

BIVARIATE METHODS TO ESTIMATE PROTEIN AND LIPID DEPOSITION EFFICIENCIES FOR BREEDING IMPROVEMENT

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INTRODUCTION

For selection purposes and the prediction of breeding progress estimates of efficiencies are necessary for individual animals. Estimates of such efficiencies cannot be obtained by the conventional multiple regression procedures due to the high correlation between protein and fat deposition in individual animals. The present approach avoids this problem of collinearity by transforming the estimation procedure from multiple regression to straightforward bivariate regression by adjoining assumptions on the energy partitioning between protein and lipid deposition as well as its control. The simplest realistic assumptions are that the proportions of growth energy devoted to protein and lipid deposition are proportional to the energetic proportions of body protein and lipid respectively and that the activities of enzymes responsible for the control of protein and lipid deposition vary with powers of the size of these chemical components. It will be shown that these assumptions lead to bivariate regression estimates of protein and lipid deposition efficiencies in agreement with multiple regression results.

THEORY

Kielanowski first formulated the generally accepted model for the description of energy requirements for maintenance and growth. For present purposes the formulation of the ARC (1981) will be transcribed as follows, $dE/dt = dF/dt/k_F + dP/dt/k_P + dA/dt/k_A$, (1) with dE/dt = the rate of energy assimilation MJ/d, measured in terms of metabolizable or effective energy ; dF/dt = the rate of fasting metabolism (MJ/d) ; dP/dt = rate of protein deposition (MJ/d) ; dA/dt = rate of lipid deposition in adipose tissue (MJ/d) ; k_F = efficiency of energy utilization for maintenance ; k_P = efficiency of energy utilization for protein deposition and k_A = efficiency of energy utilization for lipid deposition in adipose tissue. Under the assumption of constant efficiencies the cumulate form of (1) is $E = F/k_F + P/k_P + A/k_A$, with E , F , P and A measured in MJ. It is, furthermore, advantageous to write total energy retention as $R = P + A$ and $E = F/k_F + R/k_R$, with k_R the efficiency of energy utilisation for total energy retention. For some purposes it is handy to write in the alternative form $E = E_F + E_R$, with $E_F = F/k_F$ and $E_R = R/k_R$ implied. For easy reference note that $dE_R/dt = dP/dt/k_P + dA/dt/k_A$. (2) which implies that the proportion of growth energy (dE_R/dt) devoted to protein deposition is $dP/dE_R/k_P$ and that the proportion devoted to lipid deposition is $dA/dE_R/k_A$.

The hypothesis that the proportions of growth energy devoted to protein and lipid deposition is proportional to the energetic proportions of body protein and lipid implies that

$$dP/dE_R / k_P = P / (P + A) \text{ and } dA/dE_R / k_A = A / (P + A). \quad (3)$$

With $P + A = R = k_R E_R$, $dP/dE_R = (k_P/k_R) (P/E_R)$ and $dA/dE_R = (k_A/k_R) (A/E_R)$, so that the solutions to (3) are $E_R \propto P^{k_R/k_P}$ or $P \propto E_R^{k_P/k_R}$ and $E_R \propto A^{k_R/k_A}$ or $A \propto E_R^{k_A/k_R}$. (4)

$$\text{Elimination of } E_R \text{ in (4) implies } A \propto P^{k_A/k_P} \text{ or } P \propto A^{k_P/k_A}. \quad (5)$$

The hypothesis that the activities of enzymes responsible for the control of protein and lipid deposition vary with powers of the size of the chemical components implies

$$dP/dE_R / k_P = Q/c_1 P^b \text{ and } dA/dE_R / k_A = Q/c_2 A^e, \quad (6)$$

with $Q^{-1} = (1/c_1 P^b + 1/c_2 A^e)$. The values of b and e are of opposite sign and often of magnitude that would allow Q to be approximated by a constant over certain growth intervals (Roux, 2002). Then, in situations where Q can be approximated by a constant, solutions to (6) are $E_R \propto P^{b+1}$ or $P \propto E_R^{1/(b+1)}$ and $E_R \propto A^{e+1}$ or $A \propto E_R^{1/(e+1)}$. (7)

Alternatively, it follows from the elimination of dE_R and Q in (6) that $P \propto A^{(e+1)/(b+1)}$. Hence, (6) becomes

$$dP/dE_R/k_P = (e+1) k_A P / [(e+1) k_A P + (b+1) k_P A] \quad (8)$$

and $dA/dE_R/k_A = (b+1) k_P A / [(e+1) k_A P + (b+1) k_P A]$

A comparison of (3) and (8) shows that the hypotheses of division of growth energy according to body composition and control by enzyme activity are equivalent if and only if

$$(b+1)k_P = (e+1)k_A = c \text{ (constant)}. \quad (9)$$

The constant c in (9) can be evaluated from the restriction $k_A \leq 1$ and theory of Roux (2002) on enzyme activity in adipose tissue, which gives $e = -q/3$, with $0 \leq q \leq 1$ a measure of the cellular state of adipose tissue. A value of $q=0$ indicates adipose tissue growth completely by cell number and $q=1$ indicates growth completely by cell size. Since $k_A = 3c/(3-q)$ from (9),

$$c = 2/3 \text{ will cause } k_A \leq 1 \text{ as } q \leq 1. \text{ Hence it follows from (9) that } k_P = 2/3(b+1) \quad (10) \text{ and } k_A = 2/3(e+1) \quad (11) \quad k_A = 2/(3-q) \quad (12), \text{ for } e = -q/3.$$

In some growth intervals intake (E) can be approximated by constant multiples of energy devoted to fasting metabolism (E_F) (ARC, 1981). Since $E = E_F + E_R$, E must also be approximately equal to a constant multiple of E_R (energy devoted to retention), or $E \propto E_R$. (13). The relationship (13) implies that (4) and (7) are also approximately valid for E substituted for E_R , in certain growth intervals.

RESULTS AND DISCUSSION

Values of b in (10) and (6) can also be coupled to protein synthesis rates. Both theory and experimental evidence indicates that values of $b = 1/3$ and $b = 2/3$ are possible for protein synthesis rates (Roux, 2002). For $b = 1/3$ (10) predicts $k_P = 1/2$ in agreement with ARC (1981) for pigs and for $b = 2/3$ (10) predicts $k_P = 2/5 = 0.40$ in agreement with Emmans (1994), as indicated in table 1. With adipose tissue growth due to both hypertrophy and hyperplasia a value of $q = 1/2$ may be plausible. From (12) this predicts $k_A = 0.80$, near to the average value of 0.81 obtained by Klein and Hoffmann (1989) for an average of 57 different experiments reviewed by them.

The hypothesis that the division of growth energy to protein and lipid disposition is proportional to the energetic fractions of body composition {(3), (4)} can be tested on data from serial slaughter experiments on pigs from 1.8 to 90 kg reported by Campbell and Dunkin (1983a, 1983b) and Campbell *et al.* (1983, 1985). To calculate the cumulate energy for growth (E_R) the data were divided into two groups of males/high protein and females/low protein combinations, each subdivided into three groups of approximately 60%, 80% and 100% of *ad libitum* intake. E_R was calculated from energy ingestion (E) by subtraction of maintenance energy (E_F) calculated as recommended by the ARC (1981). E_R up to 1.8kg live weight was estimated for conception onwards, by assuming an energetic efficiency of 0.67. The loglinear

form of the relationship (4) with E_R as independent variable was estimated for the interval 19-90kg and did not differ significantly between the six sex/protein level/ percentage *ad libitum* intake subgroups. The calculated exponents estimate the ratios $k_p/k_R = 0.71$ (s.e. 0.025 d.f. 11) and $k_A/k_R = 1.09$ (s.e. 0.030 d.f.11). The experimental design allows a separate weighted estimate of $k_R = 0.69$ (s.e. 0.069) by conventional methods from efficiencies calculated by Campbell *et al.* (1985), in good agreement with the ARC (1981) accepted value of $k_R = 0.70$. This allows estimation of $k_p = (0.69) (0.71) = 0.49$ and $k_A = (0.69) (1.09) = 0.75$, in turn in good agreement with generally acceptable mean values calculated from ARC (1981) in table 1. The conclusion follows that the hypothesis of equation (3) receives strong support from the data of Campbell and Dunkin (1983a, 1983b) and Campbell *et al.* (1983, 1985).

The validity of the rest of the theory can be evaluated by calculating $1/(b+1)$ from the loglinear regression of P on E and $1/(e+1)$ from the loglinear regression of A on E as suggested by (7) and (13). Then, by multiplying with a factor 2/3, k_p and k_A are obtained from (10) and (11). Doing so on published estimates of regression coefficients give the estimates of k_p and k_A calculated from Roux and Kemm (1981) and Kemm *et al.* (1991) in table 1. The agreement to generally accepted values quoted in the same table is conspicuous.

Table 1. Estimates from the literature of protein (k_p) and lipid (k_A) efficiencies for pigs by either bivariate (T) or multivariate (M) regression techniques

Reference	Regr.	Interval	d.f	k_p	s.e	k_A	s.e
Roux and Kemm (1981)	T	11-31wk	51	0.39	0.009	0.81	0.016
Kemm <i>et al.</i> (1991)	T	30-90kg	11	0.49	0.010	0.71	0.008
ARC (1981)	M	15-110kg	7	0.53	0.029	0.74	0.035
Emmans (1994)	M	-	10	0.40	0.008	0.71	0.017

The agreement between estimates based on (4) and on (7) shows that the estimates of efficiencies and exponents of the powers are such that hypotheses on division of growth energy according to body composition and on power control by enzyme activity are equivalent. On the basis of (10) and (11), a comparison between (4) and (7) indicates agreement between them if the value of k_R is equal to 2/3. The average value from the ARC (1981) on pigs for the interval 13-90kg is $k_R = 0.70$ (s.e. 0.014 d.f.8), which is not significantly different from 2/3. Taken together with the results in Table 1, this is an indication that the approach of this paper may be of fairly general applicability. A further indication of the generality of the present approach is that it is in agreement, from (5) and (6), with a generally accepted power (allometric) relationship between body protein and lipid (Emmans and Whittemore, 1991).

CONCLUSIONS

The evidence from table 1 indicates that estimates obtained from the proposed bivariate regression method are in excellent agreement with generally accepted values from carefully executed multivariate studies. The difference between estimates from Roux and Kemm (1981) and Kemm *et al.* (1991) on different types of pigs suggests the possibility of genetic differences that can be exploited for breeding purposes. This indicates that studies on the

quantitative inheritance of protein and lipid deposition efficiencies from breed differences, selection experiments or the estimation of genetic parameters may be worthwhile.

In a study on energy partitioning in different types of growing pigs van Milgen and Noblet (1999) found that normally the proportion of growth energy ingestion designated for protein deposition declined with increasing body mass in the interval of 20-107 kg. Extremely lean male genotypes, however, maintained a constant partitioning for protein and lipid deposition in relation to body mass. In terms of the present theory constant partitioning implies $b = 0$ and $e = 0$, from (6). From equation (10) this suggests $k_p = 2/3$. Unless pigs can be bred with increased partitioning of growth energy to protein deposition with increased body mass, $k_p = 2/3$ may well be the maximum achievable efficiency for protein deposition. In contrast, the prediction of $k_A = 2/3$ from (11) for constant partitioning is lower than the values of k_A normally estimated. Separate estimates for extremely lean male genotypes of k_p and k_A , could, therefore, provide an interesting test of the proposed theory as well as indications of likely breeding expectations.

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