

## Evaluation of Models to Describe Temporal Growth in Local Chickens of Ghana

Research Article

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### ABSTRACT

The logistic, Gompertz, Richards and asymmetric logistic growth curve models were fitted to body weight data of local Ghanaian chickens and French SASSO T44 chickens. All four growth models provided good fit for each sex by genotype growth data with  $R^2$  values ranging from 86.7% to 96.7%. The rate constant parameter,  $k$ , ranged between 0.137 and 0.271 and were significantly different from zero for all genotype by sex groups. Predicted mature weight from the four models ranged from 2840 g to 3020 g for SASSO T44 female, 3225 g to 3448 g for SASSO T44 male, 1170 g to 1332 g for Ghanaian female and 1607 g to 1777 g for Ghanaian male chickens. For the Richards and asymmetric logistic functions, the shape parameter ( $n$ ) which influences the point of inflection ranged from -0.126 to 0.713, indicating that the shape of each of the genotype by sex sigmoid function is negatively asymmetric. Between the two simpler models, with fixed inflection point, the logistic function was characterised by a younger age at start of the growth acceleration phase, older age at the point of inflection, younger age at the end of the growth deceleration phase and lower mature body weights relative to the Gompertz function. Based on the Bayesian information criterion (BIC), the Gompertz function was preferred to the logistic function. The  $R^2$ , BIC values and predicted body weights for the asymmetric logistic function were similar to those of the Richards function. These complex models with flexible inflection point provided better goodness of fit relative to the Gompertz model. Therefore it is concluded that, where data structure and availability of adequate computing power permit, models with flexible inflection point such as the Richards function can be used to provide accurate parameter estimates for the characterization of growth of indigenous chickens.

### KEY WORDS

Bayesian information criterion, growth curve models, inflection point, maturing rate, mature weight.

### INTRODUCTION

Local chickens have survived poor management and feeding over evolutionary time and through natural selection are well-adapted to the tropics (Dana *et al.* 2011). They are therefore endowed with genes favourable for survival in harsh conditions. Exploitation of these genetically-diverse local chicken stocks for improving economic traits, such as body weight is an important approach in designing breeding programmes of chickens (Mohammed *et al.* 2005; Osei-

Amonsah *et al.* 2013) as local farmers value the size of the bird (Osei Amponsah, 2010). Growth models summarise time series data into a few parameters which enable an objective comparison of the growth efficiencies of animals. A major objective of curve fitting is to describe the course of body weight increase over time or age with mathematical parameters that are biologically interpretable (Narinc *et al.* 2010; Orheruata *et al.* 2010).

Temporal growth curve models relate body weight to age, and thus provide mathematical assessment of growth

as a function of time, and prediction of body weight at specific ages. Several growth models are available for describing temporal growth in livestock (Wellock *et al.* 2004; Roush and Branton, 2005; Orheruata *et al.* 2010). These models have different characteristics, different levels of complexities, different numbers of parameters, and different goodness of fit to different types of data sets. Given the paucity of research on local chickens in Ghana, it is not clear which of the functions best describes the growth of these chickens. There is therefore the need to assess the goodness of fit of the different growth models to growth data of local chicken as part of the process of characterising this valuable genetic resource. The aim of this study was to compare the ability of the common temporal growth models to accurately describe the growth of Ghanaian local chickens.

## MATERIALS AND METHODS

### Experimental birds and management

Sixty local chickens (10 cocks and 50 hens) were purchased between April and July, 2006 from each of two ecological zones of Ghana, i.e. Savannah and Forest. The chickens were labelled to identify the region, district, town and farmer they were purchased from. They were then maintained on deep litter at the agricultural research centre, Legon of the university of Ghana. Annual rainfall of the centre is 785 mm with a range of 128-1709 mm distributed bimodally. The long rainy season usually occurs between March and July with a peak in June and the short rainy season occurs between August and November with a peak in October. Mean monthly temperatures range from 24.8 °C in August to 28.3 °C in February with a mean of 26.9 °C. Relative humidity at 1500 hrs ranges between 58% and 83.7% and is slightly lower at 09:00 hrs. The cocks and hens were kept separate for a period of 4 weeks to purge any residual semen being carried by the hens. Chickens from the same ecozone were grouped into families comprising a cock and five hens and the collection of fertile eggs began a week later.

All eggs were labelled and incubated artificially using table top incubators. The chickens were hatched between September and November, 2006. This study was part of a West African sub-regional local chicken characterization project sponsored by the French government and so for comparative purposes, chicks of the SASSO T44 breed a French breed selected for free-range rearing (SASSO, 2010) were imported to coincide with the hatching of chicks in Ghana. The Ghanaian chicks were separated into ecozones and together with the SASSO T44 chicks were reared in three replicates on deep litter. Routine vaccination and prophylactic procedures as well as feeding and other management practices were the same for all groups. The

birds were given the same starter (0-4 weeks), grower (4-18 weeks) and layer (after 18 weeks) rations *ad libitum*. The compositions of the three rations are indicated in Table 1. A total of 571 chickens were used at the commencement (at hatch) of the study. A number of male chickens were used for carcass analyses whilst other birds died. As a result 314 chickens remained until the end of the study at 40 weeks of age. The number and mean weight of the chicken from the different genotypes, at the start and end of the study, are provided in Table 2.

**Table 1** Composition of ration fed to chickens

Diet	Chick starter	Grower ration	Layer ration
Maize (%)	50	55	55
Wheat bran (%)	25	20	20
Concentrate (%)	25	20	20
Shell grits (%)	-	-	5
CP (%)	19	15.5	17.5
ME (kcal/kg)	2770	2640	2620

CP: crude protein and ME: metabolisable energy.

Source of concentrate: agricare feed products, Ltd, Ghana.

### Traits measured and mathematical models

The chicks were weighed at hatch and subsequently every two weeks from weeks 2 to 12 and every four weeks from weeks 16 through 40 weeks of age to describe their growth rate. Four growth functions, the logistic, Gompertz, Richards and an asymmetric logistic function, were fitted to the data.

All these models have the sigmoid behaviour with either a fixed or variable point of inflection. The normal logistic function and the Gompertz function are both characterised by a fixed inflection point (Wellock *et al.* 2004). The Richards function is characterised by a flexible point of inflection (Wellock *et al.* 2004; Darmani Kuhi *et al.* 2010). The normal logistic function is relatively easier to fit but due to the fact that it has a fixed point of inflection, an asymmetric sigmoid logistic function was also used. This asymmetric logistic function allows for the fitting of a flexible point of inflection. The computational form of the growth models used, are presented in Table 3. The Gompertz and the Richards equations used were in the form similar to those used by Kebreab *et al.* (2007). For the Richards equation, the inflection occurs when  $n$  is  $> -1$ . The asymmetric logistic function used has one flexible inflection point, and was a slightly modified form (Table 2) of the one used by Kusec *et al.* (2007). In this generalised form, the function is defined as logistic when the coefficient of symmetry ( $n$ ) = 1 (at which the value of the inflection point =  $W_f/2$ ); negatively asymmetric when  $n < 1$  (at which the value of the inflection point is  $< W_f/2$ ); and positively asymmetric when  $n > 1$  (at which the value of the inflection point is  $> W_f/2$ ). In addition to the inflection point (Table 3), the growth curve for each model was divided into 4 phases.

**Table 2** Number of chickens and mean ( $\pm$ SD) body weight at the beginning and end of study

Genotype	Sex	At hatch		At 40 weeks of age	
		Number	Body weight (g)	Number	Body weight (g)
SASSO T44	Female	107	38.2 $\pm$ 2.2	63	3068.0 $\pm$ 500.2
	Male	80	37.6 $\pm$ 2.4	10	3407.0 $\pm$ 344.1
Forest	Female	114	26.5 $\pm$ 4.6	89	1184.0 $\pm$ 249.7
	Male	107	26.9 $\pm$ 4.5	39	1637.0 $\pm$ 296.6
Savannah	Female	68	25.1 $\pm$ 5.6	58	1301.0 $\pm$ 321.6
	Male	95	26.2 $\pm$ 5.5	55	1776.0 $\pm$ 301.5

SD: standard deviation.

**Table 3** Equations for models used in describing the body weight growth of chicken

Name of model	Equation <sup>1</sup>	Inflection point <sup>1</sup>
Logistic	$W = \frac{W_f}{1 + [(W_f - W_0)/W_0]e^{-kt}}$	$W = W_f / 2$
Gompertz	$W = W_0 \exp \left[ \left( \ln \frac{W_f}{W_0} \right) (1 - e^{-kt}) \right]$	$W = W_f / e$
Richards	$W = \frac{W_0 W_f}{[W_0^n + (W_f^n - W_0^n)e^{-kt}]^{1/n}}$	$W = W_f [1/(n + 1)]^{1/n}$
Asymmetric logistic <sup>2</sup>	$W = \frac{W_f}{(1 + be^{-kt})^{1/n}}$	$W = \left( \frac{1}{k} \ln \frac{b}{n}; \frac{W_f}{(1 + n)^{1/n}} \right)$

<sup>1</sup>Where: t: time (d); W<sub>0</sub>: initial body weight (g) at t=0; W<sub>f</sub>: upper asymptotic mature body weight (kg); k: a rate constant (week<sup>-1</sup>); n: > -1 and is a shape parameter influencing point of inflection and b: rate of change.

<sup>2</sup>This is similar to,  $W = W_f / (1 + be^{-ct})^{1/\gamma}$  as used by Kusec *et al.* (2007); c= k / n;  $\gamma = n$  and  $c\gamma = k$ .

The lag phase was the period from hatch until the chick attained 10% of its final body weight, followed by the accelerating phase until maximum growth rate at the inflection point, followed by the decelerating phase until it attained 90% of its final body weight, and then the stationary phase which continued until the approach of the asymptotic final body weight.

**Statistical procedures**

The weights at each age were subjected to general linear model analysis using a model which included the effect of genotype, sex, genotype by sex interaction and residual error. Means were separated using the least significant difference (LSD) method. The standard error of difference (SED) was calculated for each pair of comparisons due to unequal subclass numbers. The four mathematical models were fitted to the data. Due to significant genotype by sex interaction the models were fitted within each genotype by sex group. Selection of the preferred model was based on the Bayesian information criterion (BIC), which utilizes the significance level of the estimated parameters, the variance of the error estimate, and its standard error. The criterion imposes a penalty on more complicated models for inclusion of additional parameters. The formula for the criterion is:

$$BIC = -2 \log(L) + K \log(N)$$

Where:

K: the number of free parameters estimated.

L: the maximum value of the likelihood functions for the estimated model.

N: the sample size (Schwarz, 1978).

A lower BIC implies either fewer explanatory variables, better fit, or both, hence the model with lower BIC is the one to be preferred. The values for the residual standard deviation (RSD) for the different models were also examined, and as with the BIC, the model with a lower RSD is the one to be preferred. The values for the coefficient of determination (R<sup>2</sup>) were also studied, and in this case higher R<sup>2</sup> values are preferred. All the trait derivations, statistical analysis and mathematical modelling, were done using GenStat Release 10 (Payne *et al.* 2007).

**RESULTS AND DISCUSSION**

Least squares means of chickens of the three genotypes, at selected ages are presented in Table 4. In general the SASSO T44 chickens were heavier than the Ghanaian chickens at all ages. Within genotype, sex differences at hatch were significant (P<0.05) only in Savannah chickens. However, by 12 weeks of age sex differences in weight were significant (P<0.05) for all three genotypes, with males being heavier than females. Growth parameters for the four mathematical models evaluated are presented in Table 5. A typical growth curves predicted from the models are presented in Figure 1. In general, all the four equations provided a good fit for each sex by genotype growth data, with R<sup>2</sup> values ranging from 86.6% to 96.7%.

**Table 4** Least squares means ( $\pm$ SE) of body weight (g) at selected ages of female and male chickens from three genotypes

Genotype	Sex	Age			
		At hatch	8 weeks	12 weeks	28 weeks
SASSO T44	Female	38.3 $\pm$ 0.5 <sup>a</sup>	707.8 $\pm$ 11.3 <sup>a</sup>	1343.7 $\pm$ 18.0 <sup>b</sup>	2653.6 $\pm$ 32.3 <sup>b</sup>
	Male	36.9 $\pm$ 1.1 <sup>a</sup>	739.7 $\pm$ 23.7 <sup>a</sup>	1506.7 $\pm$ 35.4 <sup>a</sup>	3234.4 $\pm$ 67.6 <sup>a</sup>
Forest	Female	26.5 $\pm$ 0.5 <sup>b</sup>	298.9 $\pm$ 9.3 <sup>d</sup>	554.5 $\pm$ 14.9 <sup>f</sup>	1179.4 $\pm$ 37.5 <sup>f</sup>
	Male	26.8 $\pm$ 0.5 <sup>b</sup>	361.3 $\pm$ 9.6 <sup>bc</sup>	703.6 $\pm$ 15.0 <sup>d</sup>	1521.6 $\pm$ 33.0 <sup>d</sup>
Savannah	Female	25.0 $\pm$ 0.6 <sup>c</sup>	320.3 $\pm$ 11.6 <sup>cd</sup>	610.3 $\pm$ 18.4 <sup>e</sup>	1379.0 $\pm$ 62.1 <sup>e</sup>
	Male	26.1 $\pm$ 0.5 <sup>b</sup>	386.0 $\pm$ 10.0 <sup>b</sup>	773.3 $\pm$ 15.8 <sup>c</sup>	1660.8 $\pm$ 36.5 <sup>c</sup>

The means within the same column with at least one common letter, do not have significant difference ( $P < 0.05$ ).

SE: standard error.

**Table 5** Growth parameter<sup>1</sup> estimates ( $\pm$ SE) for body weight of Forest, Savannah and SASSO T44 chickens

Model	Genotype	Sex	W <sub>0</sub> (g)	W <sub>f</sub> (g)	k (week <sup>-1</sup> )	n	Var %	RSD	BIC
Logistic	SASSO T44	Female	134.2 $\pm$ 6.9	2839.5 $\pm$ 17.4	0.230 $\pm$ 0.005	-	94.0	268	23523
		Male	104.8 $\pm$ 5.4	3225.2 $\pm$ 25.1	0.271 $\pm$ 0.005	-	96.5	206	13191
	Forest	Female	50.8 $\pm$ 3.5	1169.7 $\pm$ 8.2	0.246 $\pm$ 0.006	-	89.7	150	24823
		Male	65.1 $\pm$ 4.1	1606.6 $\pm$ 12.3	0.237 $\pm$ 0.006	-	92.1	174	21888
	Savannah	Female	59.0 $\pm$ 5.9	1291.4 $\pm$ 13.6	0.239 $\pm$ 0.009	-	86.7	191	15006
		Male	66.8 $\pm$ 4.9	1702.9 $\pm$ 13.2	0.246 $\pm$ 0.007	-	91.4	197	20068
Gompertz	SASSO T44	Female	40.3 $\pm$ 5.0	2987.2 $\pm$ 22.5	0.137 $\pm$ 0.003	-	94.4	257	23148
		Male	18.1 $\pm$ 2.8	3448.4 $\pm$ 33.2	0.157 $\pm$ 0.003	-	96.6	204	13180
	Forest	Female	10.9 $\pm$ 2.2	1206.5 $\pm$ 10.3	0.154 $\pm$ 0.004	-	89.5	151	24848
		Male	14.6 $\pm$ 2.6	1688.5 $\pm$ 16.3	0.143 $\pm$ 0.004	-	92.1	173	21877
	Savannah	Female	13.7 $\pm$ 3.8	1331.6 $\pm$ 16.8	0.150 $\pm$ 0.006	-	86.6	191	15011
		Male	13.4 $\pm$ 2.8	1777.3 $\pm$ 16.8	0.150 $\pm$ 0.004	-	91.6	195	20046
Richards	SASSO T44	Female	24.7 $\pm$ 10.9	3020.0 $\pm$ 31.6	0.127 $\pm$ 0.007	-0.126 $\pm$ 0.079	94.4	257	23153
		Male	55.9 $\pm$ 9.5	3339.4 $\pm$ 34.6	0.199 $\pm$ 0.010	0.382 $\pm$ 0.088	96.6	201	13164
	Forest	Female	41.3 $\pm$ 6.6	1176.9 $\pm$ 9.8	0.219 $\pm$ 0.016	0.712 $\pm$ 0.159	89.7	150	24827
		Male	35.3 $\pm$ 7.5	1649.8 $\pm$ 17.6	0.175 $\pm$ 0.012	0.353 $\pm$ 0.119	92.2	173	21874
	Savannah	Female	41.6 $\pm$ 11.0	1304.3 $\pm$ 16.7	0.199 $\pm$ 0.021	0.555 $\pm$ 0.219	86.7	191	15010
		Male	28.3 $\pm$ 8.6	1752.5 $\pm$ 18.7	0.172 $\pm$ 0.012	0.238 $\pm$ 0.123	91.6	195	20049

<sup>1</sup> Model: W<sub>0</sub>: the lower asymptotic weight at t= 0; W<sub>f</sub>: the upper asymptote, representing mature body weight; b: rate of change; k: a rate constant; n: a shape parameter influencing point of inflection; Var %: the coefficient of determination (R<sup>2</sup>)  $\times$  100; RSD: the residual standard deviation and BIC: Bayesian information criterion, a measure of regression fit.

SE: standard error.

The rate constant parameter, k, values ranged between 0.127 and 0.271, and were significantly different from zero for all genotype by sex groups of chickens. For the Richards and asymmetric logistic functions, the shape parameter (n) which influences the point of inflection ranged from -0.126 to 0.713, indicating that the sigmoid functions were negatively asymmetric (n less than 1). The R<sup>2</sup>, RSD and BIC values for the asymmetric logistic function were similar to those of the Richards function. The predicted body weights of these two functions were also similar, hence detailed results of the asymmetric logistic function are not presented. Between the two simpler models, with fixed inflection point, the logistic function was characterised by a younger age at start of the growth acceleration phase, older age at the point of inflection, younger age at the end of the growth deceleration phase (Table 6) and lower mature body weights (Table 5), relative to the Gompertz function. The Gompertz function had lower BIC (Table 5) compared to the logistic function for all the groups except For forest female and Savannah female chicken, where the logistic function had a marginal improvement in the goodness of fit.

In general, the characteristics for the different phases of

growth for the Gompertz function were closer to those for the complex Richards and asymmetric logistic functions than to the logistic function. However for the Gompertz function the end of the growth deceleration phase was reached at older ages and predicted mature weights were higher relative to the Richards and asymmetric logistic functions for all genotype by sex groups except for SASSO T44 females. In evaluating the models for goodness of fit it is desirable to have higher R<sup>2</sup>, lower RSD and lower BIC values. Relative to the simpler models the complex models (Richards and asymmetric models) had the highest R<sup>2</sup> and lowest RSD values for half of the genotype by sex groups and equal values for the remainder. Hence the complex models had lower BIC values than the simpler models for most of the genotype by sex groups in spite of the penalty imposed on complex models by the BIC, making the complex models the best to use for this data set. Further examination of the actual data indicates that all the models were relatively accurate in predicting mid-life growth, and that it was the early life growth (0 to 6 weeks of age) and late in life growth (20 to 40 weeks of age) that the superiority of the Richards model was evident.

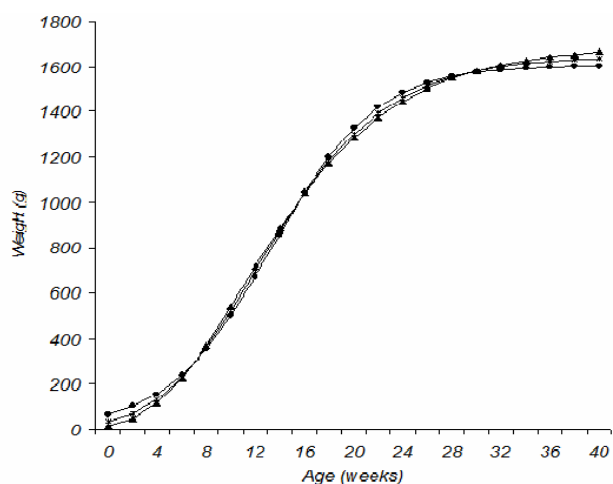
**Table 6** Computed traits for the different phases of growth in Forest, Savannah and SASSO T44 chickens

Model	Genotype	Sex	Start of growth acceleration phase <sup>1</sup>		Inflection point <sup>2</sup>		End of growth deceleration phase <sup>3</sup>	
			Age (weeks)	Weight (g)	Age (weeks)	Weight (g)	Age (weeks)	Weight (g)
Logistic	SASSO T44	Female	3.5	284	13.1	1420	22.6	2556
		Male	4.4	323	12.5	1613	20.6	2903
	Forest	Female	3.6	117	12.6	585	21.5	1053
		Male	4.1	161	13.4	803	22.6	1446
	Savannah	Female	3.5	129	12.7	646	21.9	1162
		Male	4.1	170	13.0	852	21.9	1533
Gompertz	SASSO T44	Female	4.6	299	10.6	1099	27.0	2689
		Male	5.3	345	10.6	1269	24.9	3104
	Forest	Female	4.7	121	10.0	444	24.7	1086
		Male	5.0	169	10.9	621	26.6	1520
	Savannah	Female	4.6	133	10.1	490	25.1	1198
		Male	5.0	178	10.6	654	25.6	1600
Richards	SASSO T44	Female	4.6	302	10.0	1037	27.9	2718
		Male	4.9	334	11.4	1432	22.7	3005
	Forest	Female	3.9	118	12.0	553	22.0	1059
		Male	4.7	165	12.0	701	23.3	1485
	Savannah	Female	4.0	130	11.7	589	22.9	1174
		Male	4.7	175	11.3	715	24.3	1577

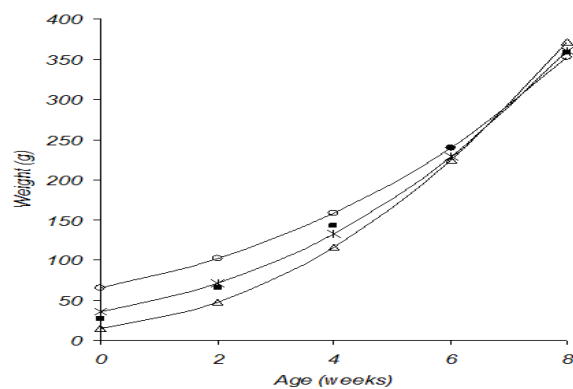
<sup>1</sup> Age at which the chick attains 10% of its final body weight and represents the beginning of the growth acceleration phase.

<sup>2</sup> Represents the end of the growth acceleration phase and the beginning of the deceleration phase.

<sup>3</sup> Age at which the chick attains 90% of its final body weight and represents the end of the growth deceleration phase.



**Figure 1** Predicted growth curves for male chicken of the Forest genotype from the Logistic (●), Gompertz (▲), and Richards (∗) functions

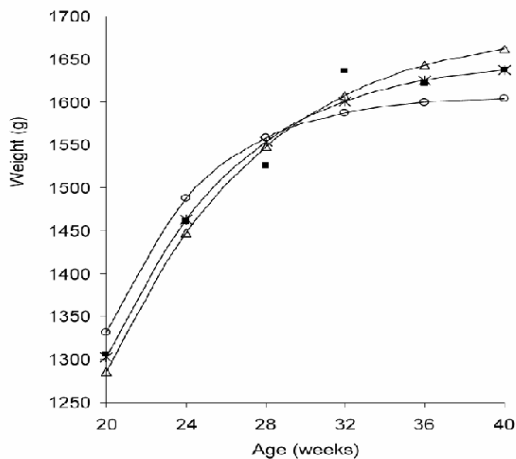


**Figure 2** Actual mean weights (■, no connecting lines) and weights predicted from the logistic (○), Gompertz (Δ) and Richards (∗) functions, for the first 8 weeks of life for male chicken of the Forest genotype

Using the data of the male chicken of the Forest genotype as an example, the predicted weights from the Richards function were closer to the actual mean weights of the chicken, whereas those from the logistic function were higher, and those from the Gompertz function were lower than the actual means from birth to 6 weeks of age (Figure 2). For late in life growth, the predicted weights from the Richards function were again closer to the actual mean weights, whereas those from the logistic and the Gompertz functions were either higher or lower than the actual means (Figure 3). The Gompertz, Richards and asymmetric logistic growth models predicted higher maturing rates and lower mature weight in the local females compared to the males, as observed by the actual data (Tables 1 and 4). Male chickens were heavier than female chickens of the same age and took a longer time to attain mature weight. This explains their lower maturing rate and the longer time taken by males to reach the point of inflection compared to females.

This finding is in agreement with the results of *Ali et al.* (2002), who reported that irrespective of genotype or the rearing system, male birds had higher adult body weights and lower maturing rates and reached the point of inflection later than female birds. In Nigeria, *Olawoyin* (2007) reported asymptotic mature weights of 1716.3 g, 1928.6 g and 1854.9 g for local cockerels based on the logistic, Gompertz and Richards growth models which were all higher than those obtained for local males in the present study using the same models (Table 5). Ghanaian local male chickens however had higher maturing rates based on these three models (Table 5) compared to Nigerian local





**Figure 3** Actual mean weights (■, no connecting lines) and weights predicted from the Logistic (○), Gompertz (Δ), and Richards (\*) functions, from 20 to 40 weeks of age for male chicken of the Forest genotype

cockerels (Olawoyin, 2007) and this can be attributed to genotype differences. The three nonlinear curves of logistic, Gompertz and Bertalanfy Growth model have been used to fit the growth model in Jinghai mixed sex yellow chickens (Yang *et al.* 2006). The three growth models were all well fitted in the prediction of growth parameters. Females reached inflection point at earlier ages (10.23 weeks, 10.26 weeks and 11.13 weeks respectively for the 3 models) than males (10.77 weeks, 11.20 weeks and 12.81 weeks respectively). Estimates from the Gompertz model of 10.26 weeks for female chickens and 11.20 weeks for male chicken are in close agreement with the average age at point of inflection of 10.49 weeks in females and 11.16 weeks in male chicken obtained in the present study. This is not surprising as both studies utilised indigenous chickens. The present study also confirms the result of females reaching the inflection point earlier than the males. Growth curves for BW, breast weight and leg weight were calculated using the Richards function (Goliomytis *et al.* 2003). The types of the curves predicted were typically sigmoid. Asymptotic weights for BW, breast weight and leg weight were estimated at 6870.2, 1744.2 and 851.5 g respectively. Age at point of inflection, at which maximum growth rate is attained, was predicted at 44.4, 47.0 and 49.1 days respectively which were lower than those obtained in the present study based on the Gompertz growth model. The difference in growth curve parameters could be attributed to the feed given to the birds, the environment and the genotypes of the birds involved.

## CONCLUSION

The results of this study indicate that all the four growth models evaluated adequately predicted the growth curve parameters. However the complex models with flexible

point of inflection were better than the simpler models, especially due to their superior prediction of early life and late life growth. Therefore it is concluded that, where data structure and availability of adequate computing power permit, the Richards function (as an example of a sigmoid model with flexible inflection point) can be used to provide accurate parameter estimates for the characterization of growth of indigenous chickens in the tropics. However, further research is required using independent data sets of chickens of the same or other local genotypes to validate and ascertain the industry-wide utility and accuracy of these prediction equations.

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