Heritability of parameters of the allometric-autoregressive model and its correlation with common growth and efficiency traits

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The heritabilities of the parameters slope (b) and intercept (ln a) of the allometric function: \( y = \ln a + bx \) [where \( y = \ln \) (body mass) and \( x = \ln \) (cumulative feed intake)] and for \( p \), which is the slope of the autoregressive relationship (t against \( t - 1 \)), were investigated using the rat as model. The heritability estimates for ln a (0.34), b (0.31) and \( p \) (0.12) agree with those of a previous study. Since ln a and b are both directly proportional to growth efficiency, it may be possible to use the model to change the entire efficiency curve of growing animals. The correlations (phenotypic, genetic, ordinary) between these parameters and common growth (growth rate, feed intake, body mass) and efficiency (three types) traits were also investigated. There are positive correlations between b and the efficiency traits (0.71; 0.82; 0.37), and growth rate (0.31). There is, however, a negative correlation between b and feed intake (−0.38). If this is true, it may be possible to increase growth rate via b without an increase in feed intake.

### Introduction

The most important advantage of using a growth function, such as the allometric-autoregressive model, is a more accurate description and evaluation of animal growth. Fitting a function to the data would minimize the effect of experimental error due to more measurements, thereby emphasizing biological differences (Meissner, 1977). A more reliable assessment of productive merit would result from the combination of more than one measurement. If the function chosen approximates reality, it is highly probable that the parameters of the equation can be related to the present knowledge of production physiology (Meissner, 1977). The model should fit the growth curve reliably. Extreme tightness of fit reduces error of measurement and consequently allows detection of small differences between animals. This is essential because within-breed differences between variables operating in growth and efficiency are usually small (Meissner, 1977).

Meissner (1977) proposed that a model should be biologically based and should incorporate current knowledge of production physiology. For example, the model should aim to incorporate the various variables relevant to growth and efficiency into a simple interrelationship. In this way, the parameters of the different variables would have biological meaning which may aid in the discovery, explanation and quantification of growth and production mechanisms (Roux, 1976). Furthermore, in developing a theory, the concept of animals as input-output devices (Parks, 1972a; 1972b) should be recognized.

In an exhaustive investigation, Meissner (1977) concluded that the allometric-autoregressive model (Roux, 1974; 1976) satisfies, on the whole, the specified prerequisites of a model for the functional description of animal growth.

Most growth functions are limited only to the description of growth in terms of output (body mass) and do not take input (feed intake) into account. However, the allometric-autoregressive model includes feed intake as a parameter, thereby taking the basic allometric nature of growth into consideration and describes growth accurately (Roux, 1974; 1976; Meissner & Roux, 1979; Roux, 1980). The model has proved to be useful in the characterization of growth responses of both breeds and feeds in nutrition studies (Meissner, Roux & Hofmeyr, 1975; Meissner, 1977; Meissner, Hofmeyr & Roux, 1977; Siebrits, 1979; Roux & Kemm, 1981; Greeff, Meissner, Roux & Janse van Rensburg, 1986a; 1986b) and also seemed to be of value in genetic studies (Scholtz & Roux, 1981a; 1981b).
For the purpose of predicting gain in selection experiments, it was decided to verify the accuracy of the heritability estimates calculated by Scholtz & Roux (1981b) for the parameters of the allometric-autoregressive model.

Since the actual correlations between the parameters of the model and common growth and efficiency traits are not known, the phenotypic and genetic correlations between these were also investigated.

**Materials and Methods**

The allometric-autoregressive model is based on the following two equations:

1. The allometric function to describe growth, viz.:
   \[ w = av^b \]
   or
   \[ y = \ln a + bx \]

   where \( w = \) body mass, \( v = \) cumulative feed intake, \( y = \ln w \) and \( x = \ln v \). Slope (\( b \)) and intercept (ln \( a \)) can thus be estimated by linear least-square procedures.

2. The equation for cumulative feed intake, viz.:
   \[ \{x(t) - \alpha_x\} = \rho[x(t-1) - \alpha_x] + \varepsilon(t) \]
   or
   \[ x(t) = [\alpha_x - x(0)]p^t + \sum_{j=0}^{t-1} p^j \varepsilon(t-j) \]

   where \( x(t) = \ln (\text{cumulative feed intake}) \) at time \( t \), \( x(0) = \ln (\text{cumulative feed intake}) \) at time \( 0 \), \( \alpha_x = \ln (\text{cumulative feed intake}) \) with \( t \to \infty \), \( \rho = \) slope of autoregression, \( \varepsilon(t) = \) error term.

   **autoregression = linear regression of \( x(t) \) as dependent variable on \( x(t-1) \) as independent variable.**

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

Rats from the outbred Wistar line, 12 families with 10 full sib individuals each, were used in this experiment to estimate the heritabilities, and correlations with the common growth and efficiency traits, of ln \( a \), \( b \) and \( \rho \) in the second growth phase of the rat. The second growth phase was selected because the rats might still be subjected to maternal effects during the first phase; the second phase is less sensitive to errors in the calculation of cumulative intake at the beginning of the experiment and most of the growth takes place during this phase (Scholtz, 1987).

The two-way analyses of variance for ln \( a \), \( b \) and \( \rho \) for the second growth phase of the rat (from ca. 35—60 days of age), are given in Table 1. From this Table, the heritabilities were calculated as follows:

\[ h^2 = \frac{2\sigma_h^2}{\sigma^2} \]

where \( \sigma_h^2 = \frac{MS_h - \sigma_w^2}{ks} \)

with \( s = \) sex = 2; \( k = \) individuals/sex/family; \( \sigma_h^2 = \sigma_H^2 + \sigma_w^2 \) (\( \sigma_w^2 \) is directly available from the analysis of variance table).

The confidence intervals of the heritabilities were calculated according to Turner & Young (1969) and Scholtz (1979).

Both \( a \) and \( b \) are directly proportional to growth efficiency, where growth efficiency may be defined as either \( w/v = av^{b-1} \) or \( dw/dv = abv^{b-1} \) (Scholtz & Roux, 1981a). Furthermore, \( \rho \) is a function of the rate constant of growth.

The common efficiency and growth traits involved were (1) efficiency (gain/intake) in the second phase, (2) local efficiency at 60 days of age \( \left( b \frac{w}{v} \right) \), (3) efficiency from conception to 60 days of age, (4) average daily gain in phase 2 (ADG), (5) daily feed intake in phase 2 and (6) body mass at 60 days of age.

The phenotypic \( (r_p) \) and genetic \( (r_G) \) correlations between both ln \( a \) and \( b \) and the common growth and efficiency traits were calculated using standard procedures (Becker, 1967).

The ordinary correlation \( (r_o) \), which ignores the group and family structure, is sometimes incorrectly referred

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>ln ( a )</td>
<td>Between sexes</td>
<td>1</td>
<td>24,451</td>
<td>26,451</td>
<td>252,2</td>
</tr>
<tr>
<td></td>
<td>Between families</td>
<td>11</td>
<td>3,521</td>
<td>0,320</td>
<td>4,619</td>
</tr>
<tr>
<td></td>
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<td>11</td>
<td>1,153</td>
<td>0,1049</td>
<td>1,514</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>96</td>
<td>6,694</td>
<td>0,0693</td>
<td></td>
</tr>
<tr>
<td>( b )</td>
<td>Between sexes</td>
<td>1</td>
<td>1,117</td>
<td>1,117</td>
<td>372,6</td>
</tr>
<tr>
<td></td>
<td>Between families</td>
<td>11</td>
<td>0,1012</td>
<td>0,0092</td>
<td>4,381</td>
</tr>
<tr>
<td></td>
<td>Sex ( \times ) family</td>
<td>11</td>
<td>0,0334</td>
<td>0,0030</td>
<td>1,429</td>
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<tr>
<td></td>
<td>Error</td>
<td>96</td>
<td>0,2041</td>
<td>0,0021</td>
<td></td>
</tr>
<tr>
<td>( \rho )</td>
<td>Between sexes</td>
<td>1</td>
<td>0,0112</td>
<td>0,0112</td>
<td>0,488</td>
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<td></td>
<td>Between families</td>
<td>11</td>
<td>0,0050</td>
<td>0,0005</td>
<td>2,368</td>
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<tr>
<td></td>
<td>Sex ( \times ) family</td>
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<td>0,0028</td>
<td>0,0025</td>
<td>1,316</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>96</td>
<td>0,0184</td>
<td>0,0019</td>
<td></td>
</tr>
</tbody>
</table>
to as the phenotypic correlation \( r_p \). The term \( r_p \) takes the group and family structure into consideration and is calculated by using variance and covariance components. Tests of significance can be applied to \( r_o \), only and not to \( r_p \) and \( r_G \) as is often done, since their distributions are unknown. The term \( r_o \) was calculated using standard procedures. Standard errors for \( r_p \) and \( r_G \) were not calculated since they cannot be used in tests of significance.

**Results**

The heritability estimates and confidence intervals are presented in Table 2, together with those of Scholtz & Roux (1981b).

The heritabilities of the current experiment are in agreement with those of Scholtz & Roux (1981b). The data of this experiment were thus combined with those of Scholtz & Roux (1981b) by adding the different sums of squares. The heritabilities estimated from the combined data are also presented in Table 2. Owing to the larger numbers involved, it is obvious that the combined heritability estimates are more accurate due to the narrower confidence intervals.

The heritability estimates of \( \ln a \) and \( b \) are moderate to high (Table 2), which indicate that progress in selection may be expected in either of the two parameters. The magnitude of these heritability estimates is in accordance with the magnitude of the heritabilities of the conventional description of efficiency. Johannson & Rendel (1986) gave the heritability estimates for efficiency as 0.26—0.60 for pigs, 0.36—0.42 for cattle and approximately 0.29 for sheep.

Since the heritability of \( \rho \) seems to be rather low, its correlations with common growth and efficiency traits were not calculated.

The phenotypic \( r_p \), genetic \( r_G \) and ordinary \( r_o \) correlations between \( \ln a \) and \( b \), and the common growth and efficiency traits are presented in Table 3. In all but two instances, the phenotypic correlation is larger than the genetic correlation. According to Searle (1961), the phenotypic correlation can only exceed the genetic correlation when the environmental correlation exceeds the genetic correlation by a sufficient margin.

Genetic correlations are difficult to estimate and large samples of related individuals are required for accurate estimates. Cheverud (1988) investigated the relationship between genetic and phenotypic correlations and determined their degree of similarity. He furthermore examined the possibility of using phenotypic correlations rather than their genetic counterparts in situations where genetic correlations cannot be precisely estimated. He concluded that much of the dissimilarity between phenotypic and genetic correlation estimates seems to be due to imprecise estimates of the genetic correlations, and that phenotypic correlations are likely to be fair estimates of their genetic counterparts in many situations.

The ordinary correlations between \( r_p \), \( r_G \) and \( r_o \) of the different traits were calculated and are presented in Table 4. From this Table, it can be seen that the correlation between \( r_p \) and \( r_G \) is 0.75, which is in agreement with the correlation of 0.81 found by Cheverud (1988) for effective sample sizes greater than 40.

The correlation between \( r_o \) and \( r_p \) is 0.96 which, together with a consideration of the similarity of their

### Table 2 Heritability estimates and confidence intervals (0.05) of \( \ln a \), \( b \) and \( \rho \)

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>( \ln a )</td>
<td>0.30—1.37</td>
<td>0.20—0.95</td>
<td>0.31—0.85</td>
</tr>
<tr>
<td>( b )</td>
<td>0.25—1.31</td>
<td>0.18—0.91</td>
<td>0.28—0.80</td>
</tr>
<tr>
<td>( \rho )</td>
<td>-0.06—0.71</td>
<td>0.02—0.58</td>
<td>0.05—0.43</td>
</tr>
</tbody>
</table>

### Table 3 Phenotypic \( r_p \), genetic \( r_G \) and ordinary \( r_o \) correlations between parameters of the allometric-autoregressive model and common growth and efficiency traits

<table>
<thead>
<tr>
<th>Traits</th>
<th>( r_p )</th>
<th>( r_G )</th>
<th>( r_o )</th>
<th>( r_p )</th>
<th>( r_G )</th>
<th>( r_o )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \ln a )</td>
<td>-0.50</td>
<td>-0.30</td>
<td>-0.54***</td>
<td>0.69</td>
<td>0.38</td>
<td>0.71***</td>
</tr>
<tr>
<td>( b )</td>
<td>-0.68</td>
<td>-0.57</td>
<td>-0.69***</td>
<td>0.81</td>
<td>0.43</td>
<td>0.82***</td>
</tr>
</tbody>
</table>

* = 5%, ** = 1% and *** = 0.1% levels of significance.
means (0.12 and 0.10 respectively), suggests that they are statistically similar. Tests of significance were done on \( r_p \) and are also given in Table 3.

**Discussion**

Both \( a \) and \( b \) are mathematically proportional to growth efficiency (Scholtz & Roux, 1981b), where growth efficiency is defined as either \( y/x = ax^{-b-1} \) or \( dy/dx = abx^{-b-1} \). These parameters are also significantly correlated with efficiency. Since the allometric parameters show significant heritabilities, it may be possible to use this model to change the efficiency curves of growing animals in a predictable manner. This appears to be of value in contrast to the conventional approach with its focus on specific time or body mass intervals.

The heritability of \( p \) appears to be low. It is speculated that \( p \) may tend to be canalized for certain environments, irrespective of the genetic constitution of a rat from a particular strain. Heritabilities close to zero may be evoluntary in origin with respect to factors such as adaptive norms, canalization, and stabilization (Scholtz & Roux, 1981b).

From Table 3, it is clear that both \( \ln a \) and \( b \) are strongly correlated with efficiency in the second growth phase of the rat, and with efficiency at 60 days. The relatively lower correlation with efficiency from conception to 60 days of age may be explained by the fact that it includes the estimated efficiency from conception, which may not be related to \( b \), thereby causing a dilution effect on this type of efficiency.

There is a significant positive correlation between ADG and \( b \). In contrast to this, the correlation between daily feed intake and \( b \) is significantly negative. Normally feed intake tends to increase as ADG increases and genetic correlations of 0.61, 0.51 (Jara-Almonte & White, 1973) and 0.71 (Sutherland, Biondini, Haverland, Pettus & Owen, 1970) between ADG and feed intake have been reported in the literature. Here, however, it seems possible that ADG may be increased via \( b \), which has a moderate heritability, while daily feed intake may decrease or at least remain at the original level.

Selection for increased growth rate tends to result in the indirect selection for feed intake (Sutherland, *et al.*, 1970; Hetzel & Nicholas, 1978; Kownacki & Jezierski, 1980), and thus the breeding of gluttons. If the correlations found in this experiment reflect the true situation, it may be advantageous to increase ADG via \( b \) without an increase in feed intake. This aspect is being checked in a selection experiment.

<table>
<thead>
<tr>
<th>Table 4 Ordinary correlation between ( r_p, r_G ) and ( r_o ) of the different traits</th>
</tr>
</thead>
<tbody>
<tr>
<td>( r_p )</td>
</tr>
<tr>
<td>0.96</td>
</tr>
<tr>
<td>0.75</td>
</tr>
</tbody>
</table>

**References**


