A Comparison of Non-Linear Models for Describing Growth in N'Dama Cattle

B. K. Ahunu[1], J. D. Kabuga[2], P. Gyawu[2] and G. Teye–Ayum[2]

[1]*Department of Animal Science, University of Ghana, Legon;* [2]*Department of Animal Science, University of Science and Technology, Kumasi.*

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Five non-linear models were fitted to growth data for female N'Dama cattle kept at the University of Science and Technology research farm, Kumasi, Ghana. Comparisons for goodness of fit provided an R^2 of approximately 96%. The Bertalanffy model was preferred because of its consistency in predicting weights at all ages, while the Richards model was more difficult to fit due to problems of non-convergence. The Brody's model over-estimated weights at all ages while the Logistic model converged too rapidly, thereby underestimating mature weights. Correlations established between estimated parameters and derived statistics indicated a tendency for early maturing animals to grow to smaller mature weights while large estimates of mature weights were associated with late maturing intervals.
KEY WORDS: N'dama cattle, non-linear models, non-convergence

Cinq modèles non linéaires étaient utilisés pour analyser les données de croissance du bétail femelle N'dama gardée à la ferme expérimentale de l'Université de Science et Technologie. Des comparaisons étaient faites pour l'adéquation des modèles pour analyser les paramètres statistiques y relatifs. Tous les modèles ont raisonablement donné une bonne adéquation avec R2 d'environ 96%. Le modèle de Bertalenffy était le plus souhaitable à cause de sa fiabilité à prédire les poids à tous les âges. Le modèle de Richards était plus difficile à ajuster et des problèmes de non-convergence y étaient souvent rencontrés. A l'exception du modèle de Richards, les poids prématurés étaient le plus souvent surestimés. Le modèle de Brody avait surestimé les poids à tous les âges alors que le modèle logistique convergeait si rapidment, sous-estimant de ce fait les poids à la maturité. Des corrélations établies entre paramètres estimés et statistiques y dérivées ont montré une tendance pour les animaux à maturité précoce à avoir un petit poids à l'âge mûr, tandis que des grandes estimations concernant des poids à la maturité étaient associées aux intervalles de maturité tardive.
MOTS CLES; bétail N'dama, modèles non-linéaires, intervalles de maturité convergente

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Introduction

Growth curves can be used to compare animals for breeding purposes. In beef cattle operations, growth curves may prove useful in predicting the ages at which individual animals will achieve specified measurements (Finney, 1978). The nature of the growth of cattle has been extensively studied (Parks, 1982) and several nonlinear regression models (Winsor, 1932; Brody, 1945; Bertalanffy, 1957; Richards, 1959 and Nelder, 1961) as well as segmented line regression procedures (Warren *et al.*, 1980) have been proposed to describe post natal growth. Studies involving the fitting of growth functions to cattle weight-age data have been limited mainly to temperate breeds (Brown *et al.*, 1976; Goonewardene *et al.*, 1981 and Doren *et al.*, 1989).

Tropical breeds of cattle are reputed to be slow growing and late maturing. For example, age at first calving in N'Dama cattle has been reported to range from 33 to 48 months (Fall *et al.*, 1982) and from 20 to 51 months (Tuah and Danso, 1985). Nonetheless, research on productivity of N'Dama cattle has generated a lot of interest. The breed is known to be trypanotolerant. Growth curve parameters for N'Dama cattle have however, not been established. Consequently, the need to compare the various growth models to identify the most appropriate ones for describing the growth patterns of N'Dama cattle.

Materials and Methods

Weight-age data for the analyses were collected on 90 N'Dama cows kept at the University of Science and Technology (UST), Kumasi from 1983 to 1988. The climate, vegetation and management of the herd have been previously described by Tuah and Danso (1985). All calvings were recorded weighed within 24 hours after birth, and weaned at about six months. Animals were sprayed against ectoparasites and weighed monthly until removed from the herd.

Body weights for the analyses were also obtained at 3, 8, 12, 18, 24, 30, 36, 48, 60 and 72 months. Only data from cattle with consecutive weights to 30 months or more were included in the analyses. The Computer software STRATGRAPHICS (1989) was used to fit the following five models to the data:

Bertalanffy (von Bertalanffy, 1957) : $Y_t = A(1-Be^{-Kt})^3$

Brody (Brody, 1945) : $Y_t = A(1-Be^{-Kt})$

Gompertz (Winsor, 1932) : $Y_t = Y_0 e^{L(1-e^{-at})/a}$

Logistic (Nelder, 1961) : $Y_t = A(1+e^{-Kt})^{-M}$

Richards (Richards, 1959) : $Y_t = A(1-Be^{-Kt})^M$

where Y_t is weight (kg) at age t months; A, B, K, L, M and a are fitted parameters.

All models were fitted to individual animal weight-age records using intrinsically non-linear regression techniques to obtain estimates of the parameters. The procedure obtains least squares estimates of the parameters by use of a search algorithim in an attempt to determine estimates which minimize the residual sum of squares. The algorithim developed by Marquardt (1963) is a compromise between using a straight linearization method and the method of steepest ascent. The Bertalanffy, Brody, Logistic and Richards models estimated three common parameters; A, the asymptote as $t \to \infty$; B, an integration constant which adjusts for a situation when $t \neq 0$ and $Y \neq 0$ and K, a maturing rate parameter which depicts growth rate relative to mature size. In addition, the Richards model estimated a fourth parameter M which is a variable inflection parameter. The Logistic model is a modification of Nelder's (1961) generalized Logisitc model which assumes a fixed value of 1 for the coefficient of e^{-Kt} and includes the parameter M permitting a variable point of inflection. The Bertalanffy and Gompertz models have fixed inflection points of 0.296A and 0.368A respectively while the Brody model has no inflection point. The Gompertz parameters require slightly different interpretation; asymptotic weight A is defined as $Y_0 e^{L/a}$ where Y_0 is the weight at age = 0 (taken as birth weight in this study) and a = K measures the rate of maturing.

The overall fit of each growth model was determined by an R^2 estimate. In addition, a percent prediction error (% PE) was calculated for each weight-age observation as % PE = $100\,(y_p-Y)/Y$ where Y is the actual or observed weight and Y_p is the predicted weight. Thus, a negative % PE value indicated underestimation of weight by the model at the particular age while a positive value indicated overestimation. Values of % PE were plotted against age. A mean percent prediction error (% MPE) was calculated over all the weight-age data for each model and this value was used as a second estimate of overall fit (Goonewardene *et al.*,1981). Differences in % MPE of the models were tested by a t-test.

Simple correlations were established among the estimated growth parameters for all five models. In addition, for the Richards model, correlations were also established among the estimated parameters and the following defined parameters; $^K/_A$, K^{-1}, t_I, Y_I and dy/dt_I where K^{-1} is a measure of the maturing interval (Brody, 1945; Taylor, 1965), t_I is the age at point if inflection (POI) defined as:

$$t_I = K^{-1} \ln MB$$

and $dy/dt_I = MK_{yI}\,(Be^{-Kt_I}/I-Be^{-Kt_I})$.

The expression in the bracket is the amount of maturity remaining to be attained as a fraction of maturity weight already attained at POI. This is analogous to relative growth rate and relative maturing rate as shown by Fitzugh and Taylor. (1971).

Results and Discussion

All growth curves appeared to provide an overall good fit to the data (Fig. 1). The Gompertz and Logistic functions underestimated birth weight with the latter grossly underestimating the quantity. Also, Bertlanffy, Gompertz and Logisitic functions tended to inflect too early thereby underestimating asymptotic weight while the Richards function showed too gradual convergence to asymptotic weight.

According to Table 1, the mean and predicted adult (60 months) weight as well as asymptotic weight A, R^2 and % MPE for each model showed no differences in the R^2 values, which were approximately 96%. This suggests that all five models provided an equal fit to the data, and agrees with Goonewardene *et al.* The R^2 values reported in this study were however slightly higher compared to those of Goonewardene *et al.* (1981) whose values ranged from 90.6 to 94.8 but which study did not include a comparison involving the Gompertz model.

Based on the mean prediction error, all models except Richards, overestimated actual weight as % MPE which turned out positive. A t-test showed that the Bertalanffy, Brody, Gompertz and Logistic models fitted the data equally well and significantly better than the Richards model. The poor % MPE of the Richards model was mainly due to its tendency to grossly underestimate early weights. This observation is contrary to that of Goonewardene *et al.* (1981) who found the Richards model to provide the best fit in Canadian beef data based on % MPE. This could be done to the rather low birth weights of N'dama and the fact that these models estimate early weights poorly compared to mature weights. On the basis of the two modes, (R_2 and % MPE), the Bertalanffy model could be said to have provided the best fit to the data, followed by the Richards, Gompertz and Logistic models. The function with no inflection point (Brody's model) provided the poorest fit to the data.

Estimation of Fit at Each Age

Fig. 2 of plots of % PE at each age by function, showed that of the five models, no accurate birth weight was predicted. Bertalanffy, Logistic and Gompertz models generally predicted 3 and 8 months weights well but not with a slight tendency to underestimate these weights. Generally, all the models estimated birth weight and weights between 12 and 24 months poorly compared to mature weights. With the exception of

Table 1. Mean observed and predicted mature adult weight, R2 and % MPE for each model

Model	Observed mature weight (kg)	Predicted mature wt. (kg)	R^2	% MPE
Bertalanffy	223.3 ± 5.0	221.7	96.04 ± 0.33	2.34 ± 1.52 a
Brody		236.7	95.54 ± 0.37	5.71 ± 2.75 a
Gompertz		222.7	96.03 ± 0.31	4.77 ± 2.35 a
Logisitc		214.4	95.95 ± 0.30	3.63 ± 3.20 a
Richards		233.0	96.22 ± 0.32	-10.38 ± 6.25 b

Richards model, early weights were mostly overestimated. Except for birth weight, the Brody function, in particular, consistently overestimated by as much as 16%, early weights highest at 12 months. Richards model consistently underestimated early weights by nearly 50% in birth weights. These deviations are quite moderate compared to reported cases of overestimation by as much as 108 to 126% in Canadian Hereford and Beef Synthetic breeds (Goonewardene *et al.*, 1981).

All five models estimated fairly well weights from 30 months onwards with the Bertalanffy and Gompertz models consistently giving the best prediction at these stages while the Brody and Richards models fitted relatively poorly. Brown *et al.* (1976) also found the Bertalanffy model to fit their data reasonably well at all ages with only a slight tendency to overestimate weights at ages prior to sis months. In general, the fit of the non-linear curves to the weight-age data varies over different time periods. In choosing between models, a model which yields differences between predicted and actual weights whose values tend to alternate in sign at short intervals is to be preferred (Brown *et al.*, 1976). It does appear, therefore, that the models with fixed inflection points (Bertalanffy and Gompertz models) provided better fit to the N'dama data that the models without inflection points (Brody) or the Richards and Logistic models which have variable inflection points. Thus, while the Richards model converged too gradually, the Logistic model converged too rapidly.

Fitted Parameter Estimates

The mean estimates of the growth constants shown in Table 2 mean that legitimate comparisons can be carried out on estimates of the asymptotic weight A. However, the other parameters measure slightly different phenomena. Estimates of A differed by only 22 kg. Estimate of A (248.86) by the Brody model was larger than estimates for the other models with the Logistic model giving the lowest estimate. The larger estimate of A by the Brody model was associated with a smaller estimate of A (215.1 kg) by the Logisitc model was associated with a large estimate of K (0.114).

The variable inflection point estimates M were 2.94 and 3.00 for the Logisitc and Richards models respectively. These figures compare favourably with those of Brown *et al.* (1976) who reported K and M values of 0.116 and 2.90 respectively. A difficulty encountered with the Richards model was the non-convergence of the iterative solution for some of the weight age relationships so that some individual animal data could not be fitted by the model. The condition of using only data from animals for which solutions to all five models were available and a restriction of the value of B<1 and 0<m<8 facilitated editing of the data. These conditions were necessary not only for ease of comparison of like estimates from same animals but also to ensure biologically plausible values and mathematically feasible computations.

It can be concluded from the foregoing that while there may be wide differences in body size of cattle breeds for which different asymptote values of A may be obtained, there appears to be a fairly constant value for growth rate relative to mature weight.

Correlations

Correlations among the growth parameters from all five models given in Table 3 demonstrate that A's ranged from 0.57 between estimates of the Logisitic and Richards' model to 0.96 for the Bertalanffy and Logisitc models. Similarly, correlations among estimates of K ranged from 0.66 between Brody and Logistic models to 0.99 between the Bertalanffy and Logistic models. With the exception of parameter B from the Richards model, which did not correlate significantly with estimate of B from other models, correlation between B's from Bertalanffy and Brody models (0.93) was highly significant. In addition, parameter M from the Logistic model was highly correlated with B's from Bertalanffy and Brody models although B and M from the Richards model did not correlate with parameters from other models. It would seem as if the parameters from the Richards model measure at least slightly different phenomena from parameters from the remaining models and may well demand slightly different biological interpretation. The difficulty of biological interpretation of the parameters of the Richards function has previously been reported (Aguilar *et al.*, 1983).

Correlations among parameter estimates for the Richards model presented in Table 4 show that monthly gain at POI (dy/dt_I) was negatively correlated to A, indicating that animals gaining rapidly at POI were likely to grow to a smaller mature weight. This is further supported by the consistently negative correlations between A and K (Table 3) suggesting animals maturing early are less likely to attain large mature weights than those individuals growing more slowly in early life. This agrees with the results of Fitzugh and Taylor (1971), Brown *et al.* (1976) and de Torre and Rankin (1978). However, a strong negative correlation (-0.75) was observed between age at inflection t_I and Y_I suggesting that animals which take a longer time to reach POI, perhaps by virtue of the fact that they are older, are also heavier at POI compared to fast growing animals which reach POI early but at a lighter weight. The present observations are consistent with reports by Smith *et al.* (1976) who reported a positive phenotypic correlation of 0.76 between weight at puberty and age at puberty and indicated that heifers heavier at any age except puberty tended to be younger at puberty.

Conclusions

The study has shown that all five growth models described growth in N'dama cattle adequately but the Bertalanffy model was preferred because of its consistency in predicting weight at all age levels. Early maturing animals are likely to grow to smaller maturing weights while large estimates of mature weights were associated with long maturing intervals.

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Table 2: Mean estimates (± S. E.) of the fitted parameters for the five growth models.

Model	A	B	K	M	L	Yo
Bertalanffy	224.8 ± 4.5	0.532 ± 0.006	0.079 ± 0.004			
Brody	248.9 ± 6.1	0.927 ± 0.004	0.049 ± 0.003			
Gompertz	219 ± 4.3		0.094 ± 0.004		0.201 ± 0.008	26.5 ± 0.87
Logisitc	215.1 ± 4.2		0.114 ± 0.006	2.94 ± 0.04		
Richards	239.1 ± 6.8	0.643 ± 0.034	0.071 ± 0.005	3.00 ± 0.28		

Table 3. Correlations among predicted growth parameters of the five models

		I Bertalanffy		II Brody			III Gompertz			IV Logistics			V Richards			
		B	K	A	B	K	Y_o	L	a	A	K	M	A	B	K	M
I	A	0.22ns	-0.63	0.85	0.30*	-0.53	0.41	-0.53	-0.63	0.96	0.51	0.19ns	0.72	0.01ns	-0.52	0.05n
	B		-0.29*	0.28*	0.93	-0.41	-0.77	0.14ns	-0.26ns	0.15ns	-0.08ns	0.99	0.20ns	0.00ns	0.23ns	0.07ns
	K			0.69	-0.49	0.93	-0.12ns	0.89	0.99	-0.53	0.80	-0.23ns	-0,63	-0.21ns	0.85	0.23ns
II	A				0.38	-0.70	--0.19ns	-0.57	-0.66	0.72	-0.40	0.28*	0.73	0.05ns	-0.56	-0.08ns
	B					-0.58	-0.65	-0.11ns	-0.47	0.23ns	-0.29*	0.88	0.30*	0.16ns	-0.45	-0.09ns
	K						0.08ns	0.74	0 .90	-0.40	0.66	-0.37	-0.57	-0.15ns	0.77	0.15ns
III	Y_o							-0.47	-0.17ns	0 48	-0.25ns	0.79	0.12ns	0.04ns	-0.13ns	-0.13ns
	L								0.91	-0.52	0.82	0.20ns	0.55	0.22ns	0.77	0.27*
	a									-0.56	0.83	-0.20ns	-0.60	-0.21ns	0.85	0.24ns
IV	A										-0.48	0.11ns	0.57	-0.03ns	-0.44	-0.01ns
	K											-.00ns	0.46	-0.10ns	0.65	0.13ns
	M												0.18ns	0.04ns	0.17ns	0.10ns
V	A													0.38*	0.61	0.34*
	B														-0.55	-0.95
	K															0.54

Table 4: Phenotypic correlations among growth parameters from Richards model.

	B	K	M	K/A	I/K	T_I	Y_I	DY/Dt
A	0.40*	-0.75	-0.35^{ns}	-0.75	0.74	0.68	0.67	-0.60
B		-0.51	-0.92	-0.47	0.62	0.16	-0.34^{ns}	-0.60^{ns}
K			0.54	0.97	-0.84	-0.75	-0.32^{ns}	0.87
M				0.49	-0.56	-0.10^{ns}	0.28^{ns}	0.14^{ns}
K/A					-0.76	-0.73	-0.46	0.86
I/K						0.76	0.17^{ns}	-0.69
T_I							0.55	-0.84
DY/Dt								-0.56

ns = not significant; * = significant ($p < 0.05$). All other correlations are significant ($p < 0.01$)

Figure 1. Variation in fitting qualities of the five models.

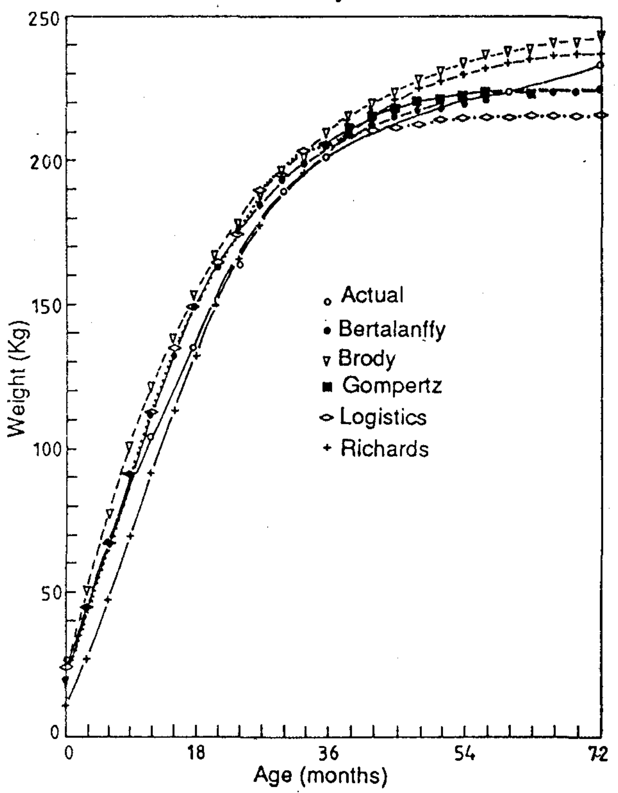

Figure 2. Plot of mean %MPE versus age for the five models.