

Comparison of Three Nonlinear and Spline Regression Models for Describing Chicken Growth Curves¹

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ABSTRACT This study compared three non-linear growth models (Richards, Gompertz, and logistic) and the spline linear regression model using BW measurements from an unselected, randombred chicken population. Based on the goodness of fit criteria, the nonlinear models (NLM) fitted the data better than the spline regression model. The four-parameter Richards model was expected to have the best overall fit; however, because the shape parameter predicted was close to 1.0, which corresponded with the Gompertz curve, there were no differences between the Richards and Gompertz models for the data used. The growth parameters predicted with the logistic model were different from those predicted by the Rich-

ards and Gompertz models. It was concluded that growth parameters predicted with different models with fixed inflection points are not directly comparable. The spline linear regression model is a compound function consisting of a series of linear models. It can be used to compartmentalize growth into segments and also substitute as an alternative to asymptotic models when the data are truncated before the asymptote is attained. The relationship between the growth trajectory (m) and carcass composition measurements were also investigated. Carcass yields among the different growth trajectories (m) were similar within sexes. However, the proportions of the major breast muscle and abdominal fat differed according to the m a bird followed.

(Key words: Richards, Gompertz, logistic, spline regression, carcass composition)

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INTRODUCTION

The process of growth measured as body mass or BW on a longitudinal time frame has often been summarized using mathematical equations fitted to growth curves. One of the objectives of curve fitting is to describe the course of BW increase over time or age with mathematical parameters that are biologically interpretable. Understanding the biology of model parameters and their relationships provides a sound basis for developing a breeding strategy to modify or change the trajectory of growth. A number of nonlinear models (NLM) have been used to describe growth curves in chickens. Sang (1962), Grossman and Bohren (1982), and Grossman et al. (1985) applied the logistic function to chicken data, although its symmetrical form does not correspond to the growth pattern of chickens (Knizetova et al., 1991a). The Laird form (Laird et al., 1965) of the Gompertz model (Gompertz, 1925) has been the model of choice for chicken data

(Tzeng and Becker, 1981; Anthony et al., 1991; Barbato, 1991; and Mignon-Grasteau et al., 1999) because of its overall fit and the biological meaning of the model parameters (Ricklefs, 1985). As pointed out by Barbato (1991), the original Gompertz equation is a function of the asymptote (or mature) weight of birds. Broiler type birds rarely attain mature BW because they are usually processed at slaughter age (42 d) or placed on a restricted breeder feeding regimen between 4 and 12 wk of age. The Laird form (Laird et al., 1965) of the Gompertz curve, however, estimates the exponential decay rate of the animal based on initial BW and the point of inflection.

The logistic and Gompertz models have fixed growth forms with points of inflection at about 50 and 37% of the asymptote, respectively (Ricklefs, 1968). These parameter models are special cases of the more flexible Richards model, which has a variable point of inflection specified by the shape parameter (m) (Richards, 1959). Although the generalized Richards model is attractive and flexible, it has not been used extensively to study poultry growth (Knizetova et al., 1991a,b; Gebhardt-Henrich and Marks, 1993), which may be due to assumptions that the four-parameter model is difficult to fit. However, Brisbin et al. (1987) suggested that the shape

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Abbreviation Key: NLM = nonlinear model.

parameter has greater propensity to change in response to environmental changes than the asymptotic weight or growth rate and may be used to study the effects of environmental stress on growth. This reasoning inherently implies that growth models with fixed shapes may not contribute to the understanding of the effects of factors such as dietary and environmental changes on growth. The trajectory of growth as defined by m may reflect the architecture of body composition and could therefore be used to manipulate the desired body composition at a given age.

High order polynomial models have also been fit to growth data (Tzeng and Becker, 1981). Although, high order polynomials tend to have a better fit for poultry data, the models do not asymptote, and the model parameters do not have any biological meaning.

The spline model is generally defined as piecewise polynomials of degree n whose function values and first $n-1$ derivatives agree at the points where they join. The abscissas of these joints are called knots. Polynomials may be considered as a special case of splines with no knots (Smith, 1979). The spline linear model is a seamless compound function consisting of a series of linear equations. Although discrete, the neighboring functions meet at the knots. The spline linear regression model can be used as an alternative to high order polynomials and complicated NLM.

The present study was designed to compare the Richards, logistic, Gompertz, and Spline linear regression models using growth data from a randombred, unselected chicken population and to study how the shape parameter, m , affects growth patterns, carcass yield, and composition

MATERIALS AND METHODS

Animals

Data were collected on an unselected, random mating Athens-Canadian chicken population (Hess, 1962). Fifty males were pedigree-mated to 120 dams (sex ratio, 1:2~3) to hatch 405 chicks in two hatches at a 14-d interval. Chicks were placed in pens with litter and fed a starter diet of 23% protein/3,200 kcal ME/kg from hatch until 18 d of age. Thereafter, they were fed a 17% protein/3,200 kcal ME/kg grower diet. All birds were weighed and sexed at hatch. Birds were weighed every third day until 54 d of age; thereafter, the birds were weighed every 14 d until 170 d of age. Only data collected to 170 d of age were used. A total of 365 birds were used for growth curve parameter estimations. At 170 d of age, birds were processed. All birds were New York dressed and weighed. The skin from the breast of the whole bird was removed, and the *Pectoralis major* (breast) muscle was filleted from the skeleton and weighed. The abdominal fat pads were also removed and weighed. Two hundred six males and 138 females had complete growth and body composition data.

Growth Models

Richards Model. To estimate the expected BW at a specific age, a four-parameter growth curve modified from Richards (1959) growth function (Sugden et al., 1981) was fitted to the BW data collected. The growth curve was of the following form:

$$W_t = W_A [1 - (1 - m) \exp[-K(t - t_i)/m^{1/(1-m)}]]^{1/(1-m)}$$

where W_t is the weight of bird at time t , W_A is the asymptotic (mature) BW, K is the maximum relative growth (per day), t_i is the age at maximum rate of growth (days), and m is a shape parameter, with the property that $m^{1/(1-m)}$ is relative weight at t_i .

Gompertz-Laird Model. The Laird form of the Gompertz equation (Laird et al., 1965) was fitted to the data. The following equation describes the Gompertz-Laird growth curve:

$$W_t = W_0 \exp[(L/K)(1 - \exp - Kt)]$$

where W_t is the weight of bird at time t , W_0 is the initial (hatch) BW, L is the instantaneous growth rate (per day), K is the rate of exponential decay of the initial specific growth rate, L (which measures the rate of decline in the growth rate). The parameters derived for the inflection point, t_i ; the BW at the inflection point; and the asymptotic body, W_A , are

$$\begin{aligned} t_i &= (1/K)\log(L/K) \\ W_i &= W_0 \exp((L/K)^{-1}) \\ W_A &= W_0 \exp(L/K). \end{aligned}$$

Logistic Model. The following equation describes the logistic (Robertson, 1923) growth model:

$$W_t = W_A/[1 + \exp - K(t - t_i)]$$

where W_t is the BW at time t , W_A is the asymptotic BW, K is the exponential growth rate, and t_i is the age at the inflection point.

Spline Linear Regression Model. The spline model fitted was of the general form

$$W_t = W_0 + b_1(t - t_1) + b_2(t - t_2) + \dots + b_n(t - t_n) + e$$

where W_t is the BW of the bird at time t , W_0 is the point of intersection (hatch weight), and $t_1 \dots t_n$ are the so-called knots (age at which the growth rate changes). As post-hatch growth is under consideration, t_1 is the age at which the first growth period starts; therefore, t_1 equals zero, $b_1 \dots b_n$ are the growth rates of the specified periods that constitute the entire spline, and e the residual error. The data were first plotted to determine how many straight lines are to be constructed in a spline. The actual model that was fitted to the data was as follows:

$$W_t = W_0 + b_1t + b_2(t - 6) + b_3(t - 18) + b_4(t - 113) + e;$$

for $t < 6$ d,

$$W_t = W_0 + b_1 t + e;$$

for $6 < t < 18$ d,

$$W_t = W_0 + b_1 t + b_2(t - 6) + e,$$

which is equivalent to

$$W_t = W_0 - 6b_2 + (b_1 + b_2) t + e;$$

for $18 < t < 113$ d,

$$W_t = W_0 + b_1 t + b_2(t - 6) + b_3(t - 18) + e,$$

which is equivalent to

$$W_t = W_0 - 6b_2 - 18b_3 + (b_1 + b_2 + b_3) t + e;$$

for $t > 113$ d,

$$W_t = W_0 + b_1 t + b_2(t - 6) + b_3(t - 18) + b_4(t - 113) + e,$$

which is equivalent to

$$W_t = W_0 - 6b_2 - 18b_3 - 113b_4 + (b_1 + b_2 + b_3 + b_4) t + e.$$

The four line segments are joined at 6, 18, and 113 d of age. Growth curve parameters for the Richards, Gompertz-Laird, and logistic curves were estimated for each bird using PROC NLIN (Marquart algorithm) (SAS Institute Inc., 1996). The spline model was fitted using PROC REG (SAS Institute Inc., 1996). Goodness of fit criteria were R^2 and the residual standard deviation. Birds with body composition data were grouped according to their shape parameter m from the Richards model. There were three male groups (0.74, 0.99, and 1.45), and two female groups (0.71 and 1.22). The differences in carcass data as classified by the m groupings were tested using PROC GLM (SAS Institute Inc., 1996).

RESULTS AND DISCUSSION

Overall means and standard deviations for BW for both sexes are presented in Table 1. For both sexes, the standard deviation increased with age. The Richards, Gompertz, and logistic curves fitted to sex are shown in Figure 1. The fitted parameters for each growth model are presented in Table 2. For the Richards model, the growth curve shape is characterized by the shape parameter m . The mean values for the shape parameter were 1.06 and 0.96 for males and females, respectively. These values are close to 1.0, which corresponds to the Gompertz model (Brisbin et al., 1987). Theoretically, the four-parameter Richards model is expected to give a higher R^2 than the three-parameter Gompertz and logistic models. However, because the growth trajectory predicted by the Richards model is close to the Gompertz model, the R^2 were similar. To date, no biological meaning has been assigned to the shape parameter of the Richards model. Nevertheless, it could potentially be of interest when

differences in the growth pattern of birds is the goal of a study. From a series of experiments, Brisbin et al. (1986a,b) concluded that the Richards shape parameter has more propensity to change in response to environmental changes than the asymptotic BW or growth rate, which inherently suggests that growth models in which the curve shape is set and not allowed to vary may not be useful in understanding the effect of environmental changes (Brisbin et al., 1987), such as dietary and temperature stresses on growth. The trajectory of growth may reflect the architecture of body composition; therefore, the shape parameter can be manipulated to obtain the desired carcass composition at a given age. Thus, some individuals may concentrate growth early, showing a short lag phase, whereas others may show abysmal growth before the spurt. Protein and energy levels or stress factors may shorten or prolong the lag phase, and these may be readily identified by the shape parameter.

The effects of m on carcass components are shown in Table 3, and the growth patterns of birds according to m (Richards model) groupings for both males and females are shown in Figure 2. Both 170-d BW and dressed carcass weight were different ($P \leq 0.05$) among the m groups for both males and females. For both males and females, birds with $m < 0.99$ had a higher 170-d BW and dressed carcass weight compared with birds with $m \geq 0.99$. Carcass yields, however, were the same for all groupings of m for both sexes. The proportions of the major breast muscle and abdominal fat differed according to the growth trajectory of the bird. Birds that followed a trajectory of $m > 0.99$ had reduced abdominal fat, both in amounts and percentage of carcass weight, when compared with birds with $m \leq 0.99$. This pattern was observed in males and females. From Table 3, it is likely that the shape of the growth curve could be used to determine the proportion of abdominal fat.

Among the parameters predicted by the Gompertz model is initial BW, W_0 (hatching weight). W_0 predicted by the Gompertz model (46.1 g) shown in Table 2 was higher (t test: $P \leq 0.001$) than the measured hatching weight (36.8 g) for both sexes. To improve fitting of the data, Grossman and Bohren (1982) have suggested constraining W_0 . Pasternak and Shalev (1994) have suggested weighting W_0 by the inverse of the variance. Mignon-Grasteau et al. (1999), on the other hand, constrained W_0 within two standard deviations of the mean, which resulted in a correlation of 0.98 between the measured and predicted W_0 . The effect of using the measured W_0 as a constant (Barbato, 1990) or constraining W_0 on the other model parameters is yet to be investigated beyond the improvement in the R^2 .

It is generally expected that individuals with lower initial growth rate would reach the age of maximum growth sooner and, consequently, show a higher exponential decay, than individuals with higher initial growth rate when the Laird form of the Gompertz model is fitted to growth models. However, reports in literature have been conflicting. In this study, females showed a lower L compared with males, which was consistent

TABLE 1. Means and standard deviations for BW at different ages in Athens-Canadian randombred chickens

Age (d)	BW	
	Males (n = 217)	Females (n = 148)
	(g)	
0	37.00 ± 3.02	36.68 ± 3.02
3	41.74 ± 3.23	40.80 ± 3.59
6	59.19 ± 6.59	57.33 ± 6.46
9	79.94 ± 9.89	77.24 ± 9.11
12	102.96 ± 13.92	97.96 ± 12.46
15	132.13 ± 20.45	121.92 ± 18.48
18	170.18 ± 26.35	155.08 ± 23.10
21	206.56 ± 32.41	184.24 ± 26.25
24	250.71 ± 37.49	218.37 ± 30.24
27	285.27 ± 42.68	247.12 ± 33.46
30	324.92 ± 47.68	279.58 ± 37.74
33	372.83 ± 53.50	319.55 ± 44.41
36	417.41 ± 59.22	355.13 ± 49.12
39	469.13 ± 68.97	396.32 ± 57.26
42	519.72 ± 78.09	436.51 ± 64.96
45	577.27 ± 85.16	480.31 ± 71.56
48	633.59 ± 94.10	522.91 ± 79.14
51	667.18 ± 101.25	547.23 ± 85.92
54	717.17 ± 106.97	583.56 ± 91.09
57	786.35 ± 123.31	631.77 ± 96.68
71	1,069.28 ± 153.77	832.57 ± 118.99
85	1,326.49 ± 176.84	1,009.48 ± 130.78
99	1,589.71 ± 191.66	1,183.80 ± 148.35
113	1,859.26 ± 207.06	1,440.18 ± 188.54
127	2,015.44 ± 226.14	1,561.89 ± 200.11
141	2,142.31 ± 243.54	1,619.34 ± 212.78
155	2,220.54 ± 269.31	1,680.29 ± 220.99
170	2,262.63 ± 286.34	1,717.78 ± 230.89

with the studies of Barbato (1991) and Mignon-Grasteau et al. (1999). The average value of L for both sexes (0.0856) was lower than that obtained by Tzeng and Becker (1981) and Barbato (1991), but similar to the estimates of Mignon-Grasteau et al. (1999). The rate of maturation, K, was higher in males than in females (Table 2), and it was in contrast to the studies of Mignon-Grasteau et al. (1999). They reported a higher K value in females compared with males. Hancock et al. (1995), on the other

hand, did not observe sexual dimorphism in K when the Gompertz model was fitted. The maximum relative growth predicted by the Richards model and the exponential growth rate predicted by the logistic curve were higher in males than in females. Grossman et al. (1985) also obtained a higher K value for males than for females using the logistic model. Among the growth parameters predicted by the Gompertz model, L and K are highly positively correlated for both sexes ($r_p = 0.96$), which is close to the correlation reported by Barbato (1991). The chickens used for this study were a randombred, unselected population, and variability within the sexes were high.

The estimated ages at maximum growth (t_i) for the three NLM are presented in Table 2. As expected, the pullets reached t_i faster than the males. The differences were 3.6, 1.9, and 1.0 d for the Richards, Gompertz, and logistic models, respectively. The mature BW estimated for males were higher than those for females (Table 2). The predictions of the Richards and Gompertz models were similar. Given that the predicted mature BW differ among sexes, individuals with higher mature BW will grow faster at a weight throughout the growing period and may require different levels of protein than slow-growing birds. Common among growth models is a pronounced correlation among the growth parameters estimated (Mignon-Grasteau et al., 1999; Barbato, 1991), suggesting that the position of the inflection point strongly influences the growth rate constant value and mature BW. For the data used in this study, the inflection

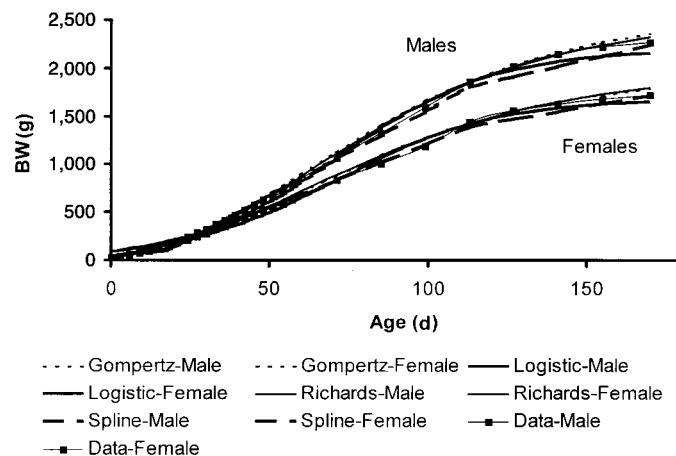


FIGURE 1. Growth curves for Athens-Canadian randombred chickens predicted by Richards, Gompertz, logistic, and spline regression models. Curves for raw data and mean model parameters were based on fitting individual birds.

TABLE 2. Estimated coefficients for Richards, Gompertz, logistic, and spline regression model growth parameters in Athens-Canadian randombred chickens

Model	Male (n = 217)	Female (n = 148)
Richards		
Asymptotic weight (W_A)	2,505.8	1,978.7
Relative growth (K)	0.0236	0.0210
Age of maximum growth (ti)	63.4	59.8
Shape parameter (m)	1.06	0.9566
R^2	0.9827	0.9812
RSD	16.46	15.23
Gompertz		
Hatching weight (W_0)	44.6	47.5
Initial growth rate (L)	0.0908	0.0804
Rate of decay (K)	0.0224	0.0216
Age of maximum growth ¹ (t*)	63.0	61.1
Asymptotic weight ¹ (W_{A*})	2,483.8	1,898.8
R^2	0.9826	0.9811
RSD	11.43	10.41
Logistic		
Asymptotic weight (W_A)	2,192.7	1,693.6
Exponential growth rate (K)	0.0422	0.0399
Age of maximum growth (ti)	72.7	71.7
R^2	0.9800	0.9780
RSD	18.27	14.81
Spline		
Hatching weight (W_0)	32.8	33.6
Growth rate for t < 6 d (b_1)	5.70	4.34
Growth rate for 6 d < t < 18 d (b_2)	4.12	5.63
Growth rate for 18 d < t < 113 d (b_3)	17.83	13.33
Growth rate for t > 113 d (b_4)	7.79	5.66
R^2	0.9642	0.9601
RSD	87.80	65.85

¹Derived parameters: R^2 = coefficient of determination and RSD = residual standard deviation.

points for the Richards and Gompertz models were similar and, consequently, had similar K values, which is contrast to the K and W_A values predicted by the logistic model. Therefore, growth model parameters from different models with fixed inflection points are not directly comparable.

The spline linear regression coefficients and points of intersection for both sexes are presented in Table 2. The point of intersection (BW at hatch) was close to the measured hatching weight values. The spline model predicted the hatching weight better than the Gompertz model. However, using goodness of fit as a measure of comparison, the spline model had the least fit to the data compared with the three NLM. Nevertheless, its model parameters are biologically meaningful. In fitting the

spline model with known knots, the data should first be plotted to determine the number and locations of the knots. The basic assumption therein is that the underlying growth rate is not the same throughout the age range from which the data were collected. This assumption can be tested by the null hypotheses that all of the coefficients of the splines defined are the same. Unlike the NLM where growth data has to be collected beyond the asymptotic weight in order for growth to be modeled, such a requirement is not necessary for the spline regression.

Ricklefs (1985) suggested that early growth may be the key response to selection for later body mass, as growth rate is evidently more flexible when it is the greatest. Hence, efforts to improve poultry meat might

TABLE 3. Effect of shape parameter (m) of the Richards growth model on carcass components

Trait	Male		Female		
	m = 0.74 (n = 57)	m = 0.99 (n = 89)	m = 1.45 (n = 60)	m = 0.71 (n = 69)	m = 1.22 (n = 69)
BW at kg 170 d, kg	2.43 ^a	2.21 ^a	2.13 ^b	1.77 ^a	1.65 ^b
Carcass wt, kg	2.03 ^a	1.91 ^b	1.77 ^c	1.53 ^a	1.41 ^b
Carcass yield ¹ , %	83.98	83.16	83.23	86.11	85.41
Breast meat, g	245.47 ^a	225.32 ^b	207.69	184.09	175.98
Breast meat yield ¹ , %	12.11	11.84	11.71	12.08	12.54
Abdominal fat, g	27.83 ^a	26.37 ^a	16.52 ^b	47.80 ^a	38.38 ^b
Abdominal fat yield ¹ , %	1.34 ^a	1.32 ^a	0.92 ^b	3.41 ^a	2.63 ^b

^{a-c}Trait means within sex with different superscripts are significantly different at $P \leq 0.05$.

¹Percentage of carcass weight.

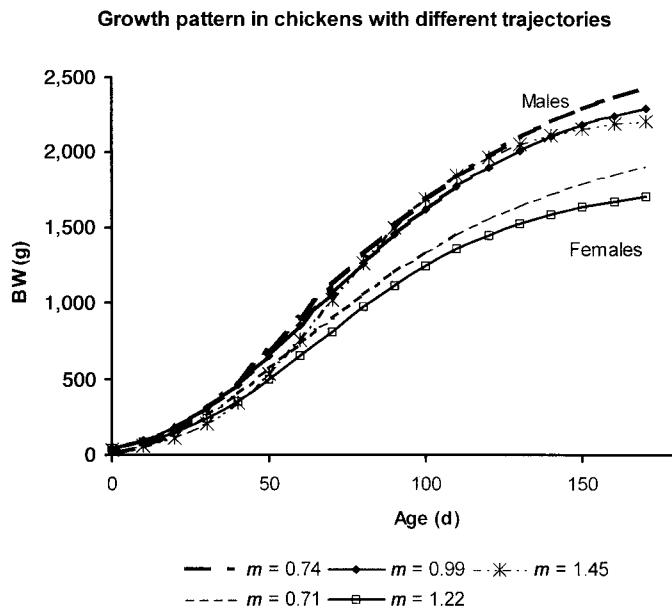


FIGURE 2. Growth curve as predicted by the Richards model in chickens with different growth trajectories (m).

best be directed toward the first 2 wk after hatching. Using the spline method, the greatest growth was attained between Days 18 and 113 for both sexes; however, for the males, growth rate between Days 6 and 18 was less than that from hatch to Day 6. Rather than using the growth rate of the first 2 wk after hatching for selection as suggested by Ricklefs (1985), using growth rate from Week 1 onward might be more useful in assessing growth potential of birds. Growth rate within the first 3 to 5 d after hatching may be misleading because most hatched chicks are not active enough to feed to their maximum.

Whereas the Laird form of the Gompertz model can be used to predict initial growth rate from hatching until the inflection point, the spline method can be used to compartmentalize growth to any degree that the researcher desires. One of the potential dangers that accompanies nonlinear growth models is their analysis of data sets that do not warrant their application, as it is possible to fit growth curves to estimate asymptotic BW when the data are truncated before the asymptotic weight is reached (Brisbin et al., 1987). In situations in which the data sets are truncated before growth approaches the asymptote (Barbato, 1990), the spline linear regression would be a good alternative to high order polynomials and nonlinear and exponential models because 1) it would avoid the problem of estimating a false asymptotic BW and 2) it would estimate growth rate on a linear scale. Splines have greater flexibility than simple regressions because they can encompass data that exhibit behavior in one region that may be unrelated to the behavior of another region. In broilers, for example, knots can be created at ages where feeding regimen is changed to ascertain the rate of growth within specific intervals.

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