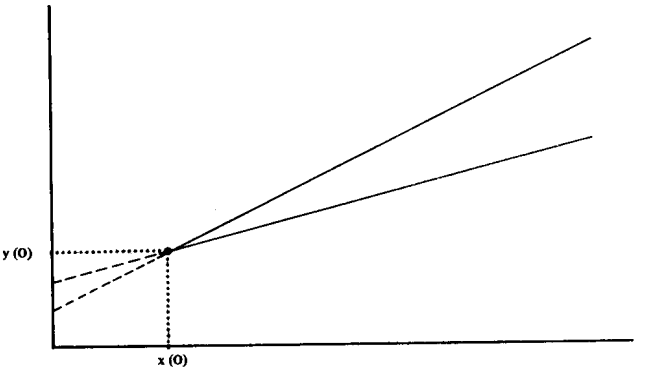

Fig. 1 Illustration of geometric effects

Fig. 1. The equation for a straight line through the point x (O), y (O) is

$$y = \ln a + b\,x$$

with

$$\ln a = y(O) - bx(O)$$

where y(O) and x(O) are respectively ln (body mass) and ln (cumulative feed intake) at the starting point, t = O. It is clear from Fig. 1 that if b increases a will decrease if y(O) and x(O) are kept constant. It thus appears that the mathematics of the model may be a contributing cause of the extremely high negative correlations between ln a and b of the same phase. It seems that, in this situation, the only suitable manner to differentiate between geometric and genetic causes would be to conduct a selection experiment.

The phenotypic correlation of all parameters between phases are low, being less than | 0,2 | (Table 4). This indicates that an animal (rat) with a good performance as measured by slope or intercept in one phase, does not necessarily have a good performance in another phase. It may, therefore, be of importance to take possible growth phases in to consideration in performance testing, since the performance of an animal in one phase may be a poor indication of its performance in another phase. These phenotypic correlations correspond with estimates of Meissner (1977) on sheep. It is, however, interesting that the genetic correlation of the same parameter between different phases is relatively high, greater than 0,65 (Table 4).

Other correlations

The phenotypic correlations between the parameters of the time relationship, ρ, α_x and α_y (Table 5) within

Table 5

The phenotypic and genetic correlations of the parameters of the allometric-autoregressive model in all the growth phases

	a_1	b_1	ρ_1	α_{x_1}	α_{y_1}	$x_1(O)$	a_2	b_2	ρ_2	α_{x_2}	α_{y_2}	$x_2(O)$	a_3	b_3	ρ_3	α_{x_3}	α_{y_3}	$x_3(O)$
a_1		− 0,97**	− 0,05	− 0,02	− 0,16	0,06	0,20	− 0,18	− 0,08	0,08	0,00	− 0,08	0,31**	0,33**	0,00	− 0,09	− 0,05	0,05
b_1	− 0,96		0,08	0,07	0,28** 0,10–0,46	0,02	− 0,05	0,06	0,05	− 0,10	0,01	− 0,09	0,30**	− 0,30**	0,01	0,08	0,07	0,08
ρ_1	− 0,02	0,03		0,92**	0,81**	0,13	0,11	− 0,11	0,13	0,06	− 0,01	− 0,05	0,05	− 0,05	0,00	− 0,16	− 0,17	− 0,11
α_{x_1}	0,14	− 0,01	0,88		0,94** 0,91–0,97	0,15	0,10	0,11	0,07	0,04	− 0,01	0,01	0,00	− 0,01	− 0,03	− 0,15	− 0,14	0,05
α_{y_1}	0,23	0,01	0,55	0,89		0,21*	0,23* 0,04–0,42	0,19	0,06	0,00	− 0,01	− 0,23*	0,01	− 0,54**	− 0,03	− 0,05	− 0,10	0,21*
$x_1(O)$	0,79	− 0,67	0,66	0,90	0,87		0,23*	− 0,19	0,05	0,05	− 0,01	− 0,17	0,18	− 0,14	− 0,02	0,03	0,04	0,48**
a_1	0,67	− 0,67	− 0,42	− 0,65	− 0,05	1,13		− 0,95** 0,93–0,97	0,27**	− 0,15	− 0,30**	− 0,46**	− 0,13	0,14	− 0,06	− 0,12	− 0,10	0,24*
b_1	− 0,67	0,65	0,55	1,04	0,41	− 0,87	− 0,96		0,34**	0,20	0,39**	0,34**	0,17	− 0,17	0,08	0,13	0,13	− 0,16
ρ_1	− 0,34	0,32	1,53	2,01	0,91	0,12	− 0,90	0,93		0,82**	0,74** 0,61–0,81	0,17	0,16	− 0,13	0,31**	− 0,08	− 0,12	− 0,14
α_{x_2}	− 0,82	0,42	3,58	5,01	0,53	0,00	− 0,94	0,46	0,27		0,71** 0,60–0,80	0,22	− 0,03	0,05	0,32**	− 0,19	− 0,33**	0,01
α_{y_2}	0,49	0,51	1,51	3,61	0,72	0,00	− 0,60	0,77	− 0,05	0,87		0,10	− 0,04	0,08	0,28**	− 0,16	− 0,13	0,07
$x_2(O)$	0,55	0,31	− 0,17	− 0,13	− 0,56	− 0,81	− 0,67	0,44	0,08	0,00	0,00		− 0,18	0,14	0,14	− 0,20	− 0,25*	− 0,27**
a_3	0,01	0,81	− 1,00	− 3,10	− 0,83	0,00	− 0,12	− 0,93	− 0,57	0,74	− 4,33	0,00		− 0,99**	− 0,30**	0,48** 0,33–0,62	0,36**	0,08
b_1	0,11	− 0,06	− 0,07	0,17	0,21	0,00	− 0,04	0,09	0,17	− 0,10	0,32	0,00	− 0,84		0,03	− 0,55**	− 0,37**	− 0,02
ρ_3	− 0,39	0,16	− 0,48	− 1,36	0,03	0,00	− 0,13	0,22	0,18	2,39	− 0,72	0,00	0,82	− 0,31		− 0,12	− 0,18	0,24*
α_{x_3}	0,00	− 0,32	0,12	0,07	− 0,61	0,00	− 0,17	− 0,05	− 0,01	0,58	− 0,27	0,00	0,54	− 0,11	0,11		0,95** 0,93–0,97	0,18
α_{y_1}	0,05	1,03	− 0,61	− 0,11	0,37	0,00	0,81	0,10	− 0,22	− 3,99	0,47	0,00	− 0,42	0,87	− 0,35	0,91		0,23
$x_3(O)$	0,62	− 0,47	0,23	0,90	0,75	0,92	0,01	− 0,64	− 0,24	0,00	0,00	− 0,55	0,00	0,00	0,00	0,00	0,00	

Phenotypic correlation – above the diagonal, genetic correlation – below the diagonal.

Subscript indicates phase.

the first two phases are high (0,71 – 0,94). This is also true for most of the genetic correlations. This confirms the belief that these parameters are functionally interrelated. The high phenotypic and genetic correlations between the time relationship parameters for feed intake (α_x) and body mass (α_y) within all 3 phases (r_P = 0,71 – 0,95 and r_G = 0,87 – 0,91) is expected, since mass (output) is dependent on intake (input) within a physiological phase (Table 5). There is, however, no significant correlation between corresponding time relationship parameters in the different physiological phases, except between ρ_2 and ρ_3 where the phenotypic correlation is 0,31. This is in agreement with the previous conclusion that the rating of a rat in one phase is a poor indication of its rating in another phase.

Conclusion

It seems that the model which has been described may be useful in understanding some of the consequences of selection for growth and efficiency, since the effect of such selection can be studied on parameters which can be biologically interpreted. Evidence for the association between the parameters of the model and the physiological processes of animals follows from the observation that the homeostatic mechanisms and limits seem to correspond with the values of the estimates of the heritabilities and genetic correlations of the parameters.

A selection experiment is presently being conducted to investigate the nature of the relationship between slope and intercept. In an additional group, with selection for a high γ (see equation 4) an immediate reduction in fitness characters, such as litter size and survival to weaning, occured as a correlated response. This strongly indicates antagonism between natural and artificial selection through the agency of embryonic deaths or low fertility of individuals with extreme values of γ.

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