Multiphasic nonlinear mixed growth models for laying hens

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ABSTRACT Appropriate evaluation of BW and gain during rearing is required for optimal extended laying performance in laying hens. The objective of this study was to compare monophasic, diphasic, and triphasic Gompertz and logistic models describing BW and gain in individually fed free-run laying hens and to study the variation between individuals in shape parameters. Fifteen Lohmann Brown Lite hens were fed ad libitum from week 0 to 43 with a precision feeding system, measuring feed intake and BW individually in a group housed setting. Random variables related to mature weight and timing of maximum gain during the pubertal growth phase were introduced into the multiphasic model for BW with the best fit. For both the weight-age and gain-age functions, the diphasic and triphasic Gompertz and logistic model models fitted the data better than the monophasic models. The Gompertz model was able to identify the ages at the highest gain at similar time points for both BW and gain, whereas the logistic models failed to do so. The derivative of the multiphasic Gompertz models for the gain-age relationship identified age at the highest gain at similar ages as compared with the logistic models for gain. The mixed models predicted that the individual mature BW ranged from 1.83 kg to 2.10 kg and the variability in the timing of the highest rate of gain during the pubertal growth spurt ranged from 15.26 wk to 19.79 wk. Including random terms associated with the mature BW and the second inflection point of the diphasic Gompertz growth model allowed for identification of variability in the growth curve shape between individuals, which can be a tool to study the relationship between the individual growth curve shape and performance parameters.

Key words: gain, modeling, growth, laying hen

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INTRODUCTION

In egg-type pullets, an appropriate BW and body composition at the end of rearing are required for optimal production results (Cheng et al., 1991). The industry direction toward extended commercial laying cycles demands accurate evaluation (allometric) of growth in laying hens (Bain et al., 2016; van Eck et al., 2019). Mathematical models have been used to describe and evaluate growth, where biologically relevant parameters could be related to performance, such as the rate of gain or mature weight (Teleken et al., 2017). Several mathematical functions have been previously proposed to describe growth in poultry, where the Gompertz, logistic, and Richards functions have shown the best fit (Sezer and Tarhan, 2005; Narinç et al., 2017; Teleken et al., 2017). It was concluded that models with a flexible point of inflection (Richards equation; Richards, 1959) would be better suitable for modeling growth than models with a fixed inflection point (Gompertz and logistic functions; Darmani Kuhi et al., 2003). However, Rizzi et al., 2013 reported optimization problems using the Richards function. In addition, the Gompertz functions often arrive at equal fit of the data (Narushin and Takma, 2003; Rizzi et al., 2013) and require one less parameter; therefore, the Gompertz functions are often used for growth modeling. Additional random terms in growth models have been proposed previously to quantify the variability in model parameters between birds (Wang and Zuidhof, 2004; Aggrey, 2009; Galeano-Vasco et al., 2014). These models have allowed variability in the mature BW and in the point of inflection, that is, the age at the highest rate of gain.

Most growth models published in the literature have been based on meat-type poultry (Darmani Kuhi et al., 2003). The objective of growth in meat-type poultry,

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lean-tissue production, differs widely from the growth objective in egg-type poultry, which focuses on establishment of critical skeleton mass to support Ca metabolism and proper development of the reproductive tract (Bain et al., 2016). In addition, Santos et al. (2018) concluded that meat- and laying-type female quail differed in the growth profile as modeled by a mixed Gompertz function, where the relative growth rate was higher and the mature weight was lower in laying-type than meat-type females (0.15 vs. 0.13% and 159 vs. 305 g, respectively).

Growth is defined as the change in the BW per time unit, also referred to as the gain-age relationship. However, most evaluated growth models in the literature are functional descriptions of the BW, the weight-age relationship. The gain-age relationship (the first derivative of the weight-age relationship) has only been mathematically studied in laying hens by Grossman and Koops (1988) and Kwakkel et al. (1993), using the first derivative of the logistic function. Growth also occurs in several phases, where growth in each phase consists of specific body components (Kwakkel et al., 1993). Grossman and Koops (1988) and Kwakkel et al. (1993) both concluded that models describing the age-gain relationship identified multiple phases of gain during rearing. However, it is not yet known whether models describing the weight-age relationship can also identify multiphasic growth and if these models would benefit from addition of random terms to identify variability in parameter estimates.

The aim of the present study was to compare Gompertz and logistic models describing the BW and gain in individually fed free-run laying hens. The models were evaluated based on their ability to identify multiple growth phases. The addition of random terms was evaluated by introducing random terms within the preferred multiphasic model. These models could allow breeding companies to evaluate the link between growth in different phases to performance parameters as the BW and egg production are genetically correlated (Dana et al., 2011).

MATERIALS AND METHODS

Animals and Housing

The animal protocol for the study was approved by the University of Alberta Animal Care and Use Committee for Livestock and followed principles established by the Canadian Council on Animal Care Guidelines and Policies (CCAC, 2009). Lohmann Brown Lite laying hen chicks (n = 15) were neck tagged for individual identification and housed in a floor pen covered with wood shavings at an approximate depth of 5 cm. Birds were fed with a precision feeding (**PF**) system (Zuidhof et al., 2016, 2017), which allocated feed and measured feed intake on an individual basis. Water was provided ad libitum with nipple drinkers during the entire experiment and a fountain style supplemental drinker was provided in each pen during the first week. From day 0 to 24, birds were trained to use the PF system. At day 24, birds were tagged with a radio frequency identification wing band, and from day 24 onward, all birds were fed individually. Birds were allowed access to 10 g of feed for a duration of 60 s when accessing the PF station. Photoschedule was set at 12L:12D during the entire experiment. For the first 3 wk, chicks received a standard wheat-based starter diet (2,726 AME, 21% CP, 1.0% Ca); from week 4 to week 23 pullets received a wheat-based grower diet (2,703 AME, 16.0% CP, and 1.1% Ca); from week 23 to week 43 hens received a wheat-based layer diet (2,689 AME, 15.0% CP, and 3.3% Ca).

Data Collection and Preparation

For the first 3 wk, pullets were weighed manually on a daily basis to confirm growth and the use of the PF system. Birds that were not growing were trained individually to use the PF system. After individual feeding started, the PF system recorded individual BW and feed intake on a per-visit basis, multiple times per day. The feed intake and visit frequency were checked on a daily basis to ensure all birds were accessing the PF system. No mortality occurred throughout the experiment. From the PF system data, the median BW per day was calculated for each bird and used as daily BW measure. Gain was calculated per week by subtracting the BW of each bird at the first day of each week from the BW at the last day of each week. Daily BW data were used to fit the weight-age relationship models. The 2-weekly moving average of weekly gain was used to fit the gain-age relationship models.

Model Specification

Two nonlinear models were evaluated to describe the BW as a function of the age: a modified Gompertz model (Tjørve and Tjørve, 2017) [1] or a logistic function (Grossman and Koops, 1988) [2].

$$\mathrm{W_t} = \sum_{\mathrm{p=1}}^{\mathrm{n}} \left\{ \mathrm{Wm}_p \mathrm{exp}^{-\mathrm{exp}^{-\mathrm{b_p} * (\mathrm{t} - \mathrm{tinf_p})}} \right\} \qquad [1]$$

$$\mathrm{W_t} = \sum_{\mathrm{p=1}}^{\mathrm{n}} \left\{ \frac{\mathrm{Wm_p}}{1 + \mathrm{exp}^{-\mathrm{b_p}\left(\mathrm{t} - \mathrm{tinf_p}\right)}} \right\} \qquad [2]$$

Where $\mathrm{W_t}$ = BW (kg) at age t (week); $\mathrm{Wm_p}$ = asymptotic BW gain of phase p (kg); $\mathrm{b_p}$ = the rate coefficient of phase p; $\mathrm{tinf_p}$ = BW inflection point in phase p, that is, the age (week) at which the BW gain occurred at the greatest rate. Single-, 2-, or 3-phase versions of each model were evaluated.

The models evaluated to describe gain as a function of age were the derivatives of the previously described

Gompertz [1] and logistic functions [2] and also included one, 2, or 3 phases.

$$G_t = \sum_{p=1}^{n} \left\{ Wm_p b_p \exp^{-\exp^{-b_p(t-tinf_p)}} \exp^{-b_p\left(t-tinf_p\right)} \right\} \quad [3]$$

$$G_t = \sum_{p=1}^{n} \left\{ Wm_p b_p \left(1 - \tanh^2\left(b_p\left(t - tinf_p\right)\right)\right) \right\} \quad [4]$$

Where G_t = BW gain at age t (kg); Wm_p [3] = asymptotic BW gain of phase p (kg); Wm_p [4] = half of the asymptotic BW gain of phase p (kg); b_p = the rate coefficient of phase p; t = age (week); $tinf_p$ = BW inflection point in phase p, that is, the age (week) at which the BW gain occurred at the greatest rate. Based on the analysis of the fit of models 1 to 4 including 1, 2, or 3 phases and the estimated parameters, the preferred model was also used to fit the Lohmann Brown Lite BW guideline (Lohmann Tierzucht, 2016).

Based on the analysis of the fit of models 1 to 4 and the estimated coefficients, 2 nonlinear mixed models were defined. The purpose of these models was to estimate the variance between individuals for coefficient estimates. The diphasic Gompertz model was used, and the models included a random term associated with the maximum gain in the first phase (Wm_1) [5] or a random term associated with Wm_1 and the inflection point of the second phase ($tinf_2$) [6].

$$\begin{aligned} W_{it} = {} & (Wm_1 + u_i) \exp^{-\exp^{-b_1*(t-tinf_2)}} \\ & + Wm_2 \exp^{-\exp^{-b_2*(t-(tinf_2))}} + \varepsilon_i \end{aligned} \quad [5]$$

$$\begin{aligned} W_{it} = {} & (Wm_1 + u_i) \exp^{-\exp^{-b_1*(t-tinf_2)}} \\ & + Wm_2 \exp^{-\exp^{-b_2*(t-(tinf_2+z_i))}} + \varepsilon_i \end{aligned} \quad [6]$$

Where W_{it} = BW (kg) at age t (week) of hen i; Wm_1 = asymptotic BW gain of phase one (kg); u_i = hen-related random term associated with Wm_1; b_1 = the rate coefficient of phase one; $tinf_1$ = BW inflection point in phase p, that is, the age (week) at which the BW gain occurred at the greatest rate, Wm_2 = asymptotic BW gain of phase 2 (kg); b_2 = the rate coefficient of phase 2; $tinf_2$ = BW inflection point in phase 2; z_i = hen-related random term associated with $tinf_2$; ε_i = residual error of hen i. One individual with an extremely high mature BW (Figure 1) was excluded from the data set for the analysis of the nonlinear mixed models, as SAS (version 9.4.; SAS Institute Inc., Cary, NC, 2012) failed to properly estimate the random variable for the second inflection point.

Statistical Analysis

All statistical analyses were performed with SAS (version 9.4.). Models [1] and [2] were fitted with the NLIN procedure and models [3-6] were fitted with the NLMIXED procedure. Root mean square errors (RMSEs) and R^2 were manually calculated from the estimated values using the following equations:

$$MSE = \frac{1}{n}\sum_{i=1}^{n}\left(Y_i - \hat{Y}_i\right)^2 \text{ and } RMSE = \sqrt{MSE}$$

$$R^2 = 1 - \frac{\sum_i \varepsilon_i^2}{\sum_i \left(y_i - \overline{y}_i\right)^2}$$

Curves within each model type (Gompertz or logistic) were evaluated using a paired F-test procedure described by Motulsky and Ransnas (1987). To determine whether fit of a curve with an additional phase was significantly better than the fit of a curve with one less phase, an F ratio was calculated:

$$F = \frac{(SS_1 - SS_2)/df_1 - df_2}{SS_2/df_2}$$

Where SS is the sum of squares and df is the number of degrees of freedom (the number of data points minus the number of parameters). The subscript 1 refers to the model with fewer phases (fewer parameters), and subscript 2 refers to the model with an additional phase. A large F-value with a corresponding low P-value indicated that the additional phase explained variation in the data better than the model without the extra phase.

RESULTS AND DISCUSSION

Animal Performance

Birds were heavier than the weight recommended by the breeder guidelines, especially during the period from week 14 to week 21 (Figure 1). The average BW was 1,471.4 ± 17.54 g at week 16 and 2,058.7 ± 22.27 g at week 43. The CV for the BW was 5.4 ± 1.45% at week 16 and 4.9 ± 1.45% at week 43. The cumulative feed intake was 5,630 ± 67.2 g from day 24 to week 16 and 17,950 ± 287.1 g from week 17 to week 43. The weekly gain was higher than the recommended gain, especially between week 7 and 14 (Figure 2). Variation in gain was relatively small during week 0 to week 14 and increased during week 18 and week 25 (Figure 2). In addition, there was variation in the timing of the decrease of gain between week 18 and week 25. It is hypothesized that during this time individual hens commenced egg production and shifted metabolic processes from growth toward egg production.

Weight-Age Functions

Convergence was achieved for all models describing the weight-age relationship. Based on the R-squared and the RMSE, all models showed a similar goodness of fit to the BW data (Table 1). In monophasic models the Gompertz curve showed a better fit than the logistic

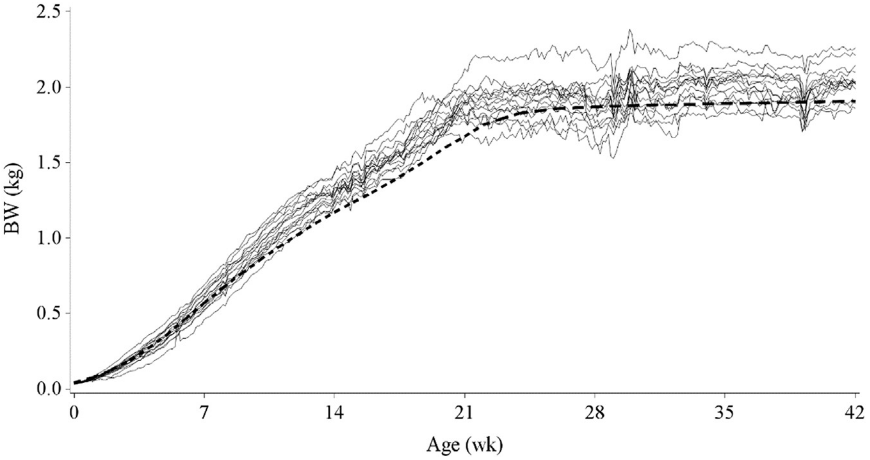

Figure 1. Individual BW of 15 ad libitum–fed Lohmann Brown Lite laying hens (black lines) and the recommended BW from the breeder guidelines (dotted line).

function, in line with previous results from Darmani Kuhi et al. (2003) and Aggrey (2002). This is likely the result of the difference in the inflection points between the Gompertz and the logistic functions, that is, the moment of the highest rate of gain. The inflection point of the Gompertz function is at 37% of its asymptote, whereas the inflection point of the logistic function is 50% of its asymptote. In practical terms, the Gompertz model being a right-skewed distribution predicts slower growth in the later stages of each growth phase. The age at the highest rate of gain was 10.2 wk and 8.7 wk as estimated by a monophasic logistic or Gompertz growth model, respectively, in Athens-Canadian random bred chickens (Aggrey, 2002). This is in line with the current results, where the monophasic logistic model estimated the highest rate of gain at 11.01 wk and the Gompertz growth model at 8.44 (Table 1).

The F-test established that the diphasic models described the data better than the monophasic models, for both the Gompertz and the logistic models. The addition of a third phase did not improve the Gompertz model ($P = 0.06$; Table 1), whereas the triphasic form fitted better than the diphasic form for the logistic model ($P < 0.049$; Table 1). However, the logistic function, having its inflection point at 50% of the asymptote, needed an extra phase between 0 and 18 wk correcting for the change in the growth rate during this time period (Figures 3A, 3B). The Gompertz function on the other hand did not require this extra phase. Extra phases increase the number of parameters in the models and therefore model complexity. Based on the number of required phases and the fit of both types of models, the Gompertz function would therefore be preferred over the logistic function.

Model selection was also based on biological meaning of incorporated coefficients. Both the Gompertz and the logistic functions include parameters that can be assigned a biological meaning (Teleken et al., 2017), such as the total gain in each phase and the age at the highest rate of gain (inflection points). The estimated mature BW, defined as the sum of the maximum gain in all phases, was slightly higher in the Gompertz model than the logistic model (2.03, 2.00, and 2.00 kg, vs. 1.99, 1.99, and 1.99 kg for the monophasic, diphasic, and triphasic

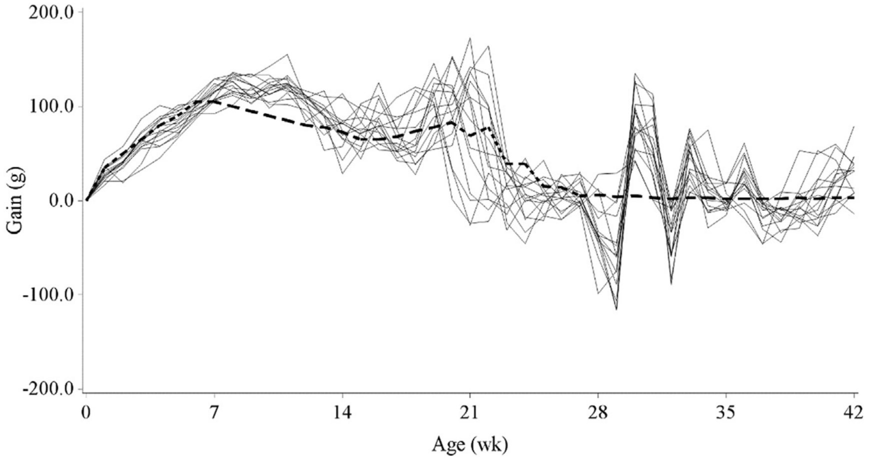

Figure 2. Weekly individual gain calculated as a moving average of 15 ad libitum–fed Lohmann Brown Lite laying hens (black lines) and the recommended weekly gain from the breeder guidelines (dotted line).

Table 1. Functional specifications, coefficients, and goodness-of-fit criteria of the single-phase and multiphase Gompertz and logistic models describing the BW as a function of age of *ad libitum*–fed Lohmann Brown Lite hens.

	Gompertz model [1]						Logistic model [2]					
Equation[1]	$W_t = \sum_{p=1}^{n}\{Wm_p \exp^{-\exp^{-b_p*(t-tinf_p)}}\}$						$W_t = \sum_{p=1}^{n}\left\{\frac{Wm_p}{1+\exp^{-b_p(t-tinf_p)}}\right\}$					
	n = 1		n = 2		n = 3		n = 1		n = 2		n = 3	
Parameters	Estimate	SEM	Estimate	SEM	Estimate	SEM	Estimate	SEM	Estimate	SEM	Estimate	SEM
Wm_1	2.03	0.003	1.83	0.015	1.81	0.016	1.99	0.003	1.01	0.067	0.65	0.137
b_1	0.16	0.001	0.18	0.002	0.18	0.002	0.24	0.002	0.45	0.019	0.56	0.064
$tinf_1$	8.44	0.029	7.73	0.061	7.67	0.066	11.01	0.032	6.74	0.195	5.05	0.708
Wm_2	-	-	0.17	0.013	0.04	0.023	-	-	0.98	0.068	0.26	0.150
b_2	-	-	1.33	0.282	2.51	4.305	-	-	0.31	0.014	1.07	0.424
$tinf_2$	-	-	18.03	0.118	16.07	0.448	-	-	16.06	0.406	9.16	0.418
Wm_3	-	-	-	-	0.15	0.024	-	-	-	-	1.08	0.066
b_3	-	-	-	-	1.58	0.452	-	-	-	-	0.31	0.014
$tinf_3$	-	-	-	-	18.40	0.216	-	-	-	-	15.68	0.402
Criterion												
R-squared[2]	0.985		0.986		0.986		0.984		0.986		0.986	
RMSE[3]	0.106		0.103		0.103		0.111		0.105		0.105	
DW[4]	0.06		0.07		0.07		0.06		0.06		0.06	
P-value[5]	-		<0.001		0.06		-		<0.001		0.046	

[1] W_t = BW (kg) at age t (week); Wm_p = maximum BW gain of phase p (kg); b_p = rate coefficient of phase p; $tinf_p$ = BW inflection point in phase p (age (week) at which the BW gain occurred at the greatest rate).

[2] Pearson correlation coefficient; higher values indicate a better fit of the model.

[3] Root mean square error; smaller values indicate a better fit of the model.

[4] Durbin-Watson statistic; values range from 0 to 4, values close to 2 indicate nonsignificant autocorrelation.

[5] The *P* value was obtained from an F-test, F value was calculated as $F = \frac{(SS_1 - SS_2)/(df_1 - df_2)}{SS_2/df_2}$, where SS is the sum of squares of the model and df is the number of degrees of freedom (the number of data points minus the number of parameters). *P*-values compare the monophasic vs. the diphasic model and the diphasic model vs. the triphasic model.

models, respectively, Table 1). This was also observed by Aggrey (2002), who estimated a 0.21-kg lower mature weight with a monophasic logistic model (1.69 kg) than with a monophasic Gompertz model (1.90 kg) in Athens-Canadian random bred chickens. In the present study, the mature BW was reduced by only 0.04 kg for the monophasic model. The distinction in the mature BW between the logistic model and the Gompertz model in the current result and previous results may have been the data record frequency. The current BW data were collected on a daily basis, whereas Aggrey (2002) collected the BW information only once every 3 d until day 54, and once every 14 d thereafter. The characteristics of the different phases in the diphasic and triphasic models for the Gompertz and logistic functions were very different. The inflection points were estimated much earlier for the triphasic logistic function than the Gompertz function (5.05, 9.16, and 15.68 wk, vs. 7.67, 16.07, and 18.40 wk, for the first, second, and third phases, respectively). The estimated maximum gain during each phase was much higher in the second and third phases for the triphasic logistic function than for the triphasic Gompertz function (0.04 kg and 0.15 kg vs. 0.26 kg and 1.08 kg, for the second and the third phases, respectively, Table 1; Figures 4A, 4B). The consecutive phases for developmental biology include immature growth (after hatch), prepubertal growth (fat gain), pubertal growth (growth of reproductive tissues, medullary bone), and mature growth (Kwakkel et al., 1995). The largest proportion of the BW gain occurred during the immature phase (Kwakkel et al., 1995). The BW gain for the prepubertal growth and pubertal growth occurred shortly before the onset of lay, close to reaching the mature BW (Kwakkel et al., 1995). In the diphasic and triphasic logistic models and the prepubertal and pubertal growth phases could not be distinguished, as the maximum gain during each phase did not reflect the expected gain for the developmental phases and the inflection points did not coincide with the expected timing. For the multiphasic Gompertz model, the phases and the amount of growth coincided with the developmental biology. In the triphasic Gompertz model, the maximum BW gain of the first phase accounted for 90.6% of the mature BW, the second phase accounted for 2.0% of the mature BW, and the third phase for 7.4% of the mature BW. The highest rates of gain were estimated at week 7.67, week 16.07, and week 18.40, for the first, second, and third phases, respectively, which would coincide with the immature, prepubertal, and pubertal phases of growth. The first phase of the triphasic Gompertz model continued into the mature phase because of the lower b value (Table 1; Figure 4A). Therefore, the first phase also accounted for growth during the mature phase. In conclusion, for models estimating the BW as a function of age, the multiphasic Gompertz model is preferred, as one less phase is required compared with the logistic model, and phases coincide with the biologically expected growth and development.

The coefficients of the triphasic Gompertz model were compared with the coefficients of the same function

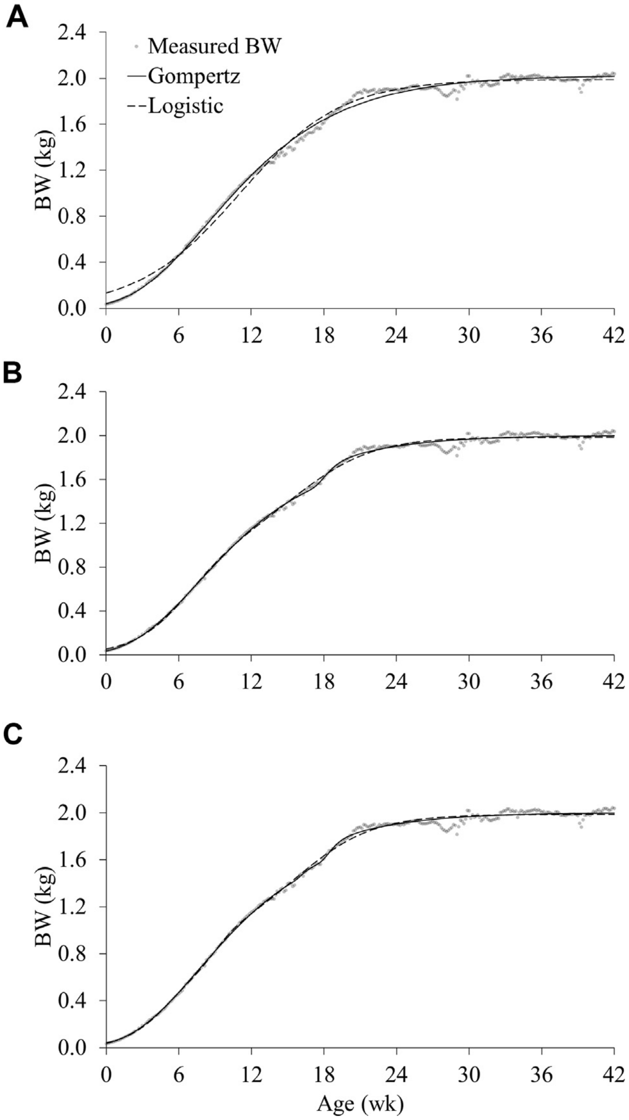

Figure 3. Monophasic (A), diphasic (B), and triphasic (C) Gompertz and logistic models fitted to BW data (measured BW) of ad libitum–fed Lohmann Brown Lite laying hens.

fitted to the Lohmann BW target (Lohmann Tierzucht, 2016). The model fitted to the Lohmann BW target showed a lower maximum gain in the first phase and a higher maximum gain in the second and third phases than the model fitted to the ad libitum–fed hens (Table 2). The rates of change (coefficient b) of the second and third phases were higher in the model fitted to the ad libitum–fed hens than those in the model fitted to the Lohmann BW target. In addition, the inflection point of the first phase was earlier in the model fitted to the Lohman BW target than that in the model fitted to data of the ad libitum–fed hens. The second phase occurred at a similar age, and the third phase occurred later in the model fitted to the Lohman BW target than in the model fitted to data of the ad libitum–fed hens (Table 2). It is hypothesized that the growth curve as recommended by the Lohmann BW target restricts the pullet BW to delay pubertal growth to delay onset of lay, thereby increasing uniformity in the onset of lay and egg weight at the first egg.

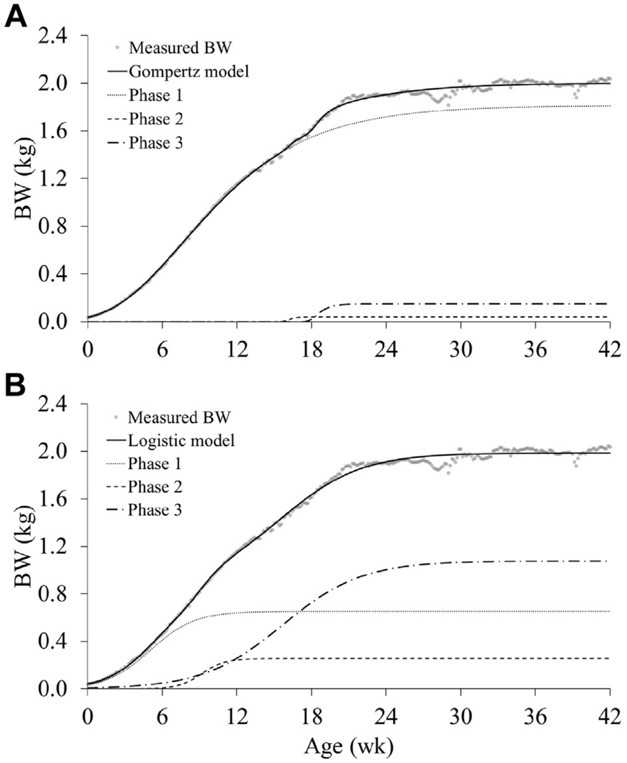

Figure 4. Triphasic Gompertz (A) and logistic (B) models fitted to gain data (measured gain) of ad libitum–fed Lohmann Brown Lite laying hens.

Gain-Age Functions

Convergence was achieved for all models describing the gain-age relationship. Based on the R-squared and the RMSE, the diphasic and triphasic models showed a better fit than the monophasic models (Table 3). The F-test established that triphasic models fitted the data better than the diphasic models for both the Gompertz and logistic functions. The asymptotic gain of the third phase of the logistic function was larger than the asymptotic gain of the third phase of the Gompertz model because the right tail of the first phase of the triphasic Gompertz function was much larger than the right tail of the logistic function. In contrast to the models describing the weight-age relationship, the triphasic Gompertz and the triphasic logistic models for gain identified similar phase characteristics (Figures 5A-5C). The age at maximum gain for the first, second, and third phases was identified at week 8.41, week 16.14, and week 19.59 for the Gompertz model and at week 9.15, week 15.94, and week 19.87 for the logistic function. Kwakkel et al. (1993) estimated slightly earlier points of inflection using a derivative of the logistic function and found the age at maximum gain at week 6.6, week 13.0, and week 19.2. However, Kwakkel et al. (1993) used a different breed (White Leghorns). There may also have been differences in environmental factors affecting gain, such as feed composition. The R-squared of the current models were lower than the results of Kwakkel et al. (1993). This is likely due to the BW loss after week 21 (Figure 2) and erroneous gain between week 28 and 35.

Table 2. Comparison between the estimated parameters of the triphasic Gompertz BW model fitted to BW data of ad libitum–fed Lohmann Brown Lite hens or fitted to the Lohmann breeder BW target.

Data	Phase 1				Phase 2				Phase 3			
	Ad lib		Lohmann		Ad lib		Lohmann		Ad lib		Lohmann	
Parameters[1]	Estimate	SEM	Estimate	SEM	Estimate	SEM	Estimate	SEM	Estimate	SEM	Estimate	SEM
Wm (kg)	1.81	0.016	1.50	0.030	0.04	0.023	0.18	0.109	0.15	0.024	0.23	0.090
B	0.18	0.002	0.19	0.004	2.51	4.305	0.41	0.201	1.58	0.452	0.62	0.115
tinf (week)	7.67	0.066	6.85	0.120	16.07	0.448	16.27	1.253	18.40	0.216	19.93	0.162

Abbreviations: Ad lib, ad libitum–fed Lohman Brown Lite hens; Lohmann, Lohmann breeder BW target.

[1] Function used: $W_t = \sum_{p=1}^{n}\{Wm_p exp^{-exp^{-b_p*(t-tinf_p)}}\}$ where W_t = BW (kg) at age t (week); Wm_p = asymptotic BW gain of phase p (kg); b_p = the rate coefficient of phase p; $tinf_p$ = BW inflection point in phase p (age (week) at which the BW gain occurred at the greatest rate).

In the present study, the direct derivatives of the Gompertz and logistic functions were used to model the gain-age relationship. The results indicate that modeling the gain-age relationship is more robust, as the biological growth phases identified by the Gompertz and logistic models are similar when modeling the gain-age relationship. This is in contrast to models describing the weight-age relationship, as discussed in the previous section. The growth phases of the Gompertz models for the BW were comparable to the derivative of the Gompertz model for gain, yet for the logistic functions, growth phases differed. The triphasic Gompertz model for the gain-age relationship had slightly later inflection points for all phases than the Gompertz model for the weight-age relationship (8.41, 16.14, and 19.59 wk vs. 7.67, 16.07, and 18.40 wk for the first, second, and third phases, respectively; Tables 1 and 3). This might be the result of the higher measuring frequency for weight data (daily) than gain data (weekly), which provided more precise information for the weight-age relationship. In addition, the gain-age relationship is a more sensitive measure for real-time changes, which allowed for better visualization of different phases, than the weight-age relationship. However, gain was highly variable and required smoothing with a 2-weekly moving average, which could have delayed the timing of the inflection points.

The differences in the comparison between the gain-age relationship for ad libitum–fed birds and the Lohman gain target are in line with the results from the comparison based on modeling the weight-age relationship (Table 4). The triphasic Gompertz gain-age model using Lohmann data estimated the age at highest rate of gain

Table 3. Functional specifications, coefficients, and goodness-of-fit criteria of the single-phase and multiphase Gompertz and Logistic derivative models describing gain as a function of age.

	Gompertz model [3]						Logistic model [4]					
Equation[1]	$G_t = \sum_{p=1}^{n}\{Wm_p b_p exp^{-exp^{-b_p(t-tinf_p)}} exp^{-b_p(t-tinf_p)}\}$						$G_t = \sum_{p=1}^{n}\{Wm_p b_p(1 - \tanh^2(b_p(t - tinf_p)))\}$					
	n = 1		n = 2		n = 3		n = 1		n = 2		n = 3	
Parameters	Estimate	SEM	Estimate	SEM	Estimate	SEM	Estimate	SEM	Estimate	SEM	Estimate	SEM
Wm_1	2.06	0.060	1.80	0.063	1.71	0.074	1.11	0.037	0.84	0.039	0.80	0.040
b_1	0.16	0.006	0.18	0.008	0.19	0.010	0.10	0.004	0.15	0.009	0.16	0.010
$tinf_1$	9.38	0.212	8.67	0.202	8.41	0.229	10.70	0.267	9.37	0.219	9.15	0.224
Wm_2	-	-	0.20	0.031	0.05	0.030	-	-	0.17	0.024	0.03	0.015
b_2	-	-	0.85	0.126	1.13	0.599	-	-	0.44	0.056	1.10	0.519
$tinf_2$	-	-	19.51	0.159	16.14	0.484	-	-	19.79	0.176	15.94	0.378
Wm_3	-	-	-	-	0.22	0.035	-	-	-	-	0.18	0.022
b_3	-	-	-	-	0.84	0.122	-	-	-	-	0.47	0.060
$tinf_3$	-	-	-	-	19.59	0.180	-	-	-	-	19.87	0.172
Criterion												
R-squared[2]	0.736		0.765		0.768		0.731		0.769		0.772	
RMSE[3]	35.097		33.173		33.059		35.473		32.923		32.794	
DW[4]	1.45		1.58		1.59		1.42		1.61		1.61	
F-test[5]	-		<0.001		0.049		-		<0.001		<0.001	

[1] G_t = gain (g) at age t (week); Wm_p [3] = maximum BW gain of phase p (g); Wm_p [4] = half of the maximum BW gain of phase p (g); b_p = the rate coefficient of phase p; $tinf_p$ = BW inflection point in phase p (age (week) at which the BW gain occurred at the greatest rate).

[2] Pearson correlation coefficient; higher values indicate a better fit of the model.

[3] Root mean square error; smaller values indicate a better fit of the model.

[4] Durbin-Watson statistic; values range from 0 to 4, values close to 2 indicate nonsignificant autocorrelation.

[5] The P value was obtained from an F-test, F value was calculated as $F = \frac{(SS_1 - SS_2)/(df_1 - df_2)}{SS_2/df_2}$, where SS is the sum of squares of the model and df is the number of degrees of freedom (the number of data points minus the number of parameters). P-values compare the monophasic vs. the diphasic model and the diphasic model vs. the triphasic model.

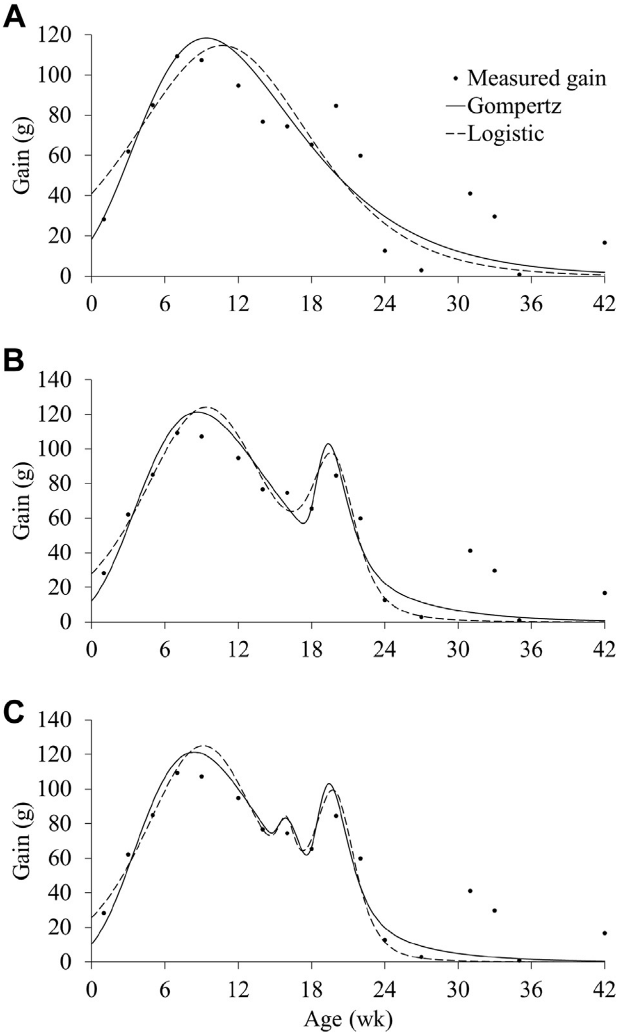

Figure 5. Monophasic (A), diphasic (B), and triphasic (C) Gompertz and logistic-derived models fitted to gain data (measured gain) of ad libitum–fed Lohmann Brown Lite laying hens.

slightly earlier for phases 1 and 3, but later for phase 2, than the Gompertz weight-age model (1.4 d, 1.8 d, and 3.7 d, respectively). The maximum gain in the first phase was estimated to be 0.10 and 0.15 kg lower when modeling the gain-age relationship than when modeling the weight-age relationship, for both the Gompertz and logistic triphasic models, respectively. It needs to be noted that a moving average was used for the data from the ad libitum–fed laying hens to account for some of the variability in gain, whereas gain calculated from the Lohmann target guideline was not converted to a moving average. The results indicate that modeling the gain-age relationship can result in slight alterations in parameter estimates compared with modeling the weight-age relationship, although gain is calculated directly from weight data and the gain-age model was the direct derivative of the original Gompertz model. Gain-age models would be more robust in identifying phases as described above; however, gain data had more variability, as the 2-weekly moving average of weekly gain needed to be used to fit the gain-age relationship models. It is suggested that further studies compare the relationship between model parameters from weight-age and gain-age models with egg-laying performance indicators.

Nonlinear Mixed Models

Two nonlinear mixed models were defined to estimate variance between birds in model parameters. Previously, Galeano-Vasco et al. (2014) concluded that a monophasic mixed Gompertz model including 2 random terms associated with the mature weight (Wm) and rate of gain (b) had the best fit to BW data of Lohmann Brown Lite hens. They also concluded that mixed logistic function on the same data did not converge. However, mixed logistic functions including 1 or 2 random terms associated with the mature weight and rate of gain converged in a study using juvenile quail (Aggrey, 2009). From the previous section, it could be concluded that the triphasic Gompertz model showed the best fit. However, the triphasic mixed Gompertz models did not converge, possibly because the timing of the second and third phases overlapped between individual hens. It is well known that convergence failures occur when models are highly complex (Kiernan et al., 2012). The inflection points of phase 2 and phase 3 were close (16.07 and 18.40 wk), and the maximum gain of each of those 2 phases were low compared with that of the first phase (0.04 and 0.15 kg vs. 1.81 kg, respectively). Therefore, the diphasic function was used for the nonlinear mixed models. The random term in equation [5] was associated with Wm_1 based on the variance in the mature weight, which was mostly determined by the first-phase weight

Table 4. Comparison between the estimated parameters of the triphasic Gompertz gain model fitted to BW data of ad libitum–fed Lohman Brown Lite hens (Ad lib) or fitted to the Lohmann breeder BW target (Lohmann).

Phase	Phase 1				Phase 2				Phase 3			
Data	Ad lib		Lohmann		Ad lib		Lohmann		Ad lib		Lohmann	
Parameters[1]	Estimate	SEM	Estimate	SEM	Estimate	SEM	Estimate	SEM	Estimate	SEM	Estimate	SEM
Wm (kg)	1.71	0.074	1.40	0.095	0.05	0.030	0.20	0.171	0.22	0.035	0.30	0.117
b	0.19	0.010	0.20	0.014	1.13	0.599	0.33	0.193	0.84	0.122	0.47	0.068
tinf (week)	8.41	0.229	7.05	0.301	16.14	0.484	15.74	1.759	19.59	0.1780	20.19	0.179

Abbreviations: Ad lib, ad libitum–fed Lohman Brown Lite hens; Lohmann, Lohmann breeder BW target.

[1] Function used: $G_t = \sum_{p=1}^{n} \{ Wm_p b_p \exp^{-\exp^{-b_p(t-tinf_p)}} \exp^{-b_p(t-tinf_p)} \}$, where G_t = Gain (kg) at age t (week); Wm_p = asymptotic BW gain of phase p (kg); b_p = the rate coefficient of phase p; $tinf_p$ = BW inflection point in phase p (age (week) at which the BW gain occurred at the greatest rate).

Table 5. Functional specifications, coefficients, and fit statistics criteria of a mixed diphasic Gompertz gain model including one or 2 random variables fitted to BW data of ad libitum–fed Lohmann Brown Lite hens.

Equation[1]	$W_{it} = (Wm_1 + u_i)\exp^{-\exp^{-b_1*(t-tinf_2)}} + Wm_2\exp^{-\exp^{-b_2*(t-tinf_2)}} + \varepsilon_i$			$W_{it} = (Wm_1 + u_i)\exp^{-\exp^{-b_1*(t-tinf_2)}} + Wm_2\exp^{-\exp^{-b_2*(t-(tinf_2+z_i))}} + \varepsilon_i$		
Parameter	Estimate	SEM	*P*-value	Estimate	SEM	*P*-Value
Wm_1	1.83	0.023	<0.001	1.78	0.023	<0.001
b_1	0.18	0.001	<0.001	0.18	0.001	<0.001
$tinf_1$	7.76	0.036	<0.001	7.57	0.032	<0.001
Wm_2	0.15	0.007	<0.001	0.20	0.006	<0.001
b_2	1.58	0.222	<0.001	1.85	0.219	<0.001
$tinf_2$	18.01	0.093	<0.001	18.09	0.408	<0.001
Variance						
V	0.00399	0.00009	<0.001	0.0035	0.00008	<0.001
V_u	0.00633	0.00240	0.021	0.0068	0.00260	0.022
V_z	-	-	-	2.2089	0.88230	0.028
Covariance	-	-	-	0.0586	0.03731	0.142
Criterion						
R-squared	0.990			0.991		
RMSE	0.063			0.059		
AIC[2]	−11,365			−11,764		
BIC[3]	−11,360			−11,757		

[1] W_{it} = BW (kg) at age t (week) of hen *i*; Wm_1 = asymptotic BW gain of phase one (kg); u_i = hen-related random term associated with Wm_1; b_1 = the rate coefficient of phase one; $tinf_1$ = BW inflection point in phase p (age (week) at which the BW gain occurred at the greatest rate), Wm_2 = asymptotic BW gain of phase 2 (kg); b_2 = the rate coefficient of phase 2; $tinf_2$ = BW inflection point in phase 2; z_i = hen-related random term associated with $tinf_2$; ε_i = residual error of hen *i*. Variance parameters $u \sim N(0,V_u)$, $z \sim N(0,V_z)$, and $\varepsilon \sim N(0,V)$ were estimated in the regressions.

[2] Akaike information criterion; smaller values indicate a better fit of the model.

[3] Bayesian information criterion; smaller values indicate a better fit of the model.

gain. In addition, monophasic versions of this function were used in previous studies for broilers (Wang and Zuidhof, 2004) and laying hens (Galeano-Vasco et al., 2014). The additional random term in equation [6] associated with the second inflection point ($tinf_2$) was based on the large variability in the moment of increase and consecutive decrease in gain before week 21 (Figure 2), identified as the (pre)pubertal growth phase. Assessing variability in this parameter may be relevant for identifying the age at maturity and association with egg production. In addition, one of the limitations of the Gompertz model was previously identified to be the fixed point of inflection (Darmani Kuhi et al., 2003). Adding the random term associated with $tinf_2$ allowed for variable points of inflection for the second growth phase in individual birds. If the model would be used in a large population of individuals with egg production and pedigree information, the heritability of the trait (the inflection point) and the genetic and phenotypic correlations between individual inflection points and production parameters could be assessed. This would provide additional tools for balanced selection for both the body weight and egg production.

The reduced Akaike and Bayesian information criteria indicated that the model including both random terms improved fit over the model including only one random term (Table 5). The parameter estimates of both models were similar. The estimated individual mature BW ($Wm_1 + u_i + Wm_2$) ranged from 1.83 kg to 2.10 kg and the SD ($\sqrt{Vu}$) was estimated at 0.082 kg in the model including 2 random terms. In female quail, the SD for individual mature weight was estimated at 0.010 kg in a monophasic logistic model including random terms associated with mature BW and the inflection point (Aggrey, 2009). This was 7.6% of the mean mature weight of 0.132 kg, a much higher proportion than the 4.1% of the total mean mature weight (1.98 kg) or 4.6% of the mean mature weight of the first phase (1.78 kg) in the current results. The use of the Gompertz function and the addition of the second phase in the current model may have captured some of the variation incorporated in the random term estimate of the mature BW in the monophasic logistic model by Aggrey (2009). Alternatively, Japanese quail may have selected to a lesser extent on the BW or egg size (correlated with BW) than laying hens, and therefore, the models from Aggrey (2009) showed proportionally more variation. The estimated individual second inflection point ($tinf_2 + z_i$) ranged from 15.26 wk to 19.79 wk, and the SD ($\sqrt{Vz}$) was 1.49 wk. This result could not be directly compared with the present literature. However, it indicates that there is considerable variation in timing of the (pre)pubertal growth phase.

The present study identified that the multiphasic mixed Gompertz growth model fitted data of *ad libitum*–fed Lohmann Brown Lite hens best. The multiphasic mixed Gompertz model identified similar growth phases by using a weight-age or gain-age function and the phases aligned with developmental biology of growth. In addition, including the random component to the inflection point of the diphasic mixed Gompertz model allowed for future study of the relationship between the individual shape of the BW function and egg production parameters.

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