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ANIMAL GROWTH IN THE CONTEXT OF TIME SERIES AND LINEAR OPTIMAL CONTROL SYSTEMS

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OPSOMMING: DIEREGROEI IN DIE KONTEKS VAN TYDSREEKSE EN SISTEME VIR LINEÊRE OPTIMALE BEHEER

Dit word bewys dat 'n singuliere tweede momentmatriks met rang een die eienskappe van 'n beheersisteem in 'n eerste orde outoregressiewe tydsreeks kan induseer. 'n Groeiwet word geassosieer met 'n nie-eenheidswortel van die herhalingsisteem, sodat groei beskryf kan word deur 'n enkel-dimensionele markovproses. Beheerwette word geassosieer met eenheidswortels van die herhalingsisteem en hulle vektore, met spesiale verwysing na die verdeling van die energie van voedselinname na hitteproduksie en die neerlegging van vet en proteïen. Dit word bewys dat die tydsreeks beskrywing getranskribeer kan word na 'n beheersisteem met optimale lineêre beheer met terugvoer en diskrete tydsintervalle.

SUMMARY:

It is shown that a singular second moment matrix with rank one may induce properties of a control system in a first order autoregressive time series. A growth law is associated with the non-unity root of the recursive system, so that it can be described by a single dimensional Markov process. Control laws are furthermore associated with the unity roots of the recursive system and their vectors, with special reference to the partitioning of feed intake energy into heat production and the deposition of fat and protein. It is shown that the time series description can be transcribed to an optimal linear discrete time feedback control system.

The origin of the present approach lies in the discovery (Roux, 1974) that ln (body mass) and ln (cumulative feed intake) are linearly related and that cumulative feed intake, like body mass, can be described over time by a Gompertz equation.

In the description of animals as input - output systems it is, however, also necessary to keep track of body composition, since it is possible that animals with the same mass may have bodies with different energy contents. In a growing animal the major pathways of utilisable energy output would be heat production and the deposition of protein and fat. Hence the number of dimensions in energy studies on growing animals is, at least, 4.

The allometric (i.e. log-linear) relationship of chemical components (i.e. protein, fat) to body mass has been known and hypothesized since Needham (1932). These relationships together with the allometric relationship between body mass and cumulative feed intake motivate an investigation into the relatonship between multivariate allometry and Gompertz relationships. To allow use of the powerful mathematical theory of linear algebra this problem is transformed to a set of interconnected first order autoregressive time series on the logarithmic scale.

In a previous paper (Roux, 1976) a somewhat intuitive connection was made between a vector stochastic differential equation with a singular matrix with rank one, and Hopkins' (1966) extension of the allometric concept to the multivariate situation. Hopkins defined the multivariate allometric situation as one in which the log-transformed variables have a covariance matrix with rank one, if the effects of individual variation or measurement error are excluded.

The first purpose of this paper is, then, to derive the relationship between multivariate allometry and difference equations in an explicit and rigorous manner. Although growth may be a continuous process, it is in practice measured at discrete time points. Difference equations or discrete time series are, therefore, preferred for the purpose of description and estimation (see also Innis, 1974). To establish a correspondence between the differential equations of Roux (1976) and discrete time series, it is necessary only to conceptualize small time units between measurements.

From Section 6 it will be clear that good evidence exists to justify the assumptions of a covariance matrix of rank one of the relevant variables and of a first order autoregressive relationship in ln (cumulative feed intake). Hence a second purpose of this paper is to attempt to construct a nontrivial theory of animal growth based on these assumptions, and to explore its possible consequences.

1. THE PROPERTIES OF VECTOR AUTOREGRESSIVE TIME SERIES INDUCED BY SECOND MOMENT MATRICES OF RANK ONE

A vector first order autoregressive time series can be written in the form

$$x(t) - \alpha = A(x(t-1) - \alpha) + \varepsilon(t), \qquad (1)$$

where A is a constant matrix and α a constant vector. The vector $\varepsilon(t)$ represents chance fluctuations. The differential equations postulated by Roux (1976) on heuristic grounds, can be written in difference form

$$\Delta x(t) = B(x(t-1) - \alpha) + \varepsilon(t) \qquad (2)$$

or in conventional time series form

$$x(t) - \alpha = (I + B)\ (x(t-1) - \alpha) + \varepsilon(t), \qquad (3)$$

where I is the identity matrix, and where comparison of (3) to (1) gives $A = I + B$. Follow Fuller (1976) in notation and write

$$\Sigma = E(\varepsilon(t)\varepsilon'(t)) = \begin{bmatrix} & \vdots & \\ \cdots & \sigma_{ij} & \cdots \\ & \vdots & \end{bmatrix}$$

and assume $E(\varepsilon(t)\varepsilon'(t-j)) = 0$, for all $j \neq 0$.

Define the time averaged second moment matrix

$$C = E\sum_{t=1}^{T} (x(t) - E\bar{x}(0))(x(t) - E\bar{x}(0))'/T \qquad (4)$$

where

$$\bar{x}(0) = \sum_{t=1}^{T} x(t)/T.$$

Note that (4) differs from a covariance matrix, since $E\,x(t) \neq E\,\bar{x}(0)$ for nonstationary time series.

Denote also

$$c_{11} = E\sum_{t=1}^{T} (x_1(t) - E\,x_1(0))^2/T,$$

with $x_1(t)$ the first component of the vector $x(t)$.

For ease in presentation statements will be formalised in theorem format, and will be given in 4 dimensions, since this is the form in which the theory will be applied most often. The extension to arbitrary dimensions will be obvious. In the ensuing development the following result is of great importance, and is, therefore, highlighted as lemma 1.

Lemma 1
With continuous variables a time averaged second moment matrix (as defined in (4)) of rank one implies a perfect fit to a straight line in 4 dimensions.

Proof
A time averaged second moment matrix (defined in (4)) of rank one must necessarily be of the general form $c_{11}F$, where F is defined as (5).

$$F = \begin{bmatrix} 1 & b_2 & b_3 & b_4 \\ b_2 & b_2^2 & b_2b_3 & b_2b_4 \\ b_3 & b_2b_3 & b_3^2 & b_3b_4 \\ b_4 & b_2b_4 & b_3b_4 & b_4^2 \end{bmatrix} \qquad (5)$$

It is also generally true that second moment correlation and covariance type matrices must be of the same rank, since the one is obtainable from the other by pre- and post multiplication of diagonal matrices. Furthermore a correlation matrix of rank one must necessarily be equal to a matrix J with all elements equal to unity. Assume also continuity of variables to enable interchange of integration and differentiation. Then a result obtainable from Kendall & Stuart (1976, pp. 294, 295) is applicable, i.e.

$$E(S^2) = p - \lambda,$$

Where S^2 is the sum of squares in standardised units of distances of sample points from a straight line in p dimensions and λ is a latent root of the relevant second moment correlation type matrix, which is defined analogously to (4). In the present situation $p = 4$ and $\lambda = 4$, since λ is a latent root of J. As S^2 is always nonnegative, $E(S^2) = 0$ implies $S^2 \equiv 0$, for all samples.

Note on the use of second moment matrices

A second moment definition, like (4), gives better justification than one of conventional covariance for the use of principal components, which is ordinarily only applicable to sequentially independent data, in the present context of nonstationary time series. Furthermore, the Yule-Walker equations of the ensuing development is identical to the usual conditional likelihood estimation procedures for the autoregressive situation as e.g. derived by Fuller (1976), if the expectation operators (E) are ignored. This will not be true for nonstationary time series in a development based on covariance matrices.

Theorem 1

Assume a first order vector autoregressive time series and a scalar first order time series for $x_1(t)$, the first member of the vector time series, i.e.

$$x_1(t) - \alpha_1 = \rho(x_1(t-1) - \alpha_1) + \varepsilon_1(t).$$

Then, if the time averaged second moment matrix C is singular with rank one, the time averaged Yule-Walker equation for a first order process will have a general solution

$$\tilde{A} = I + \tilde{B} \text{ with } \tilde{B} = cF + G(\tfrac{c}{\gamma}F - I),$$

where c is a constant, γ is the nonzero characteristic root of cF, I is the identity matrix and G is an arbitrary matrix.

Proof

Define

$$\bar{x}(0) = \sum_{t=1}^{T} x(t)/T \text{ and } \bar{x}(-1) = \sum_{t=1}^{T} x(t-1)/T.$$

Then, on taking expectations after post multiplication of (1) with $x'(t-1)$, and use of the identity

$$E(I-A)\alpha\bar{x}'(-1) = E\bar{x}(0)E\bar{x}'(-1) - AE\bar{x}(-1)E\bar{x}'(-1),$$

the time averaged multivariate Yule-Walker equation follows:

$$E\sum_{t=1}^{T}(x(t) - E\bar{x}(0))(x(t-1) - E\bar{x}(-1))'$$

$$= AE\sum_{t=1}^{T}(x(t-1) - E\bar{x}(-1))(x(t-1) - E\bar{x}(-1))'. \quad (6)$$

The general solution to (1) is of the form

$$x(t-1) = \alpha + A^{t-1}(x(0) - \alpha) + \sum_{j=0}^{t-2} A^j \varepsilon(t-1-j),$$

which explains why no term involving $\varepsilon(t)$ results on the right hand side of (6), under the assumption of the independence between vectors $\varepsilon(t)$ associated with different values of t.

Assume C in (4) has rank one. Then, by Lemma 1

$$x_i(t) = a_i + b_i x_1(t),$$

say, for i = 2, 3, 4, where the $x_i(t)$ are elements of $x(t)$ and where the parameters a_i are arbitrary intercepts allowed for by correction for the mean in C. Hence

$$x(t-1) - E\bar{x}(-1) = (x_1(t-1) - E\bar{x}_1(-1))(1, b_2, b_3, b_4)'$$

and

$$x(t) - E\bar{x}(0) = (x_1(t) - E\bar{x}_1(0))(1, b_2, b_3, b_4)'.$$

The scalar analog of (6) is

$$E\sum_{t=1}^{T}(x_1(t) - E\bar{x}_1(0))(x_1(t-1) - E\bar{x}_1(-1))$$

$$= \rho E\sum_{t=1}^{T}(x_1(t-1) - E\bar{x}_1(-1))^2.$$

Substitution of the previous three equations in (6) then results in

$$\rho F = AF.$$

Remember that the time units are conceptualized to be small enough so that $\rho = \exp(-\gamma) \doteq (1-\gamma)$; vide also Bellman (1960, p 263). Hence it follows by the use of general solutions to linear equations (vide Searle, 1966) that

$$\tilde{A} = I - cF + G(\tfrac{c}{\gamma}F - I) \quad (7)$$

and hence that

$$\tilde{B} = cF + G(\tfrac{c}{\gamma}F - I),$$

for $\gamma = c(1 + b_2^2 + b_3^2 + b_4^2)$ is a general solution to (6). G is an arbitrary matrix, because the singularity of C induces an infinite number of solutions. Direct substitution of (7) in $\rho F = AF$ provides a check, if it is noted that $F^2 = \frac{\gamma}{c} F$, where γ is the nonzero characteristic root of cF.

Theorem 2

Assume a first order vector autoregressive time series and likewise a scalar first order time series for the first member of the vector time series. Then if the time averaged second moment matrix C is singular with rank one, the covariance matrix $\ddagger = E\,\varepsilon(t)\,\varepsilon'(t)$ will be equal to $\sigma_{11}F$, where $\sigma_{11} = E\,\varepsilon_1{}^2(t)$ with $\varepsilon_1(t)$ being the first component of $\varepsilon(t)$.

Proof

The method of proof is very similar to that of Theorem 1. Hence it will be given in outline only. From the general solution to (1), it follows on post multiplication of (1) with $x'(t)$ and use of the identity

$$E(I - A) \propto \bar{x}'(0) = E\bar{x}(0)\, E\bar{x}'(0) - AE\bar{x}(-1)E\bar{x}'(0),$$

that

$$\ddagger = ET^{-1} \sum_{t=1}^{T} (x(t) - E\bar{x}(0))(x(t) - E\bar{x}(0))' -$$

$$EAT^{-1} \sum_{t=1}^{T} (x(t-1)) - E\bar{x}(-1))(x(t) - E\bar{x}(0))'$$

the so-called Yule-Walker equation.

Remember that

$$x(t) - E\bar{x}(0) = (x_1(t) - E\bar{x}(0))(1, b_2, b_3, b_4)', \text{etc.},$$

so that

$$\ddagger = ET^{-1} \sum_{t=1}^{T} (x_1(t) - E\bar{x}_1(0))^2 F -$$

$$EAT^{-1} \sum_{t=1}^{T} (x_1(t-1) - E\bar{x}_1(-1))(x_1(t) - E\bar{x}_1(0))F,$$

which on substitution of $\tilde{A}$ from (7) gives

$$\ddagger = ET^{-1} \sum_{t=1}^{T} (x_1(t) - E\bar{x}_1(0))^2 F -$$

$$E\rho T^{-1} \sum_{t=1}^{T} (x_1(t-1) - E\bar{x}_1(-1))(x_1(t) - E\bar{x}_1(0))F.$$

The scalar time averaged Yule-Walker equation which follows by assumption of a first order process is analogous to the multivariate situation:

$$\sigma_{11} = ET^{-1} \sum_{t=1}^{T} (x_1(t) - E\bar{x}_1(0))^2 -$$

$$E\rho T^{-1} \sum_{t=1}^{T} (x(t-1) - E\bar{x}(-1))(x(t) - E\bar{x}(0)).$$

Hence, immediately,

$$\ddagger = \sigma_{11}F. \tag{8}$$

Corollary 1

It follows immediately from (8) that a C of rank unity implies that $\varepsilon_i(t) = b_i\,\varepsilon_1(t), i = 2,3,4.$

Corollary 2

Since a C of rank one implies $\Delta\, x_i(t) = b_i\, x_1(t)$, it follows from (2) and corollary 1, for the rows of G in (7), that

$$g_i = b_i\, g_1,\ i = 2,3,4,$$

where $g_1, \ldots, g_4$ represent the rows of the matrix G of Theorem 1.

Theorem 3

A second moment matrix C of rank one implies a matrix B in (2) and (3) equivalent to -cF, i.e. equivalent to a singular symmetric matrix with rank one, with a nonzero root equal to that of -cF.

Proof

The proof follows immediately from (7) by the use of a set of 4 orthogonal vectors with the latent vector of F, $(1, b_2, b_3, b_4)'$, a member of the set, and from Corollary 2 of Theorem 2.

Corollary

Different matrices G will merely result in equivalent parametrizations of (1) or (3). Hence, the convenient assumption G = 0 can be made without any loss of generality.

Proof

Theorem 2 implies that $\tilde{A} = I + \tilde{B}$ must be equivalent to, say,

$$A_1 = \begin{bmatrix} \rho & a & b & c \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix},$$

since $\rho = 1 - \gamma$. This means that (2) can be transformed to

$$E(u(t) - \alpha_u) = EA_1(u(t-1) - \alpha_u),$$

with solution $E(u(t) - \alpha_u) =$

$$\begin{bmatrix} \rho^n & a\frac{(1-\rho^n)}{(1-\rho^2)} & b\frac{(1-\rho^n)}{(1-\rho^2)} & c\frac{(1-\rho^n)}{(1-\rho^2)} \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} (u(0) - \alpha_u),$$

which is clearly of the same form as $E(w(t) - \alpha_w) =$

$$\begin{bmatrix} \rho^n & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} (w(0) - \alpha_w),$$

where α_w contains

$$1/(1-\rho^2)(0, a, b, c)(u(0) - \alpha_u) + (1, 0, 0, 0)\alpha_u$$

as first element.

Theorem 4

A second moment matrix C of rank one implies the presentation of (3) as:

$$x_i(t) - \alpha_i = \rho(x_i(t-1) - \alpha_i) + \varepsilon_i(t),$$

$i = 1, 2, 3, 4.$

Proof

By the corollary to Theorem 3, α_i can be assumed to be a point on the line $x_i(t) = a_i + b_i x_1(t)$, so that the identity $(x_i(t) - \alpha_i) = b_i(x_1(t) - \alpha_1)$ follows. Substitution of this identity in (3) and writing $\rho = 1 - \gamma$, as in proof of Theorem 1, completes the proof.

2. AN EXPLICIT SOLUTION TO THE FOUR DIMENSIONAL AUTOREGRESSIVE TIME SERIES

Let $x_1 = \ln y_1$; y_1 = cumulative feed intake,

$x_2 = \ln y_2$; y_2 = cumulative heat production,

$x_3 = \ln y_3$; y_3 = mass of protein in the body,

$x_4 = \ln y_4$; y_4 = mass of fat in the body.

Let furthermore

$$x_i = a_i + b_i x_1, \text{ for } i = 2, 3, 4. \tag{13}$$

The previous theorems allow the solution of (3) under the assumption of a second moment matrix C with rank one. From Theorem 3, B = -cF, with F defined in (5). Note that cF has only one nonzero root, $\gamma = c(1 + b_2^2 + b_3^2 + b_4^2)$. Since B is symmetric any three vectors orthogonal to each other and to the vector $k_1(1, b_2, b_3, b_4)'$ associated with γ, will do as vectors associated with the zero roots. Hence to solve (3), transform

$$\begin{bmatrix} u_1(t) \\ u_2(t) \\ u_3(t) \\ u_4(t) \end{bmatrix} = \begin{bmatrix} k_1(1 & b_2 & b_3 & b_4) \\ k_2(0 & 0 & -b_4 & b_3) \\ k_3(0 & -(b_3^2 + b_4^2) & b_2 b_3 & b_2 b_4) \\ k_4(-(b_2^2 + b_3^2 + b_4^2) & b_2 & b_3 & b_4) \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \\ x_4(t) \end{bmatrix} \tag{14}$$

Hence Theorem 5 follows.

Theorem 5

The use of (14) in (3) for a second moment matrix C of rank one results in

$$u_1(t) = \alpha_u - (\alpha_u - u_1(0))\rho^t + \sum_{j=0}^{t-1} \rho^j \varepsilon_u(t-j)$$

$$u_i(t) = u_i(0), \qquad (15)$$

for i = 2, 3, 4,

where $\alpha_u = k_1(\alpha_1 + b_2\alpha_2 + b_3\alpha_3 + b_4\alpha_4)$

and $\varepsilon_u(t) = k_1(\varepsilon_1(t) + b_2\varepsilon_2(t) + b_3\varepsilon_3(t) + b_4\varepsilon_4(t))$

and where $\rho = 1 - \gamma$, or to allow for a continuous approximation to the difference equation,

$\gamma = -\ln\rho$.

The rest of the proof follows from Corollary 1 to Theorem 2.

3. CONTROL MECHANISMS

Note that it follows from (15) and (14) that $u_1(t)$ portrays movement along the lines (13) and that $u_2(t)$, $u_3(t)$ and $u_4(t)$ portray the lack of movement in directions orthogonal to the straight lines. Note furthermore that $u_2(t)$ and $u_3(t)$ contain information about the relationships between the components of the output from an animal, but that $u_4(t)$ contains all the information of the possible output versus input relationships which remain invariant with time. Hence, it follows that in (15) $u_1(t)$ can be interpreted as a growth law and $u_4(t)$ can be interpreted as the main control law.

If the second moment matrix C is of rank one and $|\rho| < 1$, then $u_1(t)$ defines the stable subspace of (1), with $u_1(t) \to \alpha_u$ as $t \to \infty$. The subspace associated with $u_i(t)$ (i = 2, 3, 4) is only stable in the sense of Lyapunov (vide Kwakernaak & Sivan, 1972).

It follows from $u_4(t)$ in (14) and (15) that

$$x_1(t) = \sum_{i=2}^{4} b_i x_i(t) / \sum_{i=2}^{4} b_i^2 + k, \qquad (16)$$

where k is a constant. Control laws associated with $u_2(t)$ and $u_3(t)$ can be similarly expressed.

Geometrically the situation of a second moment matrix C of rank one (vide (5)) can be represented by a straight line in 4 dimensions:

$$x_1 - \alpha_1 = (x_2 - \alpha_2)/b_2 = (x_3 - \alpha_3)/b_3 = (x_4 - \alpha_4)/b_4. \qquad (17)$$

It is then trivial to show that this straight line is given by the intersection of the planes associated with $u_2(t)$, $u_3(t)$ and $u_4(t)$ in (14). It is also obvious that no plane orthogonal to the vectors associated with $u_1(t)$ and $u_4(t)$ is possible with the coefficient of $x_1(t)$ unequal to zero. The vector associated with $u_1(t)$ is determined by the nonzero root of a second moment matrix like (5). Hence, once $u_4(t)$ is chosen no other plane is possible that contains information on the possible input versus output relationships. Hence, (16) is a unique member of the set of planes in which (17) is embedded.

Write

$y_i(t) = \exp(x_i(t))$, i = 1, 2, 3, 4.

Then it follows from (16) that the total differential can be expressed

$$dy_1 = y_1 \sum_{i=2}^{4} b_i\, dy_i/y_i \;\; \sum_{i=2}^{4} b_i^2. \qquad (18)$$

It follows from the uniqueness of (16) that (18) portrays the way in which an animal obeys the law of conservation of energy, since when $\frac{dy_i}{y_i} = bi\,\frac{dy_1}{y_1}$, which follows from (11), is substituted, an identity results.

The growth system (1) can be perturbed by temporarily withholding food. This will result in $dy_1 = 0$ and $dy_2 > 0$, $dy_3 \leq 0$ and $dy_4 < 0$, where the subscripts have the meaning given in (13), so that relative values of the y_i - s will change in (18). Consequently there will only be a change in intercepts in (13) if feeding is resumed soon enough for the b - s to remain unaltered. The change in intercepts can be described in terms of the initial values in (15). This description illustrates how an animal may react to all sorts of disturbances by way of a new growth path distinguishable from the old one in terms of changes in intercepts in (13). For a discussion on experiments on undernutrition from this point of view, Roux (1976) may be consulted.

In some situations a change to a new diet, for example, might enforce a change in the b - s before (18) can be obeyed. In (15) this will result in a change from γ to $\gamma' = c'(1 + (b_2')^2 + (b_3')^2 + (b_4')^2)$, say. An example is from the experiment reported on by Roux & Kemm (1981), where some increases in sawdust percentage in the diets of pigs resulted in changes from ρ to ρ', say.

4. ANIMAL GROWTH AS A CLOSED SYSTEM

The closed nature of the system developed here follows from the law of the conservation of energy and the relative constancy of the partitioning process, as portrayed by (13), by which energy is allocated to body functions. A restriction, like (16) or (18), is enough to cause a zero latent root in a system, and hence to close it. (Rosen (1970) can be consulted for a discussion of the systems theory involved). The conclusion in this paper is, therefore, in fundamental opposition to that of von Bertalanffy (1953), as formalised by Rosen (1972), who takes the point of view that growth is an open system.

If the parameters of (15) would remain unaltered by experimental treatment, its closed nature would preclude the principle of the equifinality (vide von Bertalanffy, 1953) of growth. Since, however, the parameters of (13) and (15) are influenced by diet or fasting, approximate equifinality of body mass may be achievable without contradicting the closed nature of growth.

5. ANIMAL GROWTH AS AN OPTIMAL LINEAR DISCRETE TIME FEEDBACK CONTROL SYSTEM

On a biological and biochemical level it is still far from clear in which way the regulation of growth and feed intake operates (vide Hervey, 1971). According to Bell (1971) the importance of the role of the hypothalamus is beyond dispute. Widdowson & McCance (1975) provide evidence that there is a critical period of development in any animal during which "the appetite and other regulating centres in the hypothalamus are being integrated with the size of the developing organism at that time. The plane of nutrition until this time, and consequently the size the animal has reached, determine what its final size will be, even though it may be smaller than its genetic legacy". The early determination of final size is in accordance with the importance of the vector α in eq. (1) with α_3 and α_4 (from (1), (13)) being the determinants of final size.

According to Hervey (1971) the experimental evidence in favour of feedback in control of feed intake is ambigious. This conclusion is in agreement with the theoretical result of subsection (i) below, which indicates a degenerate type of feedback control characterized by Lyapunov stability. It follows that indications from theory may be especially valuable and may suggest new experimental approaches. Hervey distinguishes between rapid and long time control mechanisms. The use of the cumulated form for all variables would place the control mechanisms proposed in this paper in Hervey's long time category, with the singularity of the matrix B in (2) reflecting the possible overriding control of growth by the hypothalamus.

(i) The feedback system

Assume that animal growth can be completely measured or sensed by the body and that measurement error is negligible. The type of description given by Kwakernaak & Sivan (1972, chapters 3 and 6) are then applicable. Conventionally the discrete time system is denoted by

$$x(t) = Px(t-1) + Qu(t-1), \qquad (19)$$

where P and Q are constant matrices, x (t) describes the state of the system and u (t - 1) is the input. The control law is described by

$$u(t) = Rx(t),$$

from which it follows that the behaviour of the system (19) is described by the roots of

$$P - QR.$$

It is almost trivial to show that (3) can be transcribed to (19). Retain the notation of (1), (3) and (5), but use the subscript r (denoting reduced) for the deletion of the first element in a vector and the first row and column in a matrix. Hence (3) can be transcribed to

$$(x_r(t) - \alpha_r) = (I_r + B_r)(x_r(t-1) - \alpha_r) - c\, b_r (x_1(t) - \alpha_1) + \varepsilon_r(t),$$

$$\text{where } b_r = (b_2, b_3, b_4). \qquad (20)$$

Then, if (17) holds, (16) gives

$$(x_1(t) - \alpha_1) = \sum_{i=2}^{4} b_i (x_i(t) - \alpha_i) \Big/ \sum_{i=2}^{4} b_i^2$$

as control law. Substitution of the control law in (20) then gives

$$x_r(t) - \alpha_r = \Big[I_r + \Big(1 + 1/\sum_{i=2}^{4} b_i^2\Big) B_r \Big] \times (x_r(t-1) - \alpha_r) + \varepsilon_r(t) \qquad (21)$$

The matrix $I_r + (1 + 1/\sum_{i=2}^{4} b_i^2) B_r$ has roots $1 - \gamma, 1, 1$, since $B_r = -cF_r$, with F defined in (5) and $\gamma = c(1 + \sum_{i=2}^{4} b_i^2)$.

On applying the same techniques as in the proof of Theorem 5, it follows from Corollary 1 of Theorem 1 that the influence of $\varepsilon_r(t)$ is eliminated from the parts of (21) associated with the unity roots. Hence with $0 < \gamma < 1$ the system (21) is stable in the sense of Lyapunov (Kwakernaak & Sivan, 1972).

(ii) The possibility of deadbeat control

In the proof of Theorem 3 use was made of the fact that C of rank one implies $\Delta x_i(t) = b_i \Delta x_1(t)$. However, a C of rank one is also consonant with a unique vector α such that

$$x_i(t) - \alpha_i = b_i(x_1(t) - \alpha_1), \tag{22}$$

which is a somewhat stronger assumption since it implies that the points α_i must always be on the corresponding straight lines. This assumption of a unique predetermined α is in contradistinction to shifts in α explicable in terms of the Corollary to Theorem 3, or the permanence of the shifts in intercepts referred to in Section 3. Hence, it is, perhaps, no surprise that the assumption of (22) as a unmutable identity would give, in the place of Theorem 1, A (from eq. (1)) equivalent to cF. The use of cF_r in the place of $I_r + B_r$ in (20) should, of course, then result in so-called deadbeat control.

Diurnal variation in growth (Sollberger, 1965) together with the possibility of growth being "sensed" by the animal body by means of a sampler (Kwakernaak & Sivan, 1972, p. 445) operating after the daily growth increments, would indicate a discrete description of growth. Since deadbeat control is the most efficient control mechanism in the discrete situation, it is, perhaps, deserving of some attention beyond that of mere intellectual curiosity.

(iii) Distinguishing between deadbeat control and Lyapunov stability

In the situation of Lyapunov stability the roots of the system (20) are $1 - \gamma, 1, 1$, with γ defined below (21). In the deadbeat situation the roots derived from (19) would be $\rho, 0, 0$, with

$$\rho = c(1 + \sum_{i=2}^{4} b_i^2). \tag{23}$$

From the discussion in Section 3 it is clear that the unity roots in Theorem 5 give rise to shifts in intercepts in the linear relationships between the $x_i(t)$ - s. This is the sort of behaviour that Roux (1976) discerned in experiments on undernutrition. Further evidence comes from the modification of body composition by the manipulation of feed intake, about which there seems to be general agreement that body composition can be modified easily only through the fat component. Hence it may be possible to choose a desired b_4 for fat deposition in (13) and to feed animals accordingly to a desired fat percentage at a given body mass. For values of γ near to *ad libitum* feed intake, this may be done on the assumption of the constancy of c, b_2 and b_3, as is shown by an experiment reported on by Meissner (1977). Here $\gamma'/\gamma = 0{,}88$ induced a ratio $b'_4/b_4 = 0{,}86$, which is significantly different from unity at the one percent level. The slopes b_2 and b_3 for heat production and protein did not differ significantly and $c = c'$ approximately. This behaviour is in line with (21) rather than (23). The evidence is, therefore, at present convincingly in favour of Lyapunov stability.

Although deadbeat control is extremely efficient it may lead to excessively large input amplitudes or to undesirable transient behaviour (Kwakernaak & Sivan, 1972). In animal growth this probably means that deadbeat control would make physiologically impossible demands. Lyapunov stability, on the other hand, means that the animal may be able to survive until adverse circumstances improve again.

(iv) The optimality properties of the control system with Lyapunov stability

From the roots of $I_r + B_r$ in (20) it is clear that (20) is not stabilisable. Hence the usual theory on the optimality of linear discrete time-invariant systems is of no avail under the present circumstances. However, a suggestion of Rosen (1967), that in a straight line situation the straight line is the minimum of the arc length between 2 points, is applicable.

Let $\Delta x_i(t) = x_i(t) - x_i(t-1)$, for $i = 1, 2, 3, 4$, and denote the arc length for the corresponding time interval by $\Delta S(t)$. A second moment matrix (4) of rank one implies a straight line in 4 dimensions, so that the idea of an arc length in 4 dimensions is meaningful in the present situation. Hence, if there are no shifts in intercepts (see Section 3), Theorem 5 or the system (21) ensure that

$$\Sigma [\Delta S(t)]^2 = \sum_{t=1}^{T} \sum_{i=1}^{4} [\Delta x_i(t)]^2$$

$$= \sum_{t=1}^{T} \Delta' x(t) I \Delta x(t), \tag{24}$$

is a minimum for a given $x_i(T) - x_i(0)$, $i = 1, 2, 3, 4$.

On the other hand Theorem 5 implies

$$u_1(t) - \alpha_u = \rho\,(u_1(t-1) - \alpha_u) + \varepsilon_u(t), \tag{25}$$

where the different terms are as defined in (15). The linear form of (25) suggests

$$\begin{aligned} &\sum_{t=2}^{T} [\Delta S(t)]^2 \\ &= \sum_{t=2}^{T} [\{\Delta u_1(t)\}^2 + \{\Delta u_1(t-1)\}^2] \\ &= \sum_{t=2}^{T} [\Delta x'(t) F \Delta x(t) + \Delta x'(t-1) F \Delta x(t-1)], \end{aligned} \tag{26}$$

from (5) and (15), as candidate for minimization by the systems (15) and (21). The deterministic nature indicated by the rank one situation of the matrix C would ensure that the minimum of (24) would be reached if there are no changes in intercepts of the linear system. In contrast the presence of an error term in (25) gives the minimum of (26) as a lower limit of the achievable minimum induced by (25). Equations (24) and (26) are similar to the quadratic forms considered for minimization in the construction of linear optimal control systems. These minima portray aspects of the law of conservation of energy and the regular partitioning of energy, as should be clear from a comparison with the development in Section 3.

6. EXPERIMENTAL EVIDENCE

At present enough experimental evidence has accumulated at the A.D.S.R.I., Irene to warrant taking the theory developed here seriously. Some results from 4 experiments will be mentioned in support.

Experiment 1

Under the usual circumstances heat production is obtained by subtraction on the arithmetic scale. To counter the objection of artificailly creating linear dependency by subtraction, 3 lambs were permanently kept in confinement and their heat production measured in an open system calorimetric unit. Measurements were taken on alternate weeks, with the other weekly values obtained by interpolation. Body composition was obtained by the tritium dilution technique, (Meissner, 1977) which depends on two independent measurements i.e. tritiated water space and body mass, so that no artificial linear dependency can be created. Nutrient uptake before birth was estimated by the method given by Meissner, Roux & Hofmeyr (1975) and added to cumulative feed intake. Since there is a break in some relationships with the onset of puberty at 13 weeks, only results of biweekly data from 13 to about 30 weeks are given. Most of the measurements fell in this period during which the lambs approximately doubled their body masses from 25 kg to about 50 kg.

Table 1

The percentage values of the latent roots of the covariance matrix of the logarithms of cumulative digestable energy intake, body protein, body fat and cumulative heat production of Mutton Merino lambs

Sheep No.	Number of observations	Largest root	Second root	Third root	Smallest root
K1	8	99,34	0,62	0,04	0,00
W15	7	99,12	0,73	0,15	0,00
W25	6	99,33	0,56	0,11	0,00
Common	21	99,01	0,88	0,11	0,00

This experiment is described by Meissner (1977), and a full discussion will be published by Roux, Meissner & Hofmeyr (1980) in which the biological aspects will be accentuated. In the present context the principal component analysis is important. The results are given in Table 1. In all 3 cases the dominant root is equal to more than 99%. This implies that more than 99% of the aggregate variation in the log measurements of cumulative feed intake, body fat, body protein and cumulative heat production can be explained by the postulated single dimensional linear relationship.

Experiment 2

The results of experiment 1 are confirmed by data on pigs from an *ad libitum* feed intake experiment of Kemm (reported by Roux & Kemm, 1981) in which feed intake was regulated by adding from zero to 32% sawdust to the experimental diets.

In this experiment nutrient uptake during pregnancy and before weaning was estimated from data on efficiency and body composition in the literature, and added to the first measurement of the metabolisable energy consumed during the course of the experiment.

Measurements on feed intake, protein and fat, with heat production obtained by subtraction on the arithmetic scale resulted in a first root of more than 99%. Kemm's data are the results of chemical analyses of carcases, so

Table 2

The percentage values of the latent roots of the covariance matrix of the logarithms of cumulative metaboliseable energy intake, body protein, body fat and cumulative heat production of pigs

Treatment No.	No. of animals	Largest root	Second root	Third root	Smallest root
1	11	99,5	0,3	0,2	0,0
2	10	99,4	0,5	0,1	0,0
3	11	99,6	0,3	0,1	0,0
4	11	99,6	0,2	0,2	0,0
5	11	99,3	0,5	0,2	0,0
6	11	99,4	0,4	0,2	0,0

that each datum represents a different animal. The spread of the data was adequate, since masses were available for pigs growing on a regular course from 11 weeks at 20 - 27 kg to 31 weeks at 83 - 121 kg, depending on treatment.

It seems, therefore, reasonable to conclude from Tables 1 and 2 that the ranks of the covariance matrices are equal to one with the nonzero values on roots 2, 3 and 4 being attributable to measurement error or individual variation, as the case may be. The mathematical plausibility of this conclusion derives from results by Bellman (1960, pp. 60 - 63) on matrices with small perturbations added to them.

With careful experimentation it is often possible to measure feed intake more accurately than body mass, which is influenced by intestinal content. To establish that a first order autoregressive process described growth adequately, h_2 was tested for significance in a model

$$x_1(t) = g + h_1\, x_1(t-1) + h_2\, x_1(t-2) + \varepsilon(t), \qquad (27)$$

where $x_1(t)$ is ln (cumulative feed intake at time t). The results are given in Table 3 for the pigs slaughtered near the end of the experiment.

Experiment 3

The procedure of eq. (27) was also repeated on the sheep data otherwise discussed by Roux (1976). The results are in Tables 4 and 5. The conclusion from Tables 3, 4 and 5 is that a first order autoregressive process fits the data adequately. One point remains. The question is if the values of the regression coefficients near one are not indicative of a root of value one. That the values of ρ $(0{,}93 < \rho < 0{,}97)$ are significantly different from unity in Tables 3 and 4 in Roux (1976) follows from Table 8.5.2. of Fuller (1976) by the use of the published standard errors, S_ρ.

Experiment 4

In an experiment on the feeding of baconers Siebrits (1979) found that pigs fed with a $\rho = 0{,}94$ [defined in (15)] grew in body mass with a $\rho = 0{,}94$ on a low protein (14%) diet and a $\rho = 0{,}92$ on a high protein (16%) diet, in both cases with a standard error of 0,003. The

Table 3

Regression coefficients and their standard errors for pigs

d.f.	Pig No.	Treatment No.	h_1	S_{h_1}	h_2	S_{h_2}
14	311	1	1,094**	0,127	-0,162	0,114
18	160	1	0,608**	0,225	0,274	0,204
12	112	2	1,048**	0,193	-0,115	0,176
14	314	2	0,435*	0,157	0,418*	0,144
16	312	3	1,056**	0,221	-0,129	0,201
14	109	3	1,382**	0,274	-0,423	0,253
16	355	4	0,995**	0,243	-0,069	0,224
14	113	4	0,571*	0,259	0,353	0,244
16	161	5	0,888**	0,249	0,046	0,234
14	310	5	0,661*	0,243	0,243	0,223
14	315	6	0,958**	0,251	-0,047	0,226
16	163	6	0,706*	0,243	0,191	0,223

* Significant at the 5% level
** Significant at the 1% level

deviant value of ρ was accompanied by slight curvilinearity in the system, as one might expect. The value of 0,92 for ρ is in the vicinity of the value of 0,91 found by Roux & Kemm (1981), for a diet with 19 percent protein. The ρ used for feed intake was, actually, more extreme than a $\rho = 0{,}93$ obtained for pigs on *ad libitum* feed intake, with their feed energy concentration diluted by 32 percent sawdust. Hence the high protein diet allowed some reversion in the direction of faster normal growth at lighter body masses.

7. SOME GENERAL PERSPECTIVES

1. An advantage in experimental design and analysis is that the usual estimators of a_i, b_i $(i = 2, 3, 4$ and 5, say, for body mass) and $x_1(0)$, α_1 and ρ, for feed intake, are sufficient statistics for normal distributions under the usual regularity assumptions. Working with sufficient statistics provides a basis for the use in data analysis of estimates of parameters for individual animals, instead of the actual observations. Hence feeds and breeds can be evaluated in terms of the parameters describing growth and its efficiency and rations can be quantified in relation to *ad libitum* feed intake, in terms of percentages of $\gamma = -\ln\rho$, and the behaviour of the slopes and intercepts can be described with reference to this percentage. To this must be added that the description of growth in terms of log-linear theory has the advantage that it provides an easy way of reducing measurement error by the combination of repeated measurements. This is of value in quantifying breeds and feeds over the whole period of active growth, if some estimate of prenatal nutrient uptake of the foetus or pre-experimental feed intake, is available. Roux (1976) and Meissner (1977) can be consulted for examples.

2. The model can only be expected to hold for the period of active growth since the log-linear system corresponds to the way in which a young animal is scaled to maturity. This involves ideas on biological similarity (vide Gunther, 1975) which are based on the mechanical similarity of Newton and the dimensional analysis of Maxwell. That the model does not hold at maturity is indicated by theorems (4) and (5), where cumulative feed intake goes to α_1 as $t \to \infty$, which indicates an intake rate of zero at that point.

3. To the best of knowledge this is at present the only theory which suggests definite error structures to observations on which appropriate statistical analyses can be based. In the other cases an error is merely tagged on, as is convenient. For further discussion, see Roux (1976).

Table 4

Regression coefficients and their standard errors for Mutton Merino ewe lambs

Sheep No.	h_1	S_{h_1}	h_2	S_{h_2}
D5	1,030**	0,263	-0,091	0,245
D6	1,050**	0,260	-0,102	0,244
D16	0,429	0,242	0,459	0,224
D17	1,029**	0,261	-0,088	0,244
D18	1,002**	0,244	-0,059	0,230
D19	1,198**	0,248	-0,248	0,231
D23	0,997**	0,195	-0,666	0,182
D25	0,299	0,200	0,589**	0,186
D29	1,283**	0,239	-0,321	0,226
D30	0,877**	0,253	0,067	0,239

* Significant at the 5% level
** Significant at the 1% level

4. The transformation to straight lines has the advantage that any sort of deviation or change in growth is easily discernable. In this way different growth phases, such as for example, a phase from birth to the onset of puberty, and from the onset of puberty to maturity, have been identified in different species, vide Roux (1976), Meissner (1977) and Scholtz (1979). In each situation the growth phase coincided with some definite identifiable physiological phase such as, say, the development to sexual maturity.

Table 5

Regression coefficients and their standard errors for Karakul lambs

Sheep No.	h_1	S_{h_1}	h_2	S_{h_2}
K2	0,918**	0,233	0,037	0,223
K3	1,156**	0,255	-0,188	0,245
K4	0,867**	0,239	0,082	0,230
K5	0,734**	0,259	0,224	0,251
K6	1,123**	0,256	-0,149	0,248
K13	0,885**	0,256	0,063	0,244
K14	0,793**	0,241	0,136	0,227
K17	0,842**	0,233	0,105	0,223
K18	0,617**	0,244	0,298	0,229
K26	0,725**	0,262	0,203	0,246

* Significant at the 5% level
** Significant at the 1% level

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