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The description of the rate of protein and lipid growth in pigs in relation to live weight

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SUMMARY

The paper seeks to compare the effectiveness of various functions as appropriate to express protein retention and lipid retention as a function of pig live weight. Linear descriptors were adequate for protein growth over the 20 to 120 kg live weight range, but not adequate when higher live weights were included. Linear descriptors were not adequate for lipid growth over any weight range. Quadratic and cubic polynomials, and the logistic function, were faulted on their failure to describe the known biology. Augmentation of the allometric function added nothing to the simple form. The Gompertz function was consistently effective for the description of daily protein retention rate. The Bridges and Richards functions are more flexible than the Gompertz with respect to the point of inflection, but when applied they resembled the Gompertz and therefore did not materially influence the descriptive outcome. The cubic polynomial, augmented allometric, Bridges and Richards functions, although favoured in other reports, were found to add nothing to the more simple functions. It is concluded that protein retention can be well expressed in relation to live weight by linear and Gompertz functions. Lipid retention could be well described by an allometric relationship with pig mass.

INTRODUCTION

Optimization of provision of dietary energy and nutrients to growing pigs requires some method for the description of expected rates for the incrementation of protein and lipid. There are differences of scientific opinion over the nature of the function that might best describe protein and lipid growth as the pig increases in weight and age (Schinckel 1999), and different functions may be considered to have different degrees of biological meaning and logic. The appropriate form for growth description is examined in the current paper through the reanalysis and comparison of the existing data sets of Tullis (1982) and Wagner *et al*. (1999); and recent propositions that more sophisticated functions with increased numbers of parameters improve description in a useful way are tested.

The reviews of Kielanowski (1969) and Rerat (1972) suggested that a single value be used to describe the daily protein retention rate (Pr_{max}) that might be expected between 20 and 120 kg live weight, which is consistent with linear growth. Apart from the linear form, other functions in the polynomial series have been discussed by NRC (1998), who recommended the use of a cubic expression to describe daily gain as a function of live weight. The description of protein growth through a part/whole allometric relationship with the live body follows from the suggestion of Huxley (1932). However Schinckel & de Lange (1996) suggested that the simple allometric form was faulted in the assumption that the body component changes according to whole body weight in a uniform way, and that an 'augmented allometric' function could account for such non-uniformity. Schinckel (1999) was of the view that the use of allometric functions to describe protein growth will underestimate early growth and overestimate later growth.

Sigmoidal functions to describe the mass of tissue as a function of time (rather than weight) have been discussed by, amongst others, Hammond (1940), Brody (1945) and Schinckel (1999). The sigmoidal descriptor is considered appropriate because it characterizes (1) a period of increasing growth at younger ages and lower live weights, (2) a period of decreasing growth rate at greater ages and higher live weights, (3) a point of inflection between the two around which

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there is apparent linearity and (4) an asymptote at which point maturity is approached. The Gompertz (1825) function requires as parameters the asymptote of the y-axis (an approximation of maturity for the tissue concerned) and a growth coefficient. The y-coordinate of the point of inflection is fixed at 1/e of the asymptote. The Bridges function (Bridges *et al.* 1986) and the Richards function (Richards 1959; described by France & Thornley 1984) are more complex and flexible than the Gompertz, each having four parameters respectively, and not having the inflection point fixed at 1/e. The Bridges function may be used with three parameters when the constant term is trivial. Different points of inflection may be an important characteristic of different pig populations. These functions may be differentiated with respect to time to give derivatives to describe the gain (dy/dx) as a function of tissue weight. In the case of the protein mass and its daily rate of gain, the differentiated function places protein mass on the right hand side of the equation (x axis of a graph), whereas in practice the requirement is to have gain expressed as a function of live weight. Parameterization of the undifferentiated equation does not therefore yield suitable values for solution of the derivative where interest is in gain as a function of live weight. The differentiated form may however be fitted to data sets where protein gains were determined over discrete weight ranges by serial slaughter. The sigmoidal functions characterize a period of increasing growth rate at lower live weights rising to a peak or maximum value, followed by a period of decreasing growth rate diminishing to approach zero as mature live weight is assumed to be attained. For the Gompertz function the peak value for protein growth rate will occur at 1/e of A, the live weight at maturity. For the Richards and Bridges functions this point is not fixed.

General and differentiated equations for all the functions reported are given as footnotes to the respective Tables.

In the case of lipid, Whittemore & Fawcett (1976) and Whittemore (1995) considered the expected maximum lipid retention (Lr_{max}) to be a function of dietary energy supply. Emmans (1988), however, proposed that the desired lipid retention of pigs (analogous to Lr_{max}) might also be described by the Gompertz (1825) function. If the growth coefficients are assumed similar, then the ultimate lipid mass (Lt_{max}) may be simply stated as a ratio of Pt_{max}, and Lr_{max} and Pr_{max} will be related allometrically. A restraint upon the upper limit for lipid retention (Lr_{max}) is often presumed to have no practical interest, but may be relevant for lean genotypes, which if assigned a lower value for Lr_{max} would also show a lower value for $Lt_{max.}$ The possibility that selection against fat in growing pigs may have led to breeding sows with reduced fat reserves is reported by Kerr & Cameron (1996).

MATERIALS AND METHODS

The published data set of Tullis (1982) was interrogated through the medium of SIGMAPLOT 5, a product of SPSS Science (Chicago, Illinois). The SigmaPlot curve fitter uses the Marquardt–Levenberg algorithm (Marquardt 1963; Press *et al.* 1986) to find the coefficients (parameters) of the independent variable(s) that give the 'best fit' between the equation and the data. This algorithm seeks, by iteration until the differences between the residual sum of squares no longer decreases significantly, the values of the parameters that minimize the sum of the squared differences between the values of the observed and predicted values of the dependent variable (convergence). For the various fitted equations the standard error of the values for the terms is given in the form ($\pm$S.E.), together with the root mean square (RMS). The RMS is the square root of the residual mean square, or the root mean square error.

The detailed data set collected by Tullis (1982) relates to the unrestricted growth of entire male, female and castrated male pigs from 20 to 200 kg live weight. Forty-one pigs were the subject of serial slaughter and full body composition analysis throughout the course of the experiment, and the chemical components determined were as reported by Whittemore *et al.* (1988). From the data of Tullis, values for the achieved daily protein retention may be obtained by difference, given the chemical analysis for body protein mass at each of the serial slaughter weights and knowledge of the number of days lapsed between them. It was not the method used by Whittemore *et al.* (1988) for the determination of the rate of protein retention as a function of increasing live weight. This earlier method, recently criticized by Schinckel (1999), divided the problem into two steps. The Gompertz function is employed not in relation to protein mass, but live body mass, and then protein mass is determined as an allometric function of live weight. Alternative approaches are now appropriate. The present analysis (in contrast to the original) presumes that the absolute mass of protein in the slaughtered pigs was representative of the absolute mass of protein in the pigs remaining on trial, irrespective of differences in live weight. Importantly, Whittemore *et al.* (1988) determined the rate of protein retention for the mean weight of pig between 20 kg (in all cases) and the subsequent respective slaughter weight at five intervals up to 200 kg. The present analysis will determine the rate of protein retention progressively for the mean of each of the five intervals. This methodology will allow a proper analysis of protein retention as a function of live weight at progressive, but discretely separated, points through growth, as opposed to the previous analysis which was 'damped' by all retentions being calculated from the experiment's origin. The present analysis will therefore be

Table 1. *Coefficients determined for fitted equations* (*with* S.E. *in parentheses*). *y = protein mass* (*kg*)*; x = time* (*days*). *Data from Tullis* (*1982*) (n = *41*)

	Linear	Gompertz	Bridges	Logistic	Richards
r^2	0·953	0·924	0·923	0·922	0·904
RMS	0·941	2·33	2·34	2·36	2·66
a	0·113 (0·0050)				
A		28·9 (1·62)	28·2 (0·187)	27·0 (1·07)	67·1 (153)
b		81·8 (11·6)	1·81 (0·213)	49·6 (5·90)	
n					−0·838 (1·28)
x^o		120 (6·40)		143 (6·47)	
m			0·0000813 (0·0000805)		
k					0·00201 (0·00790)
y_o	−2·94 (0·586)				0·0191 (4·29)

Linear: $y = y_o + a \times x$.
Gompertz: $y = A \times \exp(-\exp(-(x-x^o)/b))$ [where $1/b = B$].
Bridges: $y = y_o + A \times (1-\exp(-(m \times x^h)))$ [where $y_o = 0$].
Logistic: $y = A/(1+\exp(-(x-x^o)/b))$.
Richards: $y = (y_o \times A)/(y_o^n + (A^n - y_o^n) \times \exp(-(k \times x)))^{1/n}$.

more sensitive to the possibility of curvilinear response. Whereas in the original analysis the ultimate estimate for protein retention rate related to the 20 to 200 kg growth interval (mean 110 kg), in the present analysis the ultimate estimate will relate to the mean of the ultimate (200 kg) and penultimate (150 kg) live weight groups (mean 175 kg). In the present case, mean values are calculated for the live body weight and respective protein mass for the initial slaughter group and each of the five slaughter points. The protein retention rates are determined as the difference between the protein masses found at each slaughter point and those found at the previous slaughter point, divided by the number of days elapsed. The daily rates of protein retention thus determined were taken to relate to the live weight calculated as the mean between the two slaughter points. The data of Tullis (1982) related to three sexes. Preliminary analysis indicated that the influence of sex upon the expression of protein retention as a function of live weight was small, and the data were pooled.

Wagner *et al.* (1999) present a data set giving chemical composition and physical dissection of pigs from 25 to 152 kg live weight. For present purposes, mean values were transcribed, as it was the mean weights for the serial groups that were reported. With $n = 16$, the various functions of interest were fitted by the present authors. Further interrogation of the data with regard to the fitting of curves to incremental gains has been made possible through the kind supply by the Schinckel group at Purdue University, USA, of values for pig age at each of the eight serial-group weights, these not being required for the original interpretation of their data. The same methodology as described previously for the Tullis data set was then implemented.

RESULTS

Where y is the protein mass (kg) and x is time (days), all the functions, sigmoidal and linear, fitted rather similarly (Table 1). The Bridges and Richards functions were sensitive to the initial values chosen for the parameters. Solutions of the Bridges and Richards functions generate curves indistinguishable from the Gompertz. It was evident that the degree of prior knowledge of parameter value required is greater if the inflection point is allowed to vary. The prediction for A by Richards was associated with high error.

Differentiation of the Gompertz equation where y = protein mass and x = time (as Table 1, and where B is 1/b.), leads to the derivative where dy/dx is the daily protein gain (Pr) as a function of time (x)

$$dy/dx = A \times B \times \exp(-B \times (x-x^o) - \exp(-B \times (x-x^o))).$$

For daily protein gain ($dy/dx = Pr$) as a function of protein mass ($y = Pt$)

$$dy/dx = y \times B \times \ln(A/y)$$

where A is the protein mass (Pt) when Pr has diminished to zero.

The equivalent differentiated form for the Bridges function is

$$dy/dx = b \times m \times (A-y) \times (\ln(A/(A-y))/m)^{((b-1)/b)}$$

and that for the Richards function is

$$dy/dx = (k \times y \times (A^n - y^n))/(n \times A^n).$$

Table 2 refers to the fitting to the data of the differentiated functions to express daily protein retention ($dy/dt = Pr$) as a function of total body protein mass (Pt). After selection of appropriate initial parameter values, the Bridges and Richards functions were similar to the Gompertz in both the effectiveness of fit and in the solution.

However, as discussed above, practical interest is in the expression of daily protein gain not as a function of body protein mass, but rather of live body weight. The examination of live weight as an appropriate alternative is shown in Table 3 which refers to the fitting of the differentiated functions to express daily protein retention ($dy/dt = Pr$) as a function of live body weight (W). For the Gompertz, A indicates the live body weight at which protein retention has diminished to zero. Peak value for Pr may be estimated as ($A \times B/e$) and is 0·123 kg. Peak growth occurs at the point of inflection, being 1/e (0·37) of A, or 77 kg. The lower value for B, that occurs when live weight rather than protein mass is used, is apparent ($B = 0{\cdot}0016$ rather than $B = 0{\cdot}0108$). After selection of appropriate initial parameter values, the Bridges and Richards functions were coincident with the Gompertz in both the effectiveness of fit and in the solution. However, the adjusted r^2 value for the Gompertz was marginally higher than that for the Bridges and Richards (adjusted $r^2 = 0{\cdot}675$, 0·647, 0·655). The logistic function fitted poorly, suggesting that the constraint imposed by this function of the point of inflection and peak rate of growth occurring at 0·5 of mature weight is inappropriate.

The allometric functions expressing protein mass in relation to the whole live body weight where y = total protein mass (Pt, kg) and x = live body weight (W, kg) are given in Table 4. Linear and allometric functions were equally effective at describing the data. The augmented allometric added nothing to either description or interpretation, and error terms were high.

Table 5 shows that the third order polynomial was able to express the daily rate of protein retention (Pr) as a function of live body weight (W), but no better than the sigmoidal functions. Its advantage over the quadratic is that the cubic allows the peak rate of protein retention to occur at less than 0·5 of maturity. However, the biologically nonsensical behaviour of the cubic curve at higher live weights makes the function unsafe for wider weight ranges. The quadratic does not suffer from the same shortcoming, but its peak occurs at a constant 0·5 of maturity. The first-order polynomial function fits the 20 to 200 kg live-weight range less well, but rejection is premature because the protein retention rates achieved between 150 and 200 kg have an important bearing upon the curvature of the expression. It may legitimately be argued that, for most of the world's pig production, information covering this phase of growth is interesting but irrelevant. The data were therefore further analysed for $n = 12$, with the final values omitted. The data now presented a scattered plot. The Gompertz equation fitted with $B = 0{\cdot}00163$ ($\pm$ 0·000194), $A = 205$ ($\pm$ 19·4), with $r^2 = 0{\cdot}202$ and $RMS = 0{\cdot}0197$, while the first order polynomial fitted with $a = -0{\cdot}000029$ ($\pm$ 0·000178), $y_o = 0{\cdot}112$ ($\pm$ 0·0151), with $r^2 = 0{\cdot}00269$ and $RMS = 0{\cdot}0220$. (In these and subsequent equations presented in the text, the value in brackets is the standard error.) The peak Gompertz value for $A \times B/e$ is 0·123 kg daily, while the linear constant is 0·112 kg daily. Both functions are thus equally adept at demonstrating the relationship between the daily rate of protein retention and live weight to be flat between live weights of 20 to 150 kg, and a single value over this live weight range may well be considered a sufficient descriptor.

Live weight is the preferred x variable for practical usage, as indicated in the introduction. However for

Table 2. *Coefficients determined for fitted equations (with S.E. in parentheses). y = daily rate of protein retention (kg); x = total protein mass (kg). Data from Tullis (1982) (n = 15)*

	Gompertz	Bridges	Richards
r^2	0·536	0·531	0·547
RMS	0·0221	0·0231	0·0227
B	0·0108 (0·00100)		
b		1·71 (0·425)	
n			−0·195 (0·363)
m		0·000116 (0·000267)	
k			0·00923 (0·00307)
A	30·1 (1·71)	30·0 (3·12)	31·3 (3·41)

Gompertz: $y = x \times B \times \ln(A/x)$.
Bridges: $y = b \times m \times (A-x) \times (\ln(A/(A-x))/m)^{((b-1)/b)}$.
Richards: $y = (k \times x \times (A^n - x^n))/(n \times A^n)$.

Table 3. *Coefficients determined for fitted equations* (*with* S.E. *in parentheses*). *y = daily rate of protein retention* (*kg*)*; x = live body weight* (*kg*). *Data from Tullis* (*1982*) (n = *15*)

	Gompertz	Logistic	Bridges	Richards
r^2	0·698	0·403	0·697	0·704
RMS	0·0178	0·0251	0·0186	0·0184
B	0·00161 (0·000116)	0·0000143 (0·0000149)		
b			1·83 (0·354)	
n				−0·131 (0·271)
m			0·00000182 (0·00000518)	
k				0·00146 (0·000344)
A	207 (8·53)	190 (6·67)	202 (13·1)	212 (15·1)

Gompertz: $y = x \times B \times \ln(A/x)$.
Logistic: $y = B \times x \times (A-x)$.
Bridges: $y = b \times m \times (A-x) \times (\ln(A/(A-x))/m)^{((b-1)/b)}$.
Richards: $y = (k \times x \times (A^n - x^n))/(n \times A^n)$.

Table 4. *Coefficients determined for fitted equations* (*with* S.E. *in parentheses*). *y = protein mass* (*kg*)*; x = live body weight* (*kg*). *Data from Tullis* (*1982*) (n = *41*)

	Linear	Allometric	Augmented allometric
r^2	0·964	0·966	0·966
RMS	1·59	1·55	1·57
a	0·133 (0·0041)	0·235 (0·0402)	0·0991 (0·5387)
b		0·898 (0·0343)	0·972 (0·1951)
c			305 (825·7)
d			0·100 (0·8046)
y_o	1·17 (0·485)		

Linear: $y = y_o + a \times x$.
Simple allometric: $y = a \times x^b$.
Augmented allometric: $y = (a \times x^b) \times (c-x)^d$.

Table 5. *Coefficients determined for polynomial equations* (*with* S.E. *in parentheses*). *y = daily rate of protein retention* (*kg*)*; x = live body weight* (*kg*). *Data from Tullis* (*1982*) (n = *15*)

	Linear	Quadratic	Cubic
r^2	0·410	0·692	0·703
RMS	0·0250	0·0188	0·0192
a	−0·000385 (0·000129)	0·00119 (0·000484)	0·00233 (0·00180)
b		−0·00000760 (0·00000229)	−0·0000202 (0·0000193)
c			0·0000000403 (0·0000000615)
y_o	0·134 (0·0139)	0·0720 (0·0215)	0·0441 (0·0475)

Linear: $y = y_o + a \times x$.
Quadratic: $y = y_o + a \times x + b \times x^2$.
Cubic: $y = y_o + a \times x + b \times x^2 + c \times x^3$.

purposes of the estimation of dietary energy and nutrient requirement, and for building simulation models for pig growth, there may be convenience in expressing protein retention (Pr) in relation to protein mass (Pt) rather than live weight. In this case parameter values may be obtained from the undifferentiated function as given in Table 1, or by fitting the data for directly determined values of Pr and Pt, as employed for Table 2. In this case for the pertinent Gompertz expression [$Pr = dPt/dt = Pt \times B \times \ln(A/Pt)$], B = 0·0108, and A = 30·1. Respective values from Table 1 were 0·0122 and 28·9. Bridges and Richards functions generated curves that were indistinguishable from the Gompertz and of equal precision.

Growth rate (Pr) per unit of protein mass (Pr/Pt), the relative growth rate, will decrease with increasing mass of Pt, $Pr/Pt = y_o - B \times \ln(Pt)$, where $y_o = B \times \ln A$. Fitting this function gives $y_o = 0{\cdot}0373$ ($\pm$ 0·00219), B = 0·0110 ($\pm$ 0·000953), with the 15 data plots fitting closely to a straight line.

Table 6. *Coefficients determined for the fitted Gompertz function* (*with* S.E. *in parentheses*). *y = daily rate of lipid retention* (*kg*). *Data from Tullis* (*1982*) (n = *15*)

	x = live body weight (kg)	x = whole body protein mass (kg)	x = whole body lipid mass (kg)
r^2	0·418	0·349	0·761
RMS	0·121	0·128	0·0775
B	0·00353	0·0225	0·0152
	(0·000812)	(0·00611)	(0·00160)
A	259	39·1	74·2
	(44·1)	(8·63)	(4·43)

Gompertz: $y = x \times B \times \ln(A/x)$.

The daily rate of lipid retention expressed in relation to W, Pt and the lipid mass (Lt) is presented in Table 6. Only the Gompertz is represented, as the Bridges and Richards functions showed the same limitations as previously described. The daily lipid retention rates (Lr) from the data of Tullis (1982) produced a scattered plot, and the fit with the Gompertz function against live body weight (W, kg) was poor. Unsurprisingly, the fit against whole body protein mass (Pt, kg) was equally poor. The asymptote for lipid mass (74 kg) appears to be approximately two and a half times greater than the asymptote for protein mass (29 kg). The allometric relationship [$Lt = a \times Pt^b$] was fitted to give a = 0·760 (± 0·364) and b = 1·340 (± 0·153), with $r^2 = 0{\cdot}800$ and RMS = 11·3.

Linear and allometric functions fitted to the reported data of Wagner *et al.* (1999) are given in Table 7, which shows that the linear function fitted well for protein mass (Pt) in relation to live weight (W) over the weight range, but less well for lipid mass (Lt). The augmented allometric added little to the simple allometric, and the parameters of the augmented form were associated with higher error. The simple allometric functions fitted the data for both protein and lipid well, and were informative.

The daily rate of protein retention (Pr) determined from the incremental gains between the eight serial slaughter groups of Wagner *et al.* (1999) appeared (commonly with the Tullis data) randomly scattered in relation to live weight (W). All sigmoidal functions failed to converge. The most appropriate description was linear, $y = y_o + ax$; $Pr = 0{\cdot}117 - 0{\cdot}000138\ W$, with $r^2 = 0{\cdot}0675$, the S.E. of $y_o = \pm 0{\cdot}0142$, of a = ± 0·000148, and the RMS = 0·0192. The constant term (y_o) was highly significant, and the slope (a) not different from zero. For these data therefore, a single value would adequately describe Pr as a function of W (25 to 152 kg). This outcome for the description of protein retention rate (Pr) is a consequence both of linearity of protein growth, and the unavoidable lumpiness of data when the increments between serial points are calculated (see also Eissen 2000).

The kind provision from Purdue of the unpublished values for pig age allows an alternative approach following the failure of all sigmoidal expressions to converge. Initially, protein mass was expressed as a function of time using the Gompertz equation. The fit was good ($r^2 = 0{\cdot}995$, RMS = 0·356; A = 26·8

Table 7. *Coefficients determined for fitted equations* (*with* S.E. *in parentheses*). *y = protein mass or lipid mass* (*kg*); *x = live body weight* (*kg*). *Data from Wagner* et al. (*1999*) (n = *16*)

	y = Protein mass			y = lipid mass		
	Linear	Simple allometric	Augmented allometric	Linear	Simple allometric	Augmented allometric
r^2	0·991	0·992	0·991	0·967	0·985	0·985
RMS	0·477	0·469	0·507	2·90	1·96	2·12
a	0·117	0·168	0·0917	0·365	0·0153	0·0540
	(0·00296)	(0·0238)	(10·8)	(0·0180)	(0·00569)	(50·1)
b		0·933	0·947		1·61	1·59
		(0·0299)	(0·348)		(0·0769)	(1·30)
c			695			1066
			(86421)			(539000)
d			0·0851			−0·169
			(16·4)			(120·9)
y_o	0·589			−9·62		
	(0·289)			(1·76)		

Linear: $y = y_o + a \times x$.
Simple allometric: $y = a \times x^b$.
Augmented allometric: $y = (a \times x^b) \times (c - x)^d$.

($\pm$ 1·87), b = 87·2 ($\pm$ 7·65), x^o = 126 ($\pm$ 6·80)). The fitted values for Pt over time can now be used to generate values for dPt/dt (Pr). Subsequently, weight was fitted to time (r^2 = 0·990, RMS = 4·55; A = 216 ($\pm$ 21·3), b = 82·1 ($\pm$ 10·4), x^o = 127 ($\pm$ 9·18). This gives fitted values for W at equivalent points in the data set for the fitted values for Pr, which can now themselves be subjected to curve fitting procedures. For the Gompertz curve this method generates B = 0·00143 ($\pm$ 0·00000234) and A = 217 ($\pm$ 0·252). Pr_{max} (A × B/e) is predicted to be 0·114 kg, reached at (A/e) 79·8 kg live weight. These outcomes are similar to those obtained with the Tullis data.

DISCUSSION

Description of the outer envelope for pig growth performance, within which response to dietary energy and nutritional inputs must operate, is fraught with the self-evident impossibility of measuring performance limits in practical circumstances, and of knowing what they might be in the absence of intrinsic and extrinsic modulators. Nonetheless, the present analysis attempts to identify an appropriate form for the expression of expected protein and lipid growth over the live weight range of pigs grown for the production of meat.

Walker (1990) collected data for nitrogen retention from various (n = 22) early sources (1960 to 1980). She fitted a two-parameter equation (N retention = $W \times \exp(a + b \times W)$), where a = −0·327 and b = −0·0136. Non-linearity over the weight range may have been related to the genetically 'unimproved' nature of the pigs described. The data set of Walker (1990) was transformed by the present authors to protein by multiplying with the factor 6·25, and fitted with the Gompertz function. Values found (corresponding to those in Table 3) were r^2 = 0·742, RMS = 0·00830; B = 0·00147 (0·000051), A = 224 (6·12).

Values for 'unimproved pigs' of the early 1980s may be compared with those for 'improved' entire males collected by Urquhart (1995), who slaughtered serially a total of 14 pigs over live weight points of 90, 125, 200 and 340 kg. Protein retention rates for the three incremental periods were 0·165, 0·121 and 0·107 kg per day respectively, and ultimate protein mass (n = 2) was 53 kg. Urquhart fitted Gompertz curves to conclude an asymptotic protein mass of 55 kg and a mature live weight of 400 kg. These values thus show, in addition to curvature, the possibility of high values for A × B/e and for A. Lipid retention appeared much more erratic than that for protein, but from 90 kg onwards lay around 0·350 kg daily, and the ultimate lipid mass for these males was 102 kg.

Lorschy *et al.* (1997) reported an analogous experiment to that of Tullis (1982), with similar protocol and purpose, but over a more limited weight range (24–120 kg W). They fitted three sigmoidal functions (Gompertz, Richards and Bridges) for growth as related to time and also determined allometric relationships. Unsurprisingly, as the weight range covered the period of 'linear growth' around the point of inflection for protein and live weight, all of the sigmoidal functions fitted (equally) well. A linear function was not reported. Lorschy *et al.* (1997) selected the Richards as their preferred function because of its greater flexibility and the value of a variable inflection point for differentiating genotypes.

In the case of the present work, the Bridges function, when appropriate approximations for parameter values were selected, was similar in its point of inflection and asymptote to the Gompertz. The same was noted by Knap (2000). It is evident that the degree of prior knowledge of parameter value required is greater if the inflection point is allowed to vary. This could be a cause of difficulty where a function is sought for purposes of predicting the composition and rate of growth in order to optimize nutrient provision. Careful and knowledgeable selection of initial values for the Bridges and Richards parameters was found to be crucial; and, compared to the Gompertz, these functions have one and two more parameters. The increased complexity of the Bridges and Richards functions did not yield commensurate benefit.

Allometry relating Pt to W may be employed to calculate protein retention in relation to live weight in the manner proposed by Whittemore *et al.* (1988). The derivative of the allometric function $Pt = a \times W^b$, $dPt/dW = a \times b \times W^{b-1}$, indicates the proportion of live weight gain at W that is protein. This function is combined with the Gompertz function $dW/dt = B' \times W \times \ln(A/W)$ by means of the chain rule for differentials, to give $Pr = dPt/dt = (dPt/dW) \times (dW/dt) = (a \times b \times W^{b-1}) \times (B' \times W \times \ln(A/W))$. Values for a and b are found in Table 4 (as 0·235 and 0·898 respectively). Values for A and B′ pertain to a Gompertz curve that, in its non-differentiated form ($y = A \times \exp(-\exp(-(x - x^o)/b'))$), describes live weight as a function of time, and where $B' = 1/b'$. In respect to the Tullis (1982) data, fitting this Gompertz curve gave A = 225 ($\pm$ 9·54), b′ = 92·1 ($\pm$ 8·43), x^0 = 134·7 ($\pm$ 5·27), r^2 = 0·973, RMS = 10·4. B′, originating from the weight upon time function, = 1/b′ = 0·0109. Using these fitted values for A, B′, a, and b, at W = A/e = 83 kg the following is obtained: dPt/dW = 0·134, dW/dt = 0·899 kg, and Pr = dPt/dt = 0·121 kg.

Augmentation of the allometric function was not found to be advantageous, despite its requiring two further parameters (c and d). Schinckel & de Lange (1996) used an augmented allometric function to account for the non-uniformity of the composition of the gain. They found that the augmenting term (see footnote to Table 4) was consistently significant when

W, live body weight, was > 115 kg and P2 backfat depth was > 20 mm. The augmented allometric increased the proportion of protein retention at live body weights < 100 kg, and decreased it at weights > 100 kg. The use of the function by Lorschy *et al.* (1997) also illuminated the counterbalancing effect of the augmenting term ($c \sim 250$; $d \sim 0{\cdot}1$) upon a. Values found for the Tullis (1982) data were $c = 305$ and $d = 0{\cdot}10$. Wagner *et al.* (1999) found the equation insensitive to the value attributed to c and assigned a constant 700 kg.

Of the polynomial series of descriptors for the daily rate of protein retention as a function of weight, the present analysis would not favour the quadratic on grounds of the point of inflection occurring at 0·5 of asymptotic value (mature mass), which forces upon early growth the same dynamic as for the approach to maturity. This is counterproductive, as the predicted growth rate for pigs of lighter weight is implausibly slow, and is not consistent with growth rates normally found with young pigs in practical circumstances. This would argue for the Gompertz, with its inflection point at 1/e, or for a curve with a variable inflection point such as the Bridges or Richards functions. The cubic polynomial, as forwarded by NRC (1998), appears the more appropriate, but its form restricts its range of safe use, whereas the sigmoidal functions purport to cover the whole of growth to maturity. If the live weight range of interest is restricted to 20–120 kg, it is difficult to refute with the present analysis the effectiveness of the simple linear form of a single value to describe daily protein retention rate. The sigmoidal forms will, of course, also provide a fit to data that are essentially linear over the weight range of 20–120 kg, but may do so (as for the linear) with unreliable parameter values if used outside the restricted range. For description over an extended weight range, the sigmoidal form, particularly the Gompertz, appears most appropriate.

Attempts to find appropriate expression for the daily rate of lipid retention resulted in support for the argument of Emmans (1988), and the case for lipid to be described by an allometric relationship with protein or live weight mass. The allometric descriptor found for the Wagner *et al.* (1999) data ($Lt = 0{\cdot}0153\ W^{1{\cdot}61}$) has parameter values which are indistinguishable from those of 0·0145 and 1·65 reported for the Tullis (1982) data by Whittemore *et al.* (1988).

CONCLUSIONS

Over shorter periods of weight change, especially those excluding the early and late stages of growth, linearity in the rate of protein retention is evident. Linearity can also be effectively described by curvilinear functions that have a wider context for their use; but it is possible that some of the more complex curvilinear functions are associated with unhelpful flexibility. Generally, the description of growth performance possibilities in practice will benefit from minimizing the number of parameters in the function as far as is reasonable. It is concluded from the present analysis that the Gompertz function is a safe and appropriate descriptor for protein retention in relation to live weight, while the increase in lipid mass as the animal grows may be adequately expressed as an allometric function of the increase in protein mass.

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