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A New Form of the Gompertz Growth Curve, with Application to Broiler Chicken Growth

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SUMMARY

Several forms of the Gompertz growth curve have been used extensively to describe the live weight of poultry over time. This note reviews these current forms of the Gompertz curve and also presents a new parameterization which is particularly useful for broiler chickens. Broiler chickens are processed well before attaining their asymptotic weight, and hence their time series data have a relatively short time span compared to other poultry. The three parameters associated with the new model, all of which are insightful for broilers, are (i) the time of maximum growth, (ii) the rate of maximum growth and (iii) the weight at time of maximum growth. The estimation of these parameters directly from the new model facilitates the subsequent statistical analysis. The model and statistical analysis are illustrated with data on chicken separately for each gender, aiding comparisons. Both genders have similar times of maximum growth, however the males have a significantly larger weight at this time, and a larger maximum rate of growth. The newly parameterized Gompertz model, with its new focus for analyzing growth curves, may be applied to other poultry such as turkey, duck and goose as well.

Keywords : Logistic growth curve, Richards growth curve, Reparameterization, Autocorrelation, Point of inflection, Laird model.

1. INTRODUCTION

Scientists have been developing mathematical models to describe animal growth behavior for over 100 years. Seber and Wild (1989) review these developments for the three main growth curves often applied to poultry, namely the Gompertz, the logistic and the Richards curves. The Gompertz curve was proposed by Gompertz (1825) for life table analysis, and was first used specifically as a growth curve by Winsor (1932). The logistic curve was formulated by Verhulst (1838) and apparently first used as a growth curve by Robertson (1908). The Richards curve was developed specifically for growth curves by Richards (1959). These curves have recently found widespread application for modeling growth curves of poultry, including turkey (Sengul and Kiraz 2005), chicken (Norris *et al.* 2007), duck (Knitzetova *et al*. 1991), goose (Knitzekova *et al*. 1994), emu (Goonewardene *et al*. 2003), ostrich (Cooper 2005), quail (Hyankova *et al*. 2001) and partridge (Cetin *et al*. 2007). The growth curves are shown in these papers to fit data from the various poultry species apparently adequately, using the standard regression model assuming independent errors.

As chickens age, they become less efficient in converting feed into meat, and hence commercial practice is to process broiler chickens well before they reach a biologically mature age. Therefore, weight data for broiler chicken usually covers a relatively short time span, and thus differs qualitatively from weight data sets

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for most other poultry. The Gompertz growth curve has traditionally been favored for these short time series over other growth curves. The shortness of the time series has two other consequences. One is that such data are typically devoid of autocorrelation. The other is that it motivates a new parameterization of the Gompertz model.

Section 2 of this note reviews the various forms of the Gompertz model which are currently widely applied in poultry research. Section 3 develops a new parameterization of the model. Section 4 applies the new model to data from male and from female broilers, and Section 5 illustrates the statistical analysis using parameters from the new and the standard forms of the model. Concluding remarks are given in Section 6.

2. REVIEW OF THE GOMPERTZ GROWTH CURVE AND ITS ANALYSIS

Let $Y(t)$ be the weight of a broiler chicken at age t. As noted, the three main growth models used for poultry are the Richards curve, the logistic curve and the Gompertz curve. The commonly used forms of the Gompertz model used for poultry are reviewed and fitted to our data in this section. The appropriateness of the Richards and the logistic curves for describing broiler growth will be discussed subsequently.

2.1 Standard Parameterizations

The classical form of the Gompertz model is

$$Y(t) = K \exp\{-b \exp(-ct)\} \tag{1}$$

where K, b and $c > 0$ are parameters to be estimated. Parameter K in (1) is called the "asymptotic" or "mature" weight as $t \to \infty$, but there are no "intuitive biological" interpretations of parameters b and c. A frequently used variation is to assume that b and c are negative numbers, which would eliminate the negative signs in (1). Another small variation of this model, which is the one originally proposed by Winsor (1932), is:

$$Y(t) = K \exp\{-\exp(d - ct)\} \tag{2}$$

Both classical forms (1) and (2) are widely used for poultry, including Sengul and Kiraz (2005), Cetin *et al.* (2007), and Norris *et al.* (2007).

Maximum growth occurs at the "point of inflection". Many references, including Seber and Wild (1989), give the time of inflection of the curve, t_{inf}, the weight at this time, Y_{inf}, and the maximum growth rate which occurs at this time, X_{max}, from (1) as

$$t_{inf} = \log_e(b)/c \tag{3}$$

$$Y_{inf} = K/e \tag{4}$$

$$X_{max} = K \cdot c/e. \tag{5}$$

Each of these three new parameters is interpretable intuitively biologically, and each provides a characteristic of chicken growth curves which is useful for the subsequent model and its statistical analysis.

2.2 The Laird Parameterizations for Broiler Chickens

Aggrey (2002) observes that "the original Gompertz equation is a function of the asymptotic (or mature) weight of birds. Broiler type birds rarely attain mature body weight because they are usually processed at slaughter age (42 d)". In fact, in all our data the broilers were processed at less than 60% of their estimated asymptotic weight K. In light of this, an alternative form of the Gompertz equation, proposed originally by Laird (1966) and based on parameters related to the time of hatching, is often used for broiler chicken. The initial or "hatching weight", $Y_0 = Y(0)$, is immediate from (1) as:

$$Y_0 = Ke^{-b}, \tag{6}$$

and the "instantaneous growth rate", denoted L, found by differentiating $Y(t)$ and evaluating at $t = 0$, is:

$$L = b \cdot c. \tag{7}$$

Substituting (6) and (7) into (1) gives the new form:

$$Y(t) = Y_0 \cdot \exp\{(L/c) \cdot (1 - \exp(-ct))\} \tag{8}$$

This "Laird form" of the Gompertz equation has a compelling mechanistic interpretation, with weight starting at Y_0 and increasing initially at rate L. This rate of increase decays exponentially over time, as defined by coefficient c. This model form has been used frequently for broiler chicken data, including Mignon-Grasteau *et al.* (2001) and Aggrey (2002).

A recent variation of this model is to substitute (6) into (1), which yields

$$Y(t) = K \exp\{(\exp(-ct)) \cdot \ln(Y_0/K)\} \quad (9)$$

This form is used by Ricklefs (1985), Anthony *et al*. (1991) and Porter *et al*. (2010), and is given also in Thornley and France (2007).

3. A NEW PARAMETERIZATION

3.1 The Case for a New Parameterization

The four forms of the Gompertz model in (1), (2), (8), and (9) contain six different parameters, namely K, b, c, d, Y_0, and L, to describe a growth curve. However the parameters t_{inf}, Y_{inf}, and X_{max} in (3) – (5) are also of intrinsic interest for broiler chicken analysis. The time of maximum growth, t_{inf}, is a key characteristic of interest, and the weight, Y_{inf}, at this intermediate time is a more natural parameter for describing broiler growth than either of the other weights, Y_0 or K, at the two extreme times, namely at $t = 0$ or $t \to \infty$. Similarly X_{max} is a key descriptor of growth which has immediate application for producers. *Yet none of these three parameters is incorporated explicitly in the four commonly used forms of the Gompertz curve.*

This is often a significant problem for the following reason. These three parameters, though not incorporated explicitly into the model, have nevertheless often been used in the subsequent analysis of data. In the most common application, including in our subsequent illustration, random samples of birds are taken from a flock at specified times and the mean weights are calculated at each time. A Gompertz curve is then fitted to these mean weight data and the model parameters are estimated. As examples, Cetin *et al*. (2007) fits model (2) to mean weight data of partridge, and Aggrey (2002) fits model (8) to mean weight data of chicken. The specific parameters of the model are then transformed, using relationships such as (3) – (5), to estimate t_{inf}, Y_{inf}, and X_{max}. Comparative values of these parameters are usually given for some characteristic of interest, e.g. by gender in the two examples. However the problem with this application is that standard errors are not given for the estimates, without which formal statistical hypothesis testing is not possible. The transformations to t_{inf}, Y_{inf}, and X_{max} involve products or quotients of random variables and hence only approximations are available to calculate their standard errors (Taylor 1997). *Subsequent statistical inferences would be much simpler and more exact in these applications if the parameters t_{inf}, Y_{inf}, and X_{max} were in the model explicitly, whereby their estimates and standard errors would be calculated directly.*

In a less common application, data are recorded for individual birds over time, and a Gompertz model is fitted to each individual data set, as e.g. in Anthony *et al*. (1991). An analysis of variance (ANOVA) may then be calculated for each of the response variables, t_{inf}, Y_{inf}, and X_{max}, separately from the data on individual birds. Standards errors are estimated by the ANOVA, from which statistical inferences concerning possible treatment effects are available. This procedure clearly involves considerable data analysis. Though this application does not require that the model be parameterized explicitly in terms of t_{inf}, Y_{inf}, and X_{max} for the subsequent analysis, such a parameterization might still be enlightening.

3.2 The New Parameterization

We suggest that it is both natural and useful to parameterize the Gompertz model in terms of the new parameters, t_{inf}, Y_{inf}, and X_{max}. One step in this direction is to substitute for b in (1) a function of t_{inf} from (3). This reparameterizes (1) as

$$Y(t) = K \exp\{-\exp(-c(t - t_{inf}))\} \quad (10)$$

which is given in Seber and Wild (1989). Surprisingly, this parameterization appears not to be used for poultry.

Consider incorporating all three parameters t_{inf}, Y_{inf}, and X_{max} into the model. Substituting (4) and (5) into (10), one can show that

$$Y(t) = Y_{inf} \exp\{1 - \exp(-X_{max}(t - t_{inf})/Y_{inf})\} \quad (11)$$

We have not found form (11) of the Gompertz model used previously in the literature; *for sure it is not in common use in poultry research.* Besides being based on three biologically interpretable parameters, we will show in the following section that this parameterization has two useful properties for the subsequent statistical analysis of data. The first is that one can easily find plausible initial estimates for the nonlinear fitting by inspection from the data, and the second is that it can give standard error estimates directly. These properties are illustrated in the following section.

The derivative of $Y(t)$, denoted $X(t)$, is the curve for the growth rate. This curve is easily found to be

$$X(t) = X_{max} \exp\{1 - X_{max}(t - t_{inf})/Y_{inf} - \exp(-X_{max}(t - t_{inf})/Y_{inf})\} \quad (12)$$

This function is insightful as, by definition, its peak is X_{max}, which occurs at time t_{inf}. This time is often denoted as t_{max} for obvious reasons.

4. AN ILLUSTRATION FITTING THE GOMPERTZ MODEL TO DATA

4.1 Data on the Live Weight of Chicken

The live body weight of chicken was recorded by gender in a nutrition experiment in 2006 at the Kharabo Experimental Farm of Damascus University (Al-Rais, 2009). Random samples of 60 male and 60 female chickens were chosen every week for eight weeks from a flock of broilers. The data on their mean weight (gm) vs age (d) are given in Table 1 and illustrated in Fig. 1 for the male and the female samples.

Table 1. Observed mean weights (gm) and predicted values from the Gompertz curve for male (♂) and female (♀) chickens from 7 to 56 days of age

Age	Obs ♂	Obs ♀	Pred ♂	Pred ♀
7	129	124	135	135
14	336	320	334	321
21	667	623	665	621
28	1125	1034	1125	1030
35	1684	1529	1681	1517
42	2274	2027	2283	2042
49	2891	2559	2884	2562
56	3446	3055	3448	3049

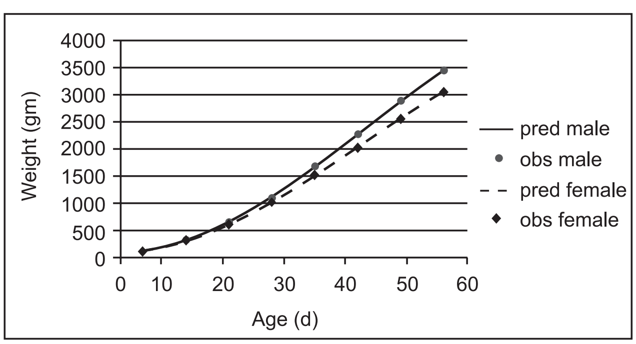

Fig. 1. Observed and fitted mean values for male and female chicken weight over time

The equality of the mean weights was tested at each time of observation using a two sample t-test (Neter *et al*. 1995). The mean weights were found to be significantly different ($p < 0.05$) between male and female chickens at each weekly age.

4.2 The Fitted Models

Considerable additional insight is provided using the proposed reparameterized Gompertz curve. The curve in (11) was fitted to the data, using the nonlinear least squares program in SPSS (2007) and assuming a regression model with independent errors. Nonlinear least squares procedures require initial parameter estimates, which are easy to provide from the data for parameters t_{inf}, Y_{inf}, and X_{max}, in (11). Note, for example, that the maximum observed weight gain for male chickens in Table 1 was about 600 gm both for the 7 days from $t = 35$ to $t = 42$, as well as from $t = 42$ to $t = 49$, and that at $t = 42$ the weight was $Y = 2274$. Hence plausible initial estimates of the parameters for male chickens are $t_{inf} = 42$ d, $Y_{inf} = 2270$ gm, and $X_{max} = 600/7 = 86$ gm/d. *Initial estimates for the other parameterizations of the Gompertz model, especially for parameter c, are not immediate from the data. This advantage of model (11) facilitates the subsequent statistical analysis of data.*

The parameter estimates and their estimated standard errors are given in Table 2. The estimates for the male and female growth curves in (11) are: for Y_{inf}, 2253 and 1981 gm; for t_{inf}, 41.655 and 41.203 d; and for X_{max}, 87 and 76 gm/d. The two curves are plotted in Fig. 1, from which the estimated parameter values are interpretable. For example, note that for the time of maximum growth for males, i.e. at $t_{inf} = 41.7$ d, the predicted size of a broiler and the slope of the curve, $Y_{inf} = 2253$ gm and $X_{max} = 87$ gm/d respectively, are consistent with visual observations from the graph. The estimated growth rate curves from (12) are plotted in Fig. 2. The estimated values of t_{inf} and of X_{max} are easily seen to be consistent with the graphs.

The fitted values for both curves are also given in Table 1, and they give an exceptionally close fit to the observed values. All residuals (ie. differences between observed and fitted values) are very small. In fact, the largest residual, for the female data at $t = 42$ d, is only 15 gm (which is less than 1% of the observed value).

Table 2. Parameter estimates and their estimated standard errors for the Gompertz curves for male (♂) and female (♀) chickens, with a statistical test of gender difference

Parameter	Est ♂	SE ♂	Est ♀	SE ♀	Difference	SE Diff	z	p-value
K	6125.0000	73.6000	5386.0000	122.1000	739.0000	142.6000	5.18	<.001
b	5.0000	0.0290	4.8100	0.0510	0.1900	0.0590	3.22	.001
c	0.0386	0.0004	0.0381	0.0008	0.0004	0.0009	0.44	.660
Y_0	41.4200	1.6060	43.8600	3.0070	–2.4400	3.4100	0.72	.480
L	0.1930	0.0032	0.1830	0.0056	0.0100	0.0064	1.56	.108
t_{inf}	41.6600	0.3410	41.2000	0.6530	0.4600	0.7400	0.62	.540
Y_{inf}	2253.0000	27.1000	1981.0000	44.9000	272.0000	52.4000	5.19	<.001
X_{max}	87.0100	0.2520	75.5400	0.4110	11.4700	0.4800	23.90	<.001

The residuals are too small to be visible in Fig. 1. *It is very unusual in the published literature in poultry for the residuals not to be visible in the graphs.*

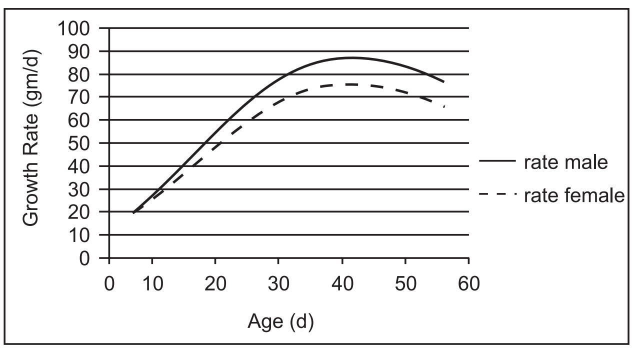

Fig. 2. Estimated growth rate functions for male and for female chicken data

The residuals have no clear pattern over time, which suggests the lack of serial correlation. The Durbin-Watson d statistics for testing for serial correlation in the two time series are 2.95 and 1.99, respectively, neither of which gives any indication of positive autocorrelation (Neter *et al*. 1995). The absence of serial correlation is likely due to the shortness of the time series. We have observed significant serial correlation in poultry data with longer series, and remedial measures are proposed in these cases (Matis *et al*. 2010 and 2011).

The goodness of fit may be assessed using the mean squared residual, denoted MSR, which is a measure of the residual variance. The MSR for the two fitted Gompertz curves are 37.9 and 107.8 gm^2. These MSR are very small due to the tiny residuals. As a contrast, the fitted logistic curves (as in Matis *et al.* 2010) for the male and female data have MSR of 2924 and 2913 gm^2, respectively. The least squares procedure failed to converge to give parameter estimates for both Richards curves (see e.g. Matis *et al.* 2011), as the model has four parameters. This failure to converge is not surprising in light of the typically very limited number of data points describing broiler chicken growth.

4.3 Fitting the Other Gompertz Forms

The standard and the Laird forms of the Gompertz model were also fitted to the data in order to obtain the standard error estimates directly. They obviously give the same fitted curve. For the standard form in (1), the parameter estimates for male and female chickens are: for K, 6125 and 5386 gm; for b, 4.996 and 4.811; and for c, 0.0386 and 0.0381d^{-1}. Only parameter K is easily interpretable from the graph in Fig. 1. For the Laird parameterization in (8), the parameter estimates are: for Y_0, 41.4 and 43.9 gm; for L, 0.193 and 0.1834d^{-1}; and for c, 0.0386 and 0.0381d^{-1} respectively. Of these, Y_0 and L are interpretable from the graph. The complete results including the standard errors are given in Table 2.

5. STATISTICAL HYPOTHESIS TESTING

The primary forms of the Gompertz model in (1), (8), and (11) contain eight different parameters, namely $K, b, c, Y_0, L, t_{inf}, Y_{inf}$, and X_{max}, to describe the growth curve. A primary question of interest is how sensitive the various parameters are in detecting treatment differences in general, in this case between the male and female growth curves.

There are two ways to test whether there are significant differences between the parameters. A simple, sufficient way is to check whether the confidence intervals overlap. For example, the 95% confidence intervals for K, which are given directly in SPSS (2007) output or can easily be calculated from the estimates and their standard errors in Table 2, are (86.4, 87.7) for male and (74.5, 76.6) for female broilers. These confidence intervals do not overlap, hence the observed 11.47 gm/d increase in X_{max} in Fig. 2 for males over females is statistically significant. In identical manner, one could show that the 272 gm increase in Y_{inf} and the 739 gm increase in K for males are also statistically significant.

An alternative, statistically more powerful method is to calculate an approximate z-statistic to test the difference directly. This test would proceed as follows:

1. For any given parameter, find the difference, denoted d, between the estimates for male and female broilers.
2. Find the estimated variance of d, denoted s_d^2. Letting s_1 and s_2 denote the standard errors for the male and female estimates, the formula is

$$s_d^2 = s_1^2 + s_2^2.$$

3. Calculate the z-statistic,

$$z = d/s_d.$$

4. Find the p-value for the test of equality assuming approximate normality.

For example, testing the hypothesis of equality of X_{max} for males and females in this case gives

$$d = 11.47,\ s_d = 0.48 \quad \text{and} \quad z = 23.9$$

which rejects the hypothesis of equality ($p < 0.001$).

Table 2 contains the results for this more powerful test. There are significant increases for the male chickens in parameters K, b, Y_{inf}, and X_{max}. As noted previously, the asymptotic weight K is not of primary interest for broiler chickens, and b is not intuitively interpretable biologically. *The parameters Y_{inf} and X_{max} which do describe differences of interest between male and female broiler chickens are the ones given directly in the new parameterization in (11).* This may not always be the case in other studies, hence we recommend investigating all variables of interest, estimating each one directly from one of the Gompertz model parameterizations. In cases where there are more than two groups to compare, one may use pairwise comparisons with the previous z-statistic, with proper error control utilizing the Bonferroni method and a pooled variance estimate (Neter *et al*. 1996)

6. DISCUSSION

Gompertz growth curves have been used to model animal growth for nearly 80 years, and they have found particular application to poultry. The Gompertz model has various forms, each with its own advantage. The original, standard forms of the model are elegant mathematically, and the Laird forms provide a clear mechanistic description of growth. We suggest that the new parameterization presented in this note has the following advantages:

1. Each of the parameters, t_{inf}, Y_{inf}, and X_{max}, is interpretable biologically and is of interest in broiler production.
2. The parameterization facilitates obtaining initial parameter estimates.
3. Standard errors estimates may be obtained directly using the parameterization.

We suggest as a rule fitting as many forms of the Gompertz curve as necessary so that all parameters of interest and their standard errors are estimated directly.

Though the new parameterization was suggested by application to broiler chicken, the statistical advantages of the new form of the model may carry over to other applications in agriculture and also engineering. In other applications, serial correlation may be likely. Research is in progress to develop methods to mitigate autocorrelation in applications with the Gompertz curve.

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