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THE ALLOMETRIC-AUTOREGRESSIVE MODEL IN GENETIC STUDIES: DIFFERENT PHYSIOLOGICAL PHASES IN THE RAT*

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(Sleutelwoorde: *Rot, groeikurwes, groeimodelle, fisiologiese fases)*

OPSOMMING: DIE ALLOMETRIESE-OUTOREGRESSIEWE MODEL IN GENETIESE STUDIES: VERSKILLENDE FISIOLOGIESE FASES BY DIE ROT

Die gebruik van 'n allometriese-outoregressiewe model vir die kwantifisering van groei en doeltreffendheid van voerverbuik vir doeleindes van seleksie vir doeltreffendhied word bespreek. Groei en doeltreffendheid tot by volwassenheid van die rot word deur hierdie model in 3 verskillende groeifases opgedeel. Elke fase word deur 'n reguit lyn in terme van helling en afsnit beskryf, en daar word aangetoon dat die verskillende groeifases geassosieer is met fisiologiese prosesse in die rot. Betekenisvolle verskille is tussen families vir sommige van die parameters in die eerste 2 fases gevind. Dit dui daarop dat die model van waarde kan wees in die seleksie van diere vir groei en doeltreffendheid. Die genetika van die parameters betrokke sal in 'n volgende artikel bespreek word.

SUMMARY:

The application of an allometric-autoregressive model for the quantification of growth and efficiency of feed utilization for purposes of selection for efficiency is discussed. To maturity rat growth and efficiency can be divided into 3 growth phases by this model. Each phase is described by a straight line in terms of slope and intercept, and the different growth phases are shown to be associated with physiological processes in the rat. There are significant differences between families for some of the parameters in the first 2 phases. This indicates that the model may have possibilities in the selection of animals for growth and efficiency. The genetics of these parameters will be discussed in a subsequent article.

The first step in any breeding programme is the formulation of breeding aims. In a production system the aim must be directed towards achieving optimal product output (meat, wool, etc.) for any input (feed intake). Existing knowledge indicates that efficiency of feed utilization varies with age and body mass. In practice this implies that the animal selected from a population will depend on the age and/or mass on which the animals are evaluated. If consumer preferences and future demand remain static, this will be no problem: it will be necessary only to fix the point of preference and to select for efficiency at that point. It is, however, known that consumer preferences and market requirements change with concommitant changes in taste and technology. An example is the consumer preference for leaner meat in recent times.

To overcome these problems the complete growth curve of an animal must be known. If this is known, comparisons can be made at any point or interval of interest, otherwise a major experimental effort will be required every time a new point of interest arises. A suitable mathematical model that approximates a set of growth and intake data well, will therefore be a valuable asset in the reliable evaluation of growth and efficiency.

Early work dates back to that of von Bertalanffy (1938) and previous workers, with revived interest in recent years as documented by von Bertalanffy (1960), Needham (1964), Lodge & Lamming (1967), Eisen, Lang & Legates (1969) and Timon & Eisen (1969), with that of Parks (1970, 1972, 1973, 1975(a), 1975(b)) representing possibly the most satisfactory attempt. However, the main objection against Parks' functions is that they show a non-random distribution of observations around the fitted curves (Roux, 1976). At least from the point of view of statistical criteria of goodness of fit, it seems, therefore, that the most acceptable model is that described by Roux (1974, 1976).

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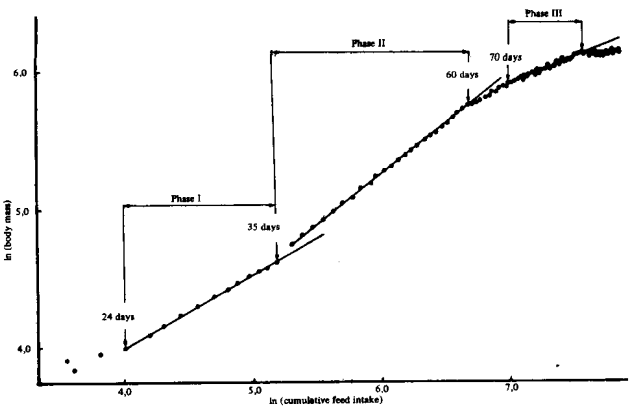

Fig. 1 Plot of ln (cumulated feed intake) against ln (body mass) of a single male rat

The theory described by Roux (1974, 1976, 1980) has been successfully used to quantify different types of growth responses in nutrition studies (Meissner, Roux & Hofmeyr, 1975; Meissner, 1977; Meissner, Hofmeyr & Roux, 1977; Siebrits, 1979; Roux & Kemm, 1980). This description of efficiency of production may also be of value in genetic studies. Its possibilities are therefore being further investigated.

It was decided to use the white rat *(Rattus domesticus)* to investigate the possibilities of this allometric-autoregressive model for genetic studies, since the experimental period and costs are reduced. The relationship between laboratory animals and farm animals is nowadays widely acknowleged. This acceptance derives from the basic similarity of the biochemical processes underlying the physiology of organisms over the whole spectrum of life. The pathways from gene to physiological action are also very similar within classes such as mammals or even within subphyla such as vertebrata. The genetic mechanism of inheritance is furthermore similar for all cross-fertilizaing organisms. There may, however, be restrictions on the extrapolation of nutritional findings

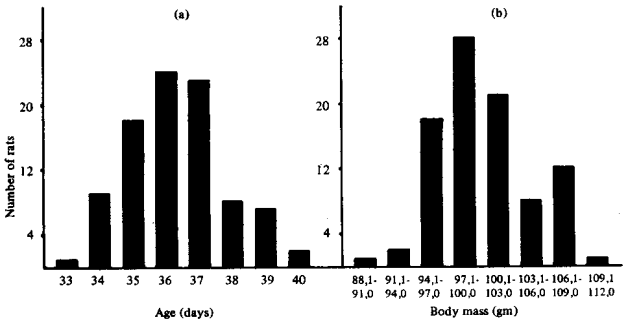

Fig. 2(a) Distribution of age on which rats reach the first breaking point
(b) Distribution of body mass on which rats reach the first breaking point

from the rat to a ruminant. Nonetheless, with the necessary care the laboratory animal can be useful in preliminary investigations or in the elucidation of general biological principles.

Materials and Methods

Model

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

$$y = ax^b$$

or

$$\ln y = \ln a + b \ln x \qquad (1)$$

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

$$(x(t) - \infty_x) = \rho(x(t-1) - \infty x) + \varepsilon(t) \qquad (2)$$

or

$$x(t) = \infty_x - (\infty_x - x_{(0)})\ \rho^t + \sum_{j=0}^{t-1} \rho^j\ \varepsilon(t-j)$$

where x (t) = ln (cumulative feed intake) at time t
x (0) = ln (cumulative feed intake at time 0.

Further, if $t \rightarrow \infty$ then $x \rightarrow \infty x$, if $|\rho| < 1$

A similar equation holds in y.

Animals

Ninety rats, from the outbred Wistar line, consisting of 10 families with 8 to 10 rats each were used in the experiment. Litter sizes were standarized at 12 pups and they were weaned at 21 days of age. The animals were maintained in standard cages under conventioanl conditions. Room temperature was kept at 21 ± 2°C with a relative humidity of 35 – 50%. There was an artificial lighting regime with 12 hours of simulated daylight. After weaning the rats were placed in individual cages, and their body mass and cumulative feed intake were measured daily without witholding them from feed and water prior to measurement. This was done up to an age of 120 days.

Estimation of preweaning energy intake

The mass of the rats at 21 days of age is a function of the milk production of the dams and the prenatal energy consumption of the foetus. It is, however, very difficult to determine the prenatal energy consumption and frequently impractical to determine the milk production

if many dams are involved. A preliminary experiment was thus carried out to find a way in which these values can be estimated by using litter mass, which is easily obtainable (Scholtz & Roux, 1980). The assumption was that the allometric equation, ln z = ln a + b ln u (where, z = cumulative energy intake and u = litter mass) gives a fair indication of the cumulative preweaning energy intake (μ). However, pups suckle as a litter and not as individuals. A method of dividing the μ of a litter within the individuals of the litter was therefore also developed by Scholtz & Roux (1980), and was used in this experiment.

Results

The relationship between growth and feed intake was established by plotting ln (cumulative feed intake)(X-axis) against ln (body mass) (Y-axis). A typical graph is presented in Fig. 1. From Fig. 1 it is evident that the post weaning growth can be divided in 3 growth phases, each described by a straight line in terms of slope and intercept. The phases are (1) a first phase from 24 to approximately 36 days, (2) a second phase from approximately 37 to 60 days, and (3) a third phase from 70 days onwards; with a transitional period between 60 and 70 days of age, which is probably the stage when sexual maturity is reached. Days 21, 22 and 23 do not fit the line describing the first phase and had to be deleted from statistical analyses. These deviations are presumably the result of weaning shock and the change in diet from milk to solids.

The first break in the growth curve (Fig. 1) at approximately 36 days is very evident, and the exact day was identified for all 90 rats involved. It does not occur at the same age for all rats, however. There is also variation in mass between rats at this point. Two histograms, Figures 2 (a) and (b), respectively show the distribution of age and mass at this point. The average age is 36,3 ± 1,5 days and the average body mass 100,2 ± 4,2 gm. The correlation between age and mass at this point is –0,35, which is significant at the 1% level. A noticable tendency for heavier rats to reach this point earlier is therefore present.

The autoregressive relationship was also plotted with ln (cumulative feed intake) at time (t-1) on the X-axis and ln (cumulative feed intake) at time t on the Y-axis (Fig. 3). Fig. 3 shows that the breaking points of the allometric and autoregressive plots correspond. The lines drawn to the graphs were fitted by hand, merely to guide the eyes of the reader. The use of a transparent ruler is suggested when scrutinising the graphs.

To eliminate the possibility that these breaking points in the growth and efficiency curves may be due to the transformation of the data, the plots were repeated on the untransformed data. Cumulative feed intake (X-axis)

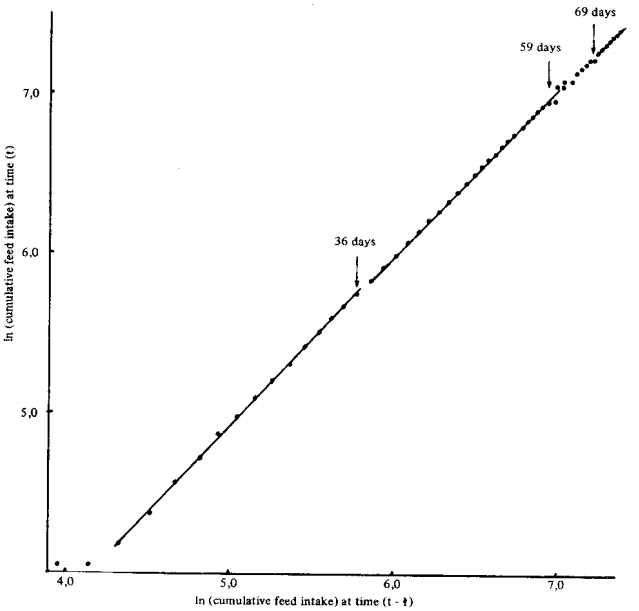

Fig. 3 Plot of autoregressive relationship of a single male rat

was plotted against body mass (Y-axis) on the arithmetic scale (Fig. 4). From Fig. 4 it is evident that the breaking points are also discernable on the arithmetic scale, so that no possibility exists of the breaking points being artefacts of the logarithmic transformation. The breaking points were probably not noticed by other workers since it is more difficult to notice systematic departures from a curve than from a straight line.

After the identification of the different growth phases, a linear regression analysis was done for each rat for each of the 3 growth phases. Slope (b) and intercept (ln a) were thus calculated for each rat in the different phases. The averages for males and females are given in Table 3. The regression analyses show an extreme accuracy of fit with averages of the individual correlation coëfficients of more than 0,99 for the first two phases. The values of the average correlation coëfficients are given in Table 1.

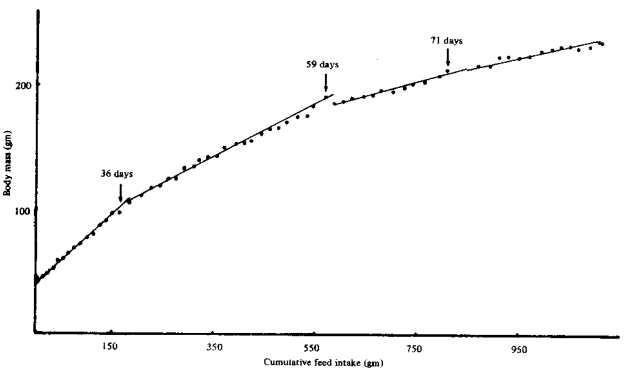

Fig. 4 Cumulative feed intake versus body mass on the arithmetic scale of a single male rat

Table 1

Average correlation coëfficients of the individual regression analyses

Phase	1	2	3
♂	0,9976	0,9983	0,9850
♀	0,9980	0,9949	0,9657

It is possible to test for the adequacy of a first order autoregressive process by testing h_2 for significance in the model (Roux, 1980):

$$x_1(t) = g + h_1 x_1(t\text{-}1) + h_2 x_2(t\text{-}2) + \varepsilon(t), \quad (3)$$

where ln (cumulative feed intake) is often the most suitable variable, since it can often be measured with greater accuracy than body mass. This test was carried out on one male and one female randomly selected from each family. The results are given in Table 2. It can be seen from Table 2 that h_2 is significant in only a few cases. Furthermore ρ (vide equation (2)) was calculated using the usual least squares estimate, namely:

$$\rho = \frac{\Sigma (w - \bar{w})\ (v - \bar{v})}{\Sigma (w - \bar{w})^2}$$

where, w = ln (cumulative feed intake) at time (t-1)
and v = ln (cumulative feed intake) at time t.

∞_x was calculated as follows:

$$\infty_x = \frac{c}{1 - \rho} \quad \text{where } c = \bar{v} - p\bar{w}$$

The values of x(0) were taken directly from the observations. The averages of ρ, ∞_x and x(0) of the different phases are also given in Table 3.

There is a considerable amount of variation between sexes and families for some of the parameters calculated for each phase. A two-way analysis of variance was therefore carried out and the F values are presented in Table 4.

Table 2

Tests of significance of the regression coëfficients of second order autoregressive process

	Phase I			Phase II			Phase III		
	df	h_1	h_2	df	h_1	h_2	df	h_1	h_2
♂	9	0,9531	0,9181	18	3,1424**	1,0878	46	8,1731**	−1,3379
	8	4,3795**	−1,0810	18	3,1854**	1,6231	34	5,5102**	0,0599
	9	2,9335*	−0,1487	18	4,7571**	−0,5075	8	1,6871	1,5838
	7	6,5884**	−0,6233	20	2,7648*	2,0852	5	1,4906	0,8920
	6	3,0092*	0,8503	21	4,6652**	−0,2288	15	2,1989**	2,3133*
	5	1,2392	2,3831	22	3,5220**	1,4028	25	3,7877**	1,2575
	8	2,6541*	1,0169	19	3,3592**	1,1598	20	3,0118**	1,5869
	9	3,1765*	0,9155	18	2,2155*	2,9528**	39	7,5113**	0,2602
	7	3,1786*	−0,6402	20	2,2332*	2,7542**	17	2,6430**	1,7293
	11	−0,0294	0,1570	16	2,3614*	2,7858**	12	2,8147**	0,8613
♀	8	6,0172**	−0,8983	19	3,5791**	0,7309	20	3,4737**	1,1555
	8	3,3809**	−0,5337	19	5,8298**	−1 8070	14	2,9275**	0,8844
	9	2,1646	3,9018**	18	17,6635**	0,0689	23	4,5195**	0,1933
	8	4,2027**	−0,9377	19	3,4182**	0,5880	11	1,9140	2,0220
	8	4,8011**	1,4100	19	7,9731**	0,2337	16	2,3826**	1 6764
	8	2,3069*	0,7224	19	4,1726**	0,0455	18	7,0914**	−2,0754
	10	3,2505*	−0,4843	17	3,1238**	1,3468	23	8,5952**	0,2725
	8	2,7836*	1,6700	19	3,5067**	2,3478*	13	2,9448*	−0,1577
	8	2,6034*	1,3048	19	4,2310**	0,4333	18	2,3403*	2,3356*
	11	4,5874**	−1,2357	16	3,6033**	0,6087	14	4,7442**	−0,9700

Table 3

Average values of the statistics

Phase		Numbers	Statistic				
			ln a	b	ρ	∝	x (0)
I	♂	48	1,7230	0,5530	0,9197	6,0797	3,8324
	♀	42	1,8413	0,5230	0,9174	4,9913	3,8268
	Std. dev.		0,1384	0,0275	0,0128	0,2308	0,0854
II	♂	48	1,111	0,6799	0,9598	7,4375	5,3316
	♀	42	2,0426	0,4959	0,9541	7,1431	5,3762
	Std. dev.		0,1969	0,-328	0,0081	0,3212	0,0558
III	♂	48	3,1028	0,3829	0,9783	7,9945	6,9340
	♀	42	2,9491	0,3485	0,9798	7,8621	6,7580
	Std. dev.		0,5414	0,0689	0,0185	0,9189	0,0573

The standard deviations were calculated as follows:

$\sqrt{\delta_e^2 + \delta_s^2}$, where δ_e^2 = within family variance and δ_s^2 = between family variance.

Discussion

Model

From the results it is clear that the allometric-auto-regressive model has the following advantages: (1) The model fits the data reliably (Fig. 1 and Table 1). Tightness of fit together with repeated observations reduce error of measurement and consequently allow detection of small differences between animals (Meissner & Roux, 1979). (2) Growth is mostly a multiplicative process and therefore non-linear in mathematical terms. This may complicate the comparison of efficiency between animals, as such functions may be difficult to fit and interpret. In the application of this model the data are transformed to linear forms (Equations 1 and 2) which are computationally easier to handle and the interpretation is in terms of the well known allometric equation. (3) The model is suitable for extrapolation as the parameters are invariant with mass and time within a growth phase. Animals can thus be compared independent of their age and/or mass within a growth phase.

The high correlation coëfficients in Table 1 are an indication of the accuracy of fit obtained with the allometric model. Furthermore, it appears from Table 2 that a first order process is adequate in describing growth. The few cases of significant h_2 are most probably due to diurnal rhythms with periods that may vary between 19 and 29 hours instead of only 24 hours (Sollberger, 1965). Hence this model appears to be an

Table 4

F- values of the two-way analysis of variance

Statistic	Between sexes	Between families	Sex x Family
ln a_1	22,07**	6,48**	1,03
b_1	45,10**	4,33**	0,73
ρ_1	2,33	1,85	0,38
α_1	9,91**	1,31	0,34
x $(0)_1$	49,67**	6,85**	0,37
ln a_2	235,36**	6,00**	2,71**
b_2	380,83**	5,28**	2,28*
ρ_2	14,38**	1,68	0,80
α_2	26,50**	0,98	0,73
x $(0)_2$	3,89	5,30**	1,67
ln a_3	1,06	0,96	1,29
b_3	2,05	0,77	1,24
ρ_3	0,29	0,49	0,63
α_3	0,34	0,68	1,52
x $(0)_3$	162,60**	10,84**	1,97

Subscripts indicate phases

accurate and useful equation for the quantifying of growth and efficiency of feed utilization. This was confirmed by Meissner (1977) working with sheep.

Growth phases

From Fig. 1 and 3 it is clear that the allometric-autoregressive model should be applied separately for each growth phase. This means that a linear regression should be done separately for each of the growth phases, as the total developmental growth of the rat is described by 3 separate straight lines in terms of slope and intercept. There is evidence from the literature that these breaking points that occur in the developmental growth of the rat have a physiological background. In plotting total metabolism (total heat production, cal/day) of rats against their body mass and age, Brody (1964, p. 406) also finds a discontinuity that corresponds to our first breaking point in fitting straight lines to the data. Von Bertalanffy & Pirozynski (1952) describe a decline in the relative growth rate of the liver and thymus somewhere in the region of a 100 gm body mass. They also find a decline in the tissue respiration of the liver and thymus at this mass (von Bertlanaffy & Pirozynski, 1953). Von Bertalanffy (1960, p. 218) furthermore finds a drastic decline in the basal metabolic rate (BMR) in rats at approximately 100 gm body mass. There are also indications from Winick & Noble (1965) that growth previous to 24 - 35 days is by mainly cell division. According to Zucker & Zucker (1963) there is a cessation of fat accretion from 21 to 35 days of age in the rat, and a rather steep course of fat accretion from then onwards. It seems, therefore, that at this body mass (± 100 gm) and at this age (± 36 days), which probably corresponds with the onset of puberty, a physiological change is taking place, and that it can be observed in different ways.

The second phase from approximately 37 days (onset of puberty) to 60 days (puberty, sexual maturation) is described by a second straight line in terms of slope and intercept. Winick & Noble (1966) found that towards the end of this phase (65 days) growth is mainly by cell enlargement, in contrast with growth by cell division and cell enlargement prior to this. Widdowson (1967) found a dramatic increase in testis mass as a percentage of body mass from 5 weeks (35 days) to 8 weeks (56 days) of age. From 8 weeks onwards there is a slight decrease in testis mass as a percentage of body mass. Data from Meyer (1976) also indicate a rapid increase in testis mass from 36 days onwards. Meyer (1976) found that this increase can be induced by the injection of HCG in the prepubertal rat, which indicates that hormones may play an important role. This is mirrored by the fact that significant differences between sexes for all parameters were accentuated in the second phase, probably due to the effect of sex hormones (see Table 4). Von Bertalanffy (1960, p. 221) found a shift in the growth cycle of body length against time at approximately 65 days. There is thus also evidence that this second growth phase has a physiological background.

The literature gives some physiological and biochemical evidence of sharp discontinuities as were obtained in this study. The metabolic rate (kcal/kg/day) of rats as reported by Kleiber (1961) dropped by 52% from day 35 to day 36. Furthermore, the hormonal induction pattern of testis mass and 3 testis enzymes measured by Meyer (1976) in the prepubertal rat shows a clear discontinuity in the enzyme concentration specific for each enzyme ranging from 2 to 6 days after the first daily injection of HCG. This indicates the exact physiological and biochemical control of genes being turned on and off. The clear breaking points obtained in the growth curves might have a similar molecular genetic origin.

The period from 60 to 70 days should perhaps not be identified as a growth phase, but merely as a transitional period in which sexual maturity is reached. During this period the daily feed intake fluctuated more than in other phases, as can be seen from the autoregressive plot (Fig. 3). It is known that the odours of one sex have an olfactory-reproductive effect on the opposite sex (Brunson, 1967), so that it is possible that the comparatively high fluctuation in daily feed intake was caused by odours related to sexual attraction by the opposite sex during this period.

From day 70 to maturity a third phase is identified which is also described by a straight line in terms of slope and intercept. Maturity was arbitrarily defined as the cessation of gain in body mass for 4 successive days. The age at which this point is reached fluctuated considerably. The mean age for the rats was 93,5 ± 8,7 days. This approach may have been too strict as mass gain commenced again in the rats, with a more fluctuating daily feed intake and daily mass gain. Calculated t-values for h_2 in equation (3) for the phase 70 to 115 days of 12 randomly selected rats are given in Table 5 to illustrate that the first order autogressive process still described at least feed intake accurately up to 115 days.

The existence of the different phases is also illustrated by the ranges and means of daily feed intake as given in Table 6. Especially the change from phase I to phase II is very clear, as there is no overlapping of the daily feed intake between the phases. Note also the high intake during puberty.

These simultaneous discontinuities in total growth, basal metabolism, and the relative growth and respiration of organs are collectively a strong indication of actual fundamental physiological changes that occur during animal growth. These different growth phases are also identified in farm animals,such as cattle (Meissner,

1980 – personal communication), sheep (Searle, Graham & O'Callaghan, 1972; Meissner *et al.*, 1975; Meissner, 1977) pigs (Kemm & Siebrits, 1980 – Personal communication) fowls (own data). Brody (1964) concludes: "It does not appear possible to represent the entire growth curve by one equation, not even by the very plastic potential series equations. In other words, growth curves appear to have metamorphosis – like discontinuities".

Significant differences betwee sexes and families

From Table 4 it is evident that there are significant sex x family interactions for both intercept and slope in phase II, which indicates that the ranking of males and females of some families differ when averages are ranked.

It is also evident (Table 4) that there are significant differences between families for both slope and intercept in the first 2 phases and for x (0) in all 3 phases. 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 selection to change the growth curves of animals. The results of the estimation of the genetic parameters necessary for this purpose will be discussed in a subsequent paper.

Table 5

Calculated t-values of the second order autoregressive process from 70 to 115 days

		b_1	b_2
♂	1	7,4**	1,2
	2	6,4**	0,1
	3	6,2**	0,0
	4	6,3**	0,0
	5	5,4**	1,1
	6	7,6**	3,6**
♀	1	6,2**	0,2
	2	5,6**	0,6
	3	5,3**	1,0
	4	5,0**	1,5
	5	4,8**	1,5
	6	8,4**	1,8

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Table 6

Range of age, body mass and daily feed intake in the different phases of a single male rat

Phase	Age (days)	Body mass (gm)	Mean Feed gm/days ± standard deviation	Range (feed)	n
I	25 – 37	49 – 95	10,40 ± 1,16	7,6 – 11,2	13
II	38 – 60	106 – 261	21,25 ± 2,76	16,2 – 25,2	23
Puberty	61 – 71	270 – 305	24,54 ± 2,16	21,0 – 28,1	11
III	72 – 106	311 – 373	21,91 ± 1,55	19,3 – 25,7	35

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ERRATA

THE ALLOMETRIC-AUTOREGRESSIVE MODEL IN GENETIC STUDIES: DIFFERENT PHYSIOLOGICAL PHASES IN THE RAT

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Equation (2) on page 28 should read:

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

or

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

where x (t) = In (cumulated feed intake) at time t

x (o) = In (cumulated feed intake) at time O.

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

Page 30:

Replace ∞_x by α_x