Multiphasic poultry growth models: method and application

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ABSTRACT Growth and development are complex phenomena. To date, most growth modeling research has focused on a single growth phase, which is sufficient and useful for describing ad libitum fed animals processed at a prepubertal age, such as broilers or turkeys produced for meat. However, multiphase growth models are necessary to describe and predict growth and further to hypothesize about optimizing growth of reproducing animals such as broiler breeder hens. Therefore, the objective of the present study was to develop and evaluate multiphasic models to describe the growth of various types of poultry raised to reproductive age. Coefficients for monophasic, diphasic, and triphasic Gompertz model forms were estimated using a variety of BW trajectories published by primary breeders. The fit of these models was evaluated for a representative laying line hen, broiler breeder hen and rooster, and turkey hen. The coefficient of determination (R^2), root mean square error, and the Bayesian information criterion were used to evaluate the fit of each model. The diphasic model was found to be the best fit for the turkey hen, while the triphasic model was the most suitable model for all the chicken lines studied. Hypotheses can be formulated based on any of the continuous model parameters, and the resulting BW trajectories can be implemented and evaluated in a systematic way. The biological relevance of the continuous parameters in multiphasic Gompertz models provides an opportunity to implement a robust hypothesis-based approach for future optimization of growth curves.

Key words: growth, nonlinear model, laying hen, broiler breeder, turkey

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INTRODUCTION

The British statistician George Box is credited with the statement “All models are wrong, but some are useful”. The present study attempts to develop a systematic and useful way to describe growth quantitatively in reproducing animals. Such a modeling approach would be useful for optimizing production systems involving egg and chick production. For example, estimating BW at any age provides a valuable basis for estimation of energy requirements, and thereafter feed intake (Emmans, 1981, 1987). For feed-restricted animals, a model with biologically meaningful parameters would facilitate the design and study of alternative growth strategies.

Single phase growth models have been used to develop software programs that intend to increase the sustainability of poultry production by minimizing excretions to the environment and maximizing profit. Modified versions of the Gompertz model, originally published in 1825 (Gompertz, 1825), have been widely adopted by biologists and livestock scientists (Gous et al., 1999; Wang and Zuidhof, 2004; Sakomura et al., 2005; Tjorve and Tjorve, 2017). However, growth occurs in multiple stages (Koops, 1986), and the Gompertz model in its basic monophasic form only adequately describes a single phase of unrestricted growth (Emmans, 1981). Thus, additional phases should be considered to model restricted growth, and particularly the growth of reproducing animals, where there are at least 3 biologically relevant growth phases: prepubertal, pubertal, and postpubertal. There have been few contributions to the study of multiphasic growth in poultry. Kwakkel et al. (1993) are among the few who have attempted to describe the growth of the body and chemical components of laying hens in a multiphasic manner. They described functional relationships with the growth of protein, fat, and ash. Notably, they reported that after 11 wk of age, protein deposition was mainly related to the development of the reproductive tract, and fat deposition was primarily in the form of abdominal fat. They also pursued the question of the impact of different multiphasic growth patterns on body composition and onset of lay and

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Table 1. Estimated coefficients and model fit statistics for 1-, 2-, and 3-phase Gompertz models[1] for the laying hen line females (Lohmann Brown Lite).

	Monophasic			Diphasic			Triphasic		
Parameter	Estimate	SEM	Pr > |t|	Estimate	SEM	Pr > |t|	Estimate	SEM	Pr > |t|
g_1	1.9579	0.0042	<0.001	1.0857	0.2753	<0.001	1.561	0.0145	<0.001
b_1	0.1398	0.0024	<0.001	0.2409	0.0514	<0.001	0.18	0.0023	<0.001
I_1	8.8654	0.0962	<0.001	5.2928	1.0857	<0.001	7.1504	0.0648	<0.001
g_2				0.866	0.2769	0.002	0.3315	0.0133	<0.001
b_2				0.1777	0.0171	<0.001	0.4964	0.0249	<0.001
I_2				15.92	1.795	<0.001	18.706	0.083	<0.001
g_3							0.1217	0.0059	<0.001
b_3							0.0583	0.0047	<0.001
I_3							58.907	1.0212	<0.001
SD	0.0326	0.0024	<0.001	0.0311	0.0022	<0.001	0.0054	0.0004	<0.001
Model fit statistics									
BIC	−361.9			−366.4			−684.3		
R^2	0.9964			0.9961			0.9999		
RMSE	0.0311			0.0326			0.0054		

Abbreviations: BIC, Bayesian Information Criterion; RMSE, root mean square error.

[1]General model form was $BW_t = \sum_{i=1}^{p} g_i exp^{-exp^{-b_i(t-I_i)}} + \varepsilon_t$, where BW_t was BW at time t (wk); $P = 1$ for the single phase (monophasic) model; $P = 2$ for the 2-phase (diphasic) model; and $P = 3$ for the 3-phase (triphasic) model; g_i was the total amount of gain accruing in phase i; b_i was the rate of growth in phase i; I_i was the inflection point for phase i, or age (wk) at which growth for that phase reached its maximum rate; and SD was the standard deviation of the residuals ε_t.

hypothesized that there may be a fat-free tissue threshold that must be reached before pubertal development (Kwakkel et al., 1995). Very little development of the concept of multiphasic growth has occurred in the last 30 yr since this pioneering work was completed.

There is a key driving motivation behind this work: to design optimal target BW curves for broiler breeders. Current levels of feed restriction are becoming so severe that some pullets do not have sufficient fat reserves to undergo sexual maturation (van Emous et al., 2015; van der Klein et al., 2018a,b; Zuidhof, 2018). High energy intake can stimulate pubertal development (Hadinia et al., 2020). An optimization strategy is needed to redefine suitable BW trajectories for broiler breeders. Thus, the objective of the current research was to evaluate the suitability of monophasic, diphasic, and triphasic models for various types of poultry grown to reproductive age and to explore their suitability for development of optimal growth recommendations for modern broiler breeders.

Figure 1. Fit of 1-, 2-, and 3-phase models to target Lohmann Brown-Lite BW trajectories.

MATERIAL AND METHODS

Experimental Design and Data

No animals were used in this study. Published target BW data for laying hens (Lohmann Brown-lite; Lohmann Tierzucht, 2017), broiler breeders (Ross 308; Aviagen, 2016), and turkey hens (Hybrid Converter; Hendrix Genetics BV, 2017) were used to evaluate the various Gompertz model forms. The lines chosen were arbitrary because once evaluated, coefficients for the most appropriate models can be estimated for the serial BW data of additional lines. Published BW data for turkey lines were only provided to the point of lay. Typically, turkey hens lose weight immediately after they start to lay, and it can be argued that BW at the point of lay is representative of their mature BW. Thus, one additional data point, the 29-wk BW for the turkey growth trajectory, was repeated in the data set 10 wk later, to prevent the turkey growth model from predicting high rates of continued growth after the onset of lay. Nonlinear regression was used to estimate the models described in the following section.

Models

All models were estimated using the NLMIXED procedure of SAS (SAS Institute, Inc., Cary, NC). One-, two-, and three-phase models were fit to the published BW data. The general form of the model was modified from previously published Gompertz forms (Wang and

Table 2. Estimated coefficients and model fit statistics for 1-, 2-, and 3-phase Gompertz models[1] for broiler breeder line female birds (Ross 308).

	Monophasic			Diphasic			Triphasic		
Parameter	Estimate	SEM	Pr > |t|	Estimate	SEM	Pr > |t|	Estimate	SEM	Pr > |t|
g_1	4.0565	0.027	<0.001	3.4962	0.0727	<0.001	2.1179	0.1157	<0.001
b_1	0.0922	0.0025	<0.001	0.0879	0.0021	<0.001	0.1499	0.0097	<0.001
I_1	13.575	0.1899	<0.001	12.254	0.2395	<0.001	7.3056	0.4307	<0.001
g_2				0.5259	0.0659	<0.001	1.5365	0.1163	<0.001
b_2				0.583	0.1434	<0.001	0.2466	0.0143	<0.001
I_2				21.62	0.5075	<0.001	21.449	0.1806	<0.001
g_3							0.6371	0.0829	<0.001
b_3							0.0929	0.0145	<0.001
I_3							51.733	1.4662	<0.001
SD	0.098	0.0086	<0.001	0.0631	0.0055	<0.001	0.0234	0.0021	<0.001
Model fit statistics									
BIC	−145.6			−100.8			−261.8		
R^2	0.9976			0.9942			0.9997		
RMSE	0.0631			0.098			0.0234		

Abbreviations: BIC, Bayesian Information Criterion; RMSE, root mean square error.
[1]General model form was $BW_t = \sum_{i=1}^{p} g_i exp^{-exp^{-b_i(t-I_i)}} + \varepsilon_t$, where BW_t was BW at time t (wk); $P = 1$ for the single phase (monophasic) model; $P = 2$ for the 2-phase (diphasic) model; and $P = 3$ for the 3-phase (triphasic) model; g_i was the total amount of gain accruing in phase i; b_i was the rate of growth in phase i; I_i was the inflection point for phase i, or age (wk) at which growth for that phase reached its maximum rate; and SD was the standard deviation of the residuals ε_t.

Zuidhof, 2004; Zuidhof et al., 2014; Tjorve and Tjorve, 2017):

$$BW_t = \sum_{i=1}^{p} g_i exp^{-exp^{-b_i(t-I_i)}} + \varepsilon_t$$

where BW_t was body weight (kg) at time t (wk); p was the number of phases ($P = 1$, 2, or 3 for monophasic, diphasic, and triphasic models, respectively); g_i was the total amount of gain accruing in phase i; b_i was the rate of growth in phase i; I_i was the inflection point for phase i or age (wk) at which growth for that phase reached its maximum rate; and ε_t was the residual error with an expected value of 0, and a normally distributed variance estimated by the software $\varepsilon_t \sim N(0, SD^2)$.

Expanded, the monophasic [1], diphasic [2], and triphasic [3] models were as follows:

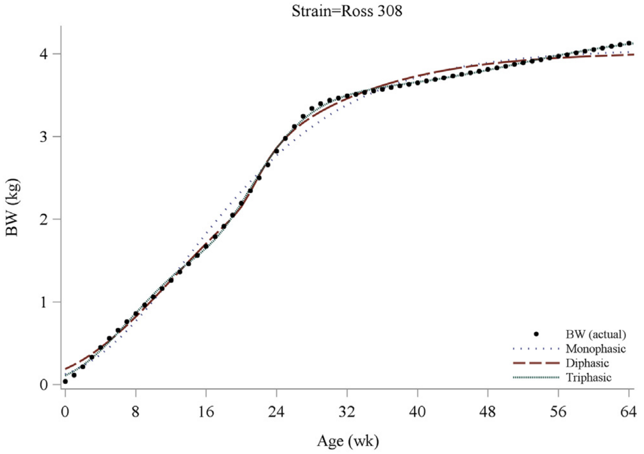

Figure 2. Fit of 1-, 2-, and 3-phase models to target Ross 308 BW trajectories.

$$BW_t = g_1 exp^{-exp^{-b_1(t-I_1)}} + \varepsilon_t \quad [1]$$

$$BW_t = g_1 exp^{-exp^{-b_1(t-I_1)}} + g_2 exp^{-exp^{-b_2(t-I_2)}} + \varepsilon_t \quad [2]$$

$$BW_t = g_1 exp^{-exp^{-b_1(t-I_1)}} + g_2 exp^{-exp^{-b_2(t-I_2)}} + g_3 exp^{-exp^{-b_3(t-I_3)}} + \varepsilon_t \quad [3]$$

Model Evaluation

In addition to the SD of the residuals, which was directly estimated in the NLMIXED procedure, models were evaluated using 3 different criteria. The Bayesian Information Criterion (**BIC**), root mean square error (**RMSE**), and the coefficient of determination (**R^2**) were as follows: BIC = − 2LL + ln(n)K, where LL was the log likelihood estimate, K was the number of model parameters, and n was the number of observations used to estimate the model. The BIC statistic rewards fit and penalizes extra model parameters. Lower BIC values indicate better models. $RMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(y_i - \widehat{y}_i)^2}$, where y_i was the i^{th} BW observation, $\hat{y}_i$ was the predicted value for the i^{th} BW observation, and n was the number of observations. $R^2 = 1 - \frac{\sum_i \varepsilon_i^2}{\sum_i (y_i - \overline{y})^2}$, where ε_i was the i^{th} residual, y_i was the i^{th} BW observation, and $\overline{y}$ was the average of all BW observations.

RESULTS

For the diphasic and triphasic models, the terms prepubertal, pubertal, and postpubertal will be used

Table 3. Estimated coefficients and model fit statistics for 1-, 2-, and 3-phase Gompertz models[1] for broiler breeder line males (Ross).

	Monophasic			Diphasic			Triphasic		
Parameter	Estimate	SEM	Pr > |t|	Estimate	SEM	Pr > |t|	Estimate	SEM	Pr > |t|
g_1	4.9932	0.0344	<0.001	4.7847	0.0457	<0.001	2.1858	0.0849	<0.001
b_1	0.0866	0.0024	<0.001	0.0958	0.0026	<0.001	0.2543	0.0161	<0.001
I_1	11.547	0.1968	<0.001	10.978	0.1795	<0.001	4.4874	0.1973	<0.001
g_2				0.5836	0.3596	0.11	2.2139	0.1049	<0.001
b_2				0.1254	0.0821	0.13	0.1997	0.0095	<0.001
I_2				56.102	5.6982	<0.001	19.279	0.2516	<0.001
g_3							1.0551	0.1171	<0.001
b_3							0.0836	0.0107	<0.001
I_3							51.098	1.2587	<0.001
SD	0.1198	0.0105	<0.001	0.0912	0.008	<0.001	0.028	0.0025	<0.001
Model fit statistics									
BIC	−97.63			−74.68			−238.8		
R^2	0.9962			0.9935			0.9996		
RMSE	0.0912			0.1198			0.028		

Abbreviations: BIC, Bayesian Information Criterion; RMSE, root mean square error.
[1]General model form was $BW_t = \sum_{i=1}^{p} g_i exp^{-exp^{-b_i(t-I_i)}} + \varepsilon_t$, where BW_t was BW at time t (wk); $P = 1$ for the single phase (monophasic) model; $P = 2$ for the 2-phase (diphasic) model; and $P = 3$ for the 3-phase (triphasic) model; g_i was the total amount of gain accruing in phase i; b_i was the rate of growth in phase i; I_i was the inflection point for phase i, or age (wk) at which growth for that phase reached its maximum rate; and SD was the standard deviation of the residuals ε_t.

interchangeably with phases 1, 2, and 3, respectively. The results presented are focused on the best fitting model for each poultry line.

Model coefficients and fit statistics for the layer line hens are shown in Table 1, and the best fit lines are shown in Figure 1. The triphasic model had the best fit, with the lowest RMSE and BIC values and the highest R^2 value. The model predicts 1.561 kg of growth during the prepubertal phase, 0.332 kg of growth in the pubertal phase, and 0.122 kg of growth in the postpubertal phase. A pubertal phase rate coefficient (b_2) of 0.4964 predicted accumulation of 98% of the total growth for that phase in approximately 12 wk, from 16 to 28 wk of age, peaking at I_2 = 18.71 wk of age. By 33 wk of age, 99% of phase 1 growth was complete, and 88% of phase 3 growth was complete by 95 wk of age.

Model coefficients and fit statistics for the broiler breeder line hens are shown in Table 2, and the best fit lines are shown in Figure 2. The triphasic model had the best fit, with the lowest RMSE and BIC values and the highest R^2 value. The model predicts 2.118 kg of growth during the prepubertal phase, 1.537 kg of growth in the pubertal phase, and 0.637 kg of growth in the postpubertal phase. A pubertal phase rate coefficient (b_2) of 0.2466 predicted accumulation of 98% of the total growth for that phase in approximately 25 wk, from 16 to 40 wk of age, peaking at I_2 = 21.45 wk of age. By 38 wk of age, 99% of phase 1 growth was complete, and 72.6% of phase 3 growth was complete by 64 wk of age.

Model coefficients and fit statistics for the broiler breeder line male birds are shown in Table 3, and the best fit lines are shown in Figure 3. The triphasic model had the best fit, with the lowest RMSE and BIC values and the highest R^2 value. The model predicts 2.186 kg of growth during the prepubertal phase, 2.214 kg of growth in the pubertal phase, and 1.055 kg of growth in the postpubertal phase. A pubertal phase rate coefficient (b_2) of 0.1997 predicted accumulation of 98% of the total growth for that phase in approximately 31 wk, from 12 to 43 wk of age, peaking at I_2 = 19.28 wk of age. By 23 wk of age, 99% of phase 1 growth was complete, and 97.5% of phase 3 growth was complete by 64 wk of age.

Model coefficients and fit statistics for the turkey line hens are shown in Table 4, and the best fit lines are shown in Figure 4. For turkey hens, the diphasic model had the best fit, with the highest BIC value. In the turkey line, the RMSE and R^2 values did not decrease with the addition of a third growth phase. The model predicts 10.352 kg of growth during the prepubertal phase and 2.15 kg of growth in the pubertal phase. A pubertal phase rate coefficient (b_2) of 0.3149 predicted accumulation of 98% of the total growth for that phase in approximately 19 wk, from 17 to 36 wk of age, peaking

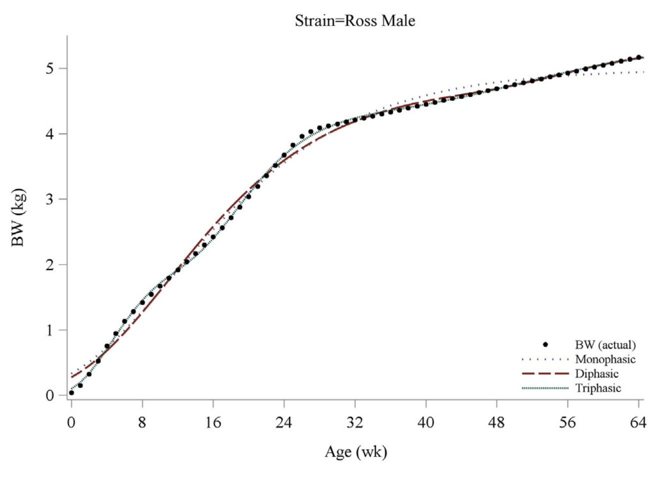

Figure 3. Fit of 1-, 2-, and 3-phase models to target Ross male BW trajectories.

Table 4. Estimated coefficients and model fit statistics for 1-, 2-, and 3-phase Gompertz models[1] for turkey line hens (Hybrid Converter).

	Monophasic			Diphasic			Triphasic		
Parameter	Estimate	SEM	Pr > |t|	Estimate	SEM	Pr > |t|	Estimate	SEM	Pr > |t|
g_1	13.129	0.1675	<0.001	10.352	0.3778	<0.001	10.352	0.3778	<0.001
b_1	0.1217	0.0034	<0.001	0.158	0.0066	<0.001	0.158	0.0066	<0.001
I_1	10.665	0.1607	<0.001	8.6302	0.2735	<0.001	8.6302	0.2735	<0.001
g_2				2.1502	0.3592	<0.001	2.1502	0.3592	<0.001
b_2				0.3149	0.0449	<0.001	0.3149	0.0449	<0.001
I_2				21.024	0.3743	<0.001	21.024	0.3743	<0.001
g_3							1E-8		
b_3							1E-8		
I_3							42.092	0	<0.001
SD	0.1986	0.0252	<0.001	0.0868	0.011	<0.001	0.0868	0.011	<0.001
Model fit statistics									
BIC	1.4894			−39.5			−29.2		
R^2	0.9975			0.9995			0.9995		
RMSE	0.1986			0.0868			0.0868		

Abbreviations: BIC, Bayesian Information Criterion; RMSE, root mean square error.

[1]General model form was $BW_t = \sum_{i=1}^{p} g_i exp^{-exp^{-b_i(t-I_i)}} + \varepsilon_t$, where BW_t was BW at time t (wk); $P = 1$ for the single phase (monophasic) model; $P = 2$ for the 2-phase (diphasic) model; and $P = 3$ for the 3-phase (triphasic) model; g_i was the total amount of gain accruing in phase i; b_i was the rate of growth in phase i; I_i was the inflection point for phase i, or age (wk) at which growth for that phase reached its maximum rate; and SD was the standard deviation of the residuals ε_t.

at $I_2 = 21.02$ wk of age. By 38 wk of age, 99% of phase 1 growth was complete.

DISCUSSION

Model Goodness of Fit

The best fit lines in Figures 1–4 visually reflected the objective comparisons of model fit. In every poultry line currently considered, the monophasic model showed evidence of biased predictions, that is, there were regions where adjacent BW estimates were overpredicted or underpredicted. Figure 5 shows the residual error of the BW predictions for the Ross 308 hens. Addition of the second and third phases reduced residuals, but did not eliminate them. Addition of a third phase for the turkey line did not improve the model fit, and as such, the diphasic and triphasic BW predictions were overlaid (Figure 4), and the fit criteria were not improved.

Biological Relevance

Reasonable multiphasic models were estimable for both unrestricted (laying hen and turkey) and feed-restricted (broiler breeder) lines. Furthermore, the model parameters make biological sense. The concept of prepubertal growth of the body as a whole, then growth and development of the reproductive organs, and finally of longer term tissue accumulation in a mature animal has long been recognized in species ranging from humans to cattle and pigs. Koops (1986) discussed the existence of superimposed phases, cycles, or spurts that could be distinguished upon careful observation of growth. Three superimposed growth phases of the Ross 308 hen are illustrated in Figure 6. Superimposed growth phases were hypothesized to be manifestations of environmental (including nutritional) changes, temporal variations in hormonal stimuli, temporary predominance of secretory glands, changes in cell size and

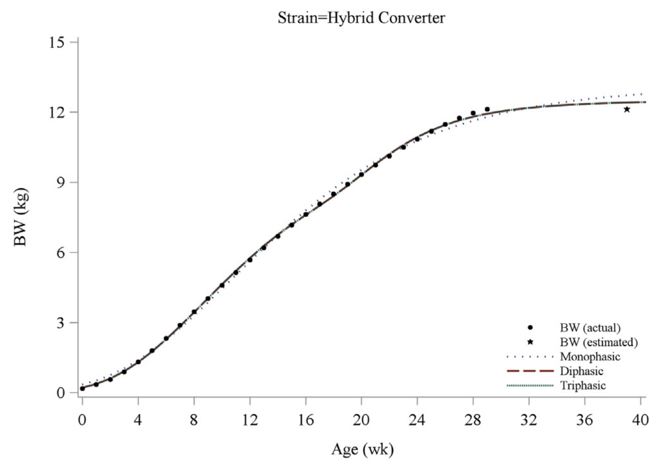

Figure 4. Fit of 1-, 2-, and 3-phase models to target Hybrid converter hen BW trajectories.

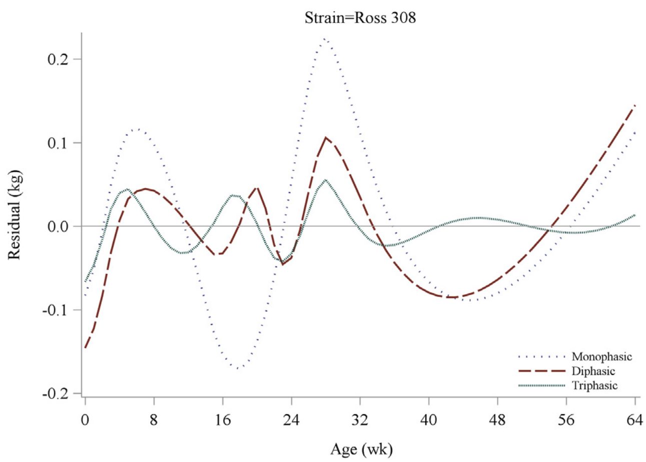

Figure 5. Body weight residuals from best fit 1-, 2-, and 3-phase growth models for Ross 308 hens.

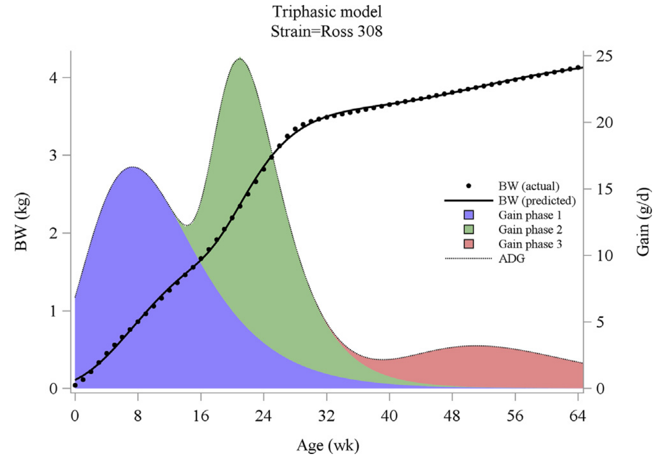

Figure 6. Growth rate during the first, second, and third growth phases fit to Ross 308 hen target BW trajectory.

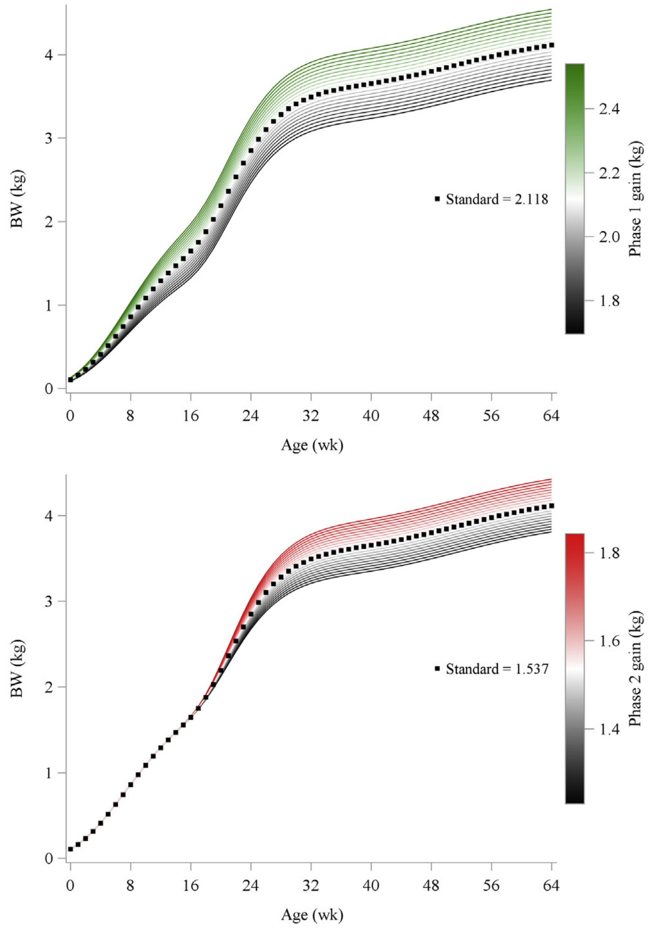

Figure 7. Examples of BW curves created by modifying the prepubertal phase gain coefficient (g_1; top) or pubertal phase gain coefficient (g_2; bottom) by −20 to 20%.

number, and successive development of tissues (Koops, 1986). To date, formal investigation and quantification of multiphasic growth in poultry over a lifetime is limited to few studies (Kwakkel et al., 1993, 1995, 1998).

The estimated prepubertal phase growth accounted for 77.5% of the total lifetime BW gain for laying hens and 82.8% for turkey hens. This was similar to estimates of 83.5% for Rhode Island Red hens and 80.2% for White Leghorn hens (Grossman and Koops, 1988). In contrast, the prepubertal phase growth coefficient was 49.4% of total lifetime BW gain for feed-restricted broiler breeder hens and 40.1% for feed-restricted broiler breeder roosters. Galeano-Vasco et al. (2014) concluded that a monophasic Gompertz model was preferable to von Bertalanffy, Richards, Brody, and Logistic monophasic models for describing laying hen growth. They reported an R^2 of 0.991 for the monophasic Gompertz model, which was an acceptable fit, and likely aided by the fact that most of the growth of laying hens occurs in the first phase.

The higher proportion of growth in the second and third phases in broiler breeders suggests that the natural multiphasic growth pattern has been altered. This raises interesting questions about the design of appropriate BW trajectories for feed-restricted animals, specifically broiler breeders. One rather obvious hypothesis is that feed restriction programs, more aptly named BW control programs, might follow a more natural pattern of distribution of BW gain. However, we can only speculate about the commercial implications, as data documenting alternative body weight trajectories for broiler breeders are too scarce to draw conclusions about the value of basing growth trajectories on a more natural pattern of growth.

Table 5. Estimated coefficients and model fit statistics for a triphasic Gompertz model[1] describing BW profile treatments of a previous experiment (Robinson et al., 2007).

	Treatment			
Parameter	Low	Standard	Moderate	High
g_1	1.9896	2.1207	2.8462	3.1194
b_1	0.1181	0.1429	0.1696	0.2178
I_1	8.9426	7.9063	7.808	7.0062
g_2	1.6842	1.4843	0.7001	0.1862
b_2	0.2367	0.2452	0.2251	0.7031
I_2	22.263	21.22	22.026	13.055
g_3	0.2421	0.2997	0.3892	0.6307
b_3	0.1289	0.118	0.0921	0.0753
I_3	51.862	48.526	46.681	37.427

[1]General model form was $BW_t = \sum_{i=1}^{p} g_i exp^{-exp^{-b_i(t-I_i)}} + \varepsilon_t$, where BW_t was BW at time t (wk); $P = 3$ for the 3-phase (triphasic) model; g_i was the total amount of gain accruing in phase i; b_i was the rate of growth in phase i; I_i was the inflection point for phase i, or age (wk) at which growth for that phase reached its maximum rate; and SD was the standard deviation of the residuals ε_t.

Hypothesis Generation From Model Coefficients

Relevance of the biological significance of the coefficients g, b, and I has been previously noted. This draws attention to the potential to use the triphasic model to evaluate growth trajectories more strategically than in the past. For example, Robinson et al. (2007) extensively evaluated discrete 4 BW profiles which they described as,

> "standard (mean target BW profile of the 3 strains used), low (12-wk BW target = 25% lower than standard followed by rapid gain to 32 wk), moderate

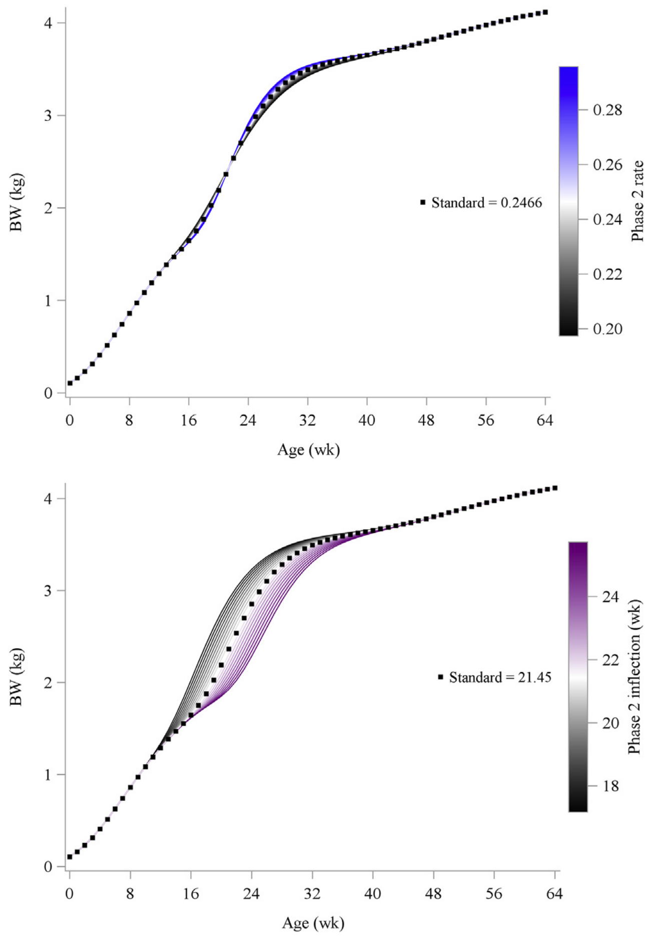

Figure 8. Examples of BW curves created by modifying the pubertal phase rate coefficient (b_2; top) or pubertal phase age at inflection coefficient (I_2; bottom) by −20 to 20%.

(12-wk BW target = 150% of standard followed by lower rate of gain to 32 wk), and high (12-wk BW target = 200% of standard followed by minimal growth to 32 wk)".

Fitting these BW profiles to a triphasic model (Table 5) reveals insights into the way that the various growth phases were manipulated. Not surprisingly, progressively from low to high, the g_1 coefficient increased incrementally, while the rate b_1 increased and the inflection point I_1 was advanced (decreased). Growth in the second phase g_2 was conversely decreased in the respective profiles from low to high, and the rate coefficient b_2 in the high treatment increased markedly. The inflection point of the high treatment was very low (13.06 wk), such that the biological relevance was questionable. The high treatment had a longer duration (low b_3 rate coefficient) and larger magnitude (g_3 gain coefficient) in the third phase. Overall, however, the coefficients reveal that the BW curves were somewhat random in their design.

Over 5 decades of selection for broiler traits, broiler growth potential and efficiency have increased greatly (Havenstein et al., 2003; Zuidhof et al., 2014). On the other hand, breeder BW recommendations have changed very little during the same time frame (Renema et al., 2007). Recent broiler breeder research suggests that feed restriction required to achieve these low-BW targets may be reaching a limit such that some broiler breeder pullets have insufficient body fat to undergo sexual development (van der Klein et al., 2018a,b; Zuidhof, 2018). Thus, new targets are needed, but identifying an optimum one is overwhelmingly complex.

The current triphasic model could be used to strategically develop hypothesis-based BW trajectories. These strategic hypotheses could be tested in a manner that will lead efficiently to optimization of growth recommendations. For example, we could hypothesize that altering the amount of gain in the prepubertal phase would allow the birds to build a better foundation for sexual maturation. Alternatively, we could hypothesize that altering the amount of gain during the pubertal phase is more important for achieving appropriate fat levels at the time sexual maturation actually occurs. To test these hypotheses, the parameters g_1 and g_2, respectively, could be changed to develop growth trajectories in the desired testing range. Figure 7 shows the hypothetical BW trajectories based on changes of −20 to 20% in the b_1 and b_2 coefficients. The magnitude and range of changes are somewhat arbitrary and for illustrative purposes. Based on recent observations that BW restrictions may already be too severe in modern broiler breeders, there would be little motivation to decrease BW recommendations further. Thus, increases in the g_1 and g_2 parameters would be more strategic hypotheses to explore. However, an important characteristic of these parameters is that they are continuous, and an optimum response curve could be developed for each hypothesis. Furthermore, one could hypothesize that changing the b_2 rate coefficient or the I_2 inflection point coefficient of the pubertal phase in a similar manner could achieve a desired reproductive outcome (Figure 8). Based on recent observations, for example, by van der Klein et al. (2018b), decreasing rather than increasing the age at the inflection point would be a more logical range of I_2 to explore. Of course, any combination of model parameters could be manipulated to test the effect of interactions or combinations of variables to be tested. This would generate a response surface or matrix from which an optimal growing strategy could be derived.

Growth and development is a complex phenomenon. The present study outlines a method for quantitatively describing growth that occurs in superimposed phases. Turkey hen growth was best described by a diphasic model, and chicken growth (laying hens and broiler breeder hens and roosters) was best described with a triphasic model. The triphasic model with its biologically relevant continuous parameters presents an opportunity to implement a more robust quantitative BW optimization approach, which is imminently needed for broiler breeders. There remain infinite BW trajectories and many optimization hypotheses that could be tested, but the triphasic model provides a way to begin to test key hypotheses in a systematic and strategic manner.

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