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Prediction in animal production models based on the allometric hypothesis when the size variable is random

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ABSTRACT

The expected value of the solution of the differential equation arising from the allometric hypothesis when the variables are random is found. This solution differs from the deterministic solution, so that predictions using the allometric equation which ignore the stochastic nature of the differential equation are biased.

When least squares estimation is carried out using the deterministic solution, ignoring the stochastic nature of the size variable, the estimate of the constant coefficient of the allometric equation may be severely biased. An example shows mild bias in estimates of the maturity parameter, but large bias in the estimate of the constant coefficient.

To obtain unbiased estimates of the parameters in the allometric equation a factor equal to the reciprocal of the square of the size variable must be added to the usual log-log regression used to calculate estimates of the parameters.

These results have application to models based on the allometric hypothesis, in particular models which are used in studies of carcass composition and the description of maintenance requirements in animal nutrition. When these models are used for prediction they need to be modified to account for any random variation occurring in the size variable.

Keywords: allometric, size variable, stochastic, estimators, bias.

INTRODUCTION

Huxley, (1932) formulated the allometric hypothesis to describe the relationships between the components of biological organisms. He inferred that in order to cope with the physical environment the relative growth of an organ of an animal is in constant proportion to the relative growth of the animal. Thus the growth of bone of an animal would be in some constant proportion to the growth of the whole animal.

Because of the perceived fundamental nature of the allometric hypothesis as an organising principle in animal structure, the allometric equation has become the basis for computer models of carcass composition for farm animals. The role of these models is to predict carcass composition when various animal management strategies are applied.

Two types of allometry are distinguished, growth allometry and size allometry (Sprent, 1972). Growth allometry refers to a sequence of observations made on organs of the same animal through time. Size allometry refers to a series of observations made on the organs of different animals, usually at the same time when each animal would be at a different stage of maturity. These measurements are combined to make inferences about development in the population of animals from which the sample was drawn.

It is important that the random nature of the variables involved in the allometric equation be taken into account, particularly for size allometry which must consider the effect of variation between animals on the allometric hypothesis. This paper reports the results of a theoretical investigation of this problem.

THE STOCHASTIC ALLOMETRIC EQUATION

The allometric hypothesis states that the relative growth of an organ (part) is directly proportional to the relative growth of the organism (whole).

One tool for expressing such a hypothesis in mathematical terms precise enough to study the consequences is a differential equation. The consequences are derived from the solution of the differential equation, and can be evaluated for agreement with reality.

The differential equation of the allometric hypothesis can be derived as follows: Let y be the weight of the part(eg. lean weight in an animal carcass), and x be the weight of the whole (eg. carcass weight). The instantaneous growth rates are dy/dt and dx/dt where t is time. The specific growth rates are in each case 1/y dy/dt and 1/x dx/dt.

The allometric hypothesis states simply that these two specific growth rates are proportional to each other; ie.

$$\frac{1}{y}\frac{dy}{dt} = \frac{k}{x}\frac{dx}{dt} \quad (1)$$

where k is the constant of proportionality between the part (y) and the whole (x), often called the maturity, or the maturing rate.

In most applications interest is in the relationship between y and x, not involving the independent variable time.

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Thus time can be eliminated from equation (1) to give:

$$\frac{dy}{dy} = \frac{k}{x} \quad (2)$$

The solution of equation (2) is by separation of variables (see for example Zill, 1979) to give:

$$y = ax^k \quad (3)$$

where a is the constant of integration.

Equation (3) is commonly referred to as the allometric equation, and the impression may sometimes be given that this equation is fundamental. This is misleading. The differential equations (1) and (2) are the fundamental equations of allometry because these equations express the allometric hypothesis precisely. Equation (3) merely defines the consequences of this definition. Extensions to the allometric hypothesis should proceed from equations (1) and (2), not from equation (3).

However, when the variables involved in the allometric hypothesis are random then equations (1) and (2) become stochastic differential equations. The solution of a stochastic differential equation is, in general, not the same solution as for its' deterministic counterpart.

Pleasants *et al.*, (in press) have shown that the solution of the expected value (mean) of the stochastic differential equation (2) is:

$$y = ax^k e^{\frac{k(k-1)(k-2)\sigma^2}{4x^2}} \quad (4)$$

Estimation of the Parameters of the Allometric Equation

When fitting the deterministic allometric equation (3) to data it is usual to transform the nonlinear equation to a linear equation by taking logs, thus:

$$\ln y = \ln a + k \ln x$$

This model may be fitted by ordinary linear regression.

However this formulation assumes that the deviations of observations from the equation are multiplicative rather than additive. This may not be a reasonable assumption in some circumstances. If additive deviations are assumed then equation (3) must be fitted with a nonlinear regression.

Pleasants *et al.*, (in press) have shown that when the size variable is random, but the coefficient of variation of the size variable is constant, then :

1. Estimates of the integration constant a are severely biased when k does not equal 0, 1 or 2 under additive and multiplicative errors.
2. Estimates of the maturity k are unbiased under additive errors.
3. Estimates of the maturity k are biased under multiplicative errors unless k equals 0, 1 or 2.

When the coefficient of variation of the size variable is not constant then both k and a will be biased under both additive and multiplicative errors.

Equation (4) suggests that unbiased estimates of the parameters of allometry can be found by fitting the multiple regression equation (for multiplicative errors)

$$\ln y = a + k \ln x + \frac{z}{x^2}$$

Similarly for additive errors equation (4) can be used directly.

To illustrate these issues results from a study by Butler-Hogg, (1984) into carcass composition of lambs were used to construct simulated data for an allometric equation having parameters a = 0.05, and maturity k = 1.5. Carcass weights were simulated from a normal probability distribution with a standard deviation of 3 kg. The error structure was additive.

Using least squares to estimate the coefficients of the allometric equation without taking account of the random nature of the size variable yields estimates of a = 0.09, and k = 1.3 ± 0.07. Both parameters are biased, especially the parameter a. Adding the reciprocal of the square of x to the regression equation produced estimates of a = 0.04 and k = 1.5 ± 0.25, which are both close to the values used in the simulation.

DISCUSSION

The allometric principle is the basis for statistical models which describe changes in carcass composition of domestic animals (Butler-Hogg, 1984; Seebeck, 1983; Korver *et al.*, 1987). When the parameters of these models are estimated ignoring the random nature of the size variable the resulting bias, especially in the estimation of the integration coefficient a will ensure systematic errors of prediction in the model. This problem will be compounded when predictions are to be made far from the mean of the statistical model used to obtain the estimates.

When models designed to predict carcass composition are based on the allometric hypothesis (Keele *et al.*, 1992; Williams *et al.*, 1992; Emmans, 1988), error will arise if the estimates of the parameters of these models have ignored any randomness in the values of the size variable.

When the size variable in an allometric model is random the regression equation used to estimate the allometric parameters should include a term in the reciprocal of the square of the size variable. If the range of the size variable in an experiment is small then multicollinearity problems may be encountered due to a high correlation between the log of the size variable and the reciprocal of the square of the size variable. In this case it may be advisable to regress on the Principal Components (Wonnacott and Wonnacott, 1979).

The model used to describe maintenance energy in animal nutrition has the same general form as the allometric hypothesis. The heat generated in maintaining a resting animal is considered to be proportional to the change in volume of the animal relative to a change in the surface area of the animal. Treating an animal as an approximate cylinder, and considering a proportional relationship between relative rates of change, the hypothesis suggests that the maintenance energy should be related to animal liveweight (w) by:

$$\textit{energy intake} = cw^k$$

where c and k are parameters to be estimated.

The parameter c in this relationship is the maintenance energy which is the proportion of energy intake not used for lactation, growth etc. It is estimated by partitioning the energy intake amongst lactation, growth etc. and w^k for a number of animals of differing liveweight. Thus liveweight, the size variable, is stochastic. Therefore from the results summarised in this paper it would be expected that the coefficient of maintenance c would be biased. The example suggests that this bias may be very substantial, and therefore very misleading about animal nutrition. The review of Joyce *et al.*, (1975), which quotes large variances in the estimates of the maintenance coefficient over a number of trials, would support the existence of bias in the estimates of this parameter.

The formulation of this problem at the fundamental level of differential equations has enabled modifications to the allometric state equation to be found. This illustrates the value of using this kind of formulation in agricultural systems generally. Agricultural problems involving dynamical systems can be analysed and understood very well with this approach in either a deterministic or stochastic way. We believe this approach is under utilised at present, yet holds great promise.

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