Evaluation of Growth Functions on Japanese Quail Lines

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The aim of present study was to fit the best predictive equation to describe the growth curve of different Japanese quail lines. Moreover the effect of short-term divergent selection on the growth curve parameters was investigated. The quail lines utilized in the current study were two divergently selected lines for high (HW) and low (LW) 4-wk body weight (BW) and a control line (C). Determination and adjusted determination coefficients, relative error mean and standard deviation, mean square error, Akaike’s information criteria and Schwarz Bayesian information criteria were used to evaluate the accuracy of prediction with the growth functions of Hyperbolastic (H1, H2, H3), Richards, Gompertz, Logistic and Von bertalanffy. Based on model behavior and statistical performance, the Gompertz and Logistic functions were not able to show a suitable fit for all three lines. The overall goodness of fit statistics in the HW line showed that the Richards function has the best fit to the data followed by H3, H2, H1, Von bertalanffy, Gompertz and Logistic functions, respectively. The overall results in the LW and C lines were similar to the HW line, except that Logistic function provided a better fit to the data than Gompertz. The study of growth pattern using Richards function revealed that short-term divergent selection altered the growth trajectory of selected lines through the changing of shape parameters and relative intensity of growth rates.

Key words: divergent selection, growth curve, Japanese quail

Introduction

Growth is a priority trait in poultry industry. Recently, researches are focused primarily on the Japanese quail, because of its low maintenance costs and short intergeneration interval. Moreover Japanese quail is considered to be a low-cost and useful function for poultry growth researches (Aggrey and Cheng, 1994; Jones, 1996; Decuyper et al., 2002).

A major step toward understanding growth process would be to explain the observed growth distribution. Traditionally, the mathematical functions called ‘growth models’ have been used to investigate the relationship between live weight and age (Fitzhugh, 1976; Anthony et al., 1996; Hyánková et al., 2001; Aggrey et al., 2003; Aggrey et al., 2009; Darmani-Kuhi et al., 2010). A useful growth function should describe data well and it must contain the biologically and physically meaningful parameters (France et al., 1996; Darmani-Kuhi et al., 2010). The growth functions have different specialities which must be noted prior to select them for description of observed growth data: The Logistic and Gompertz functions have fixed growth forms with the point of inflection at about 50 and 37% of the asymptote, respectively (Ricklefs, 1968). These parameter models are special cases of the more flexible Richards function, which a variable point of inflection has specified by the shape parameter (γ) (Richards, 1959). The flexible functions are often generalized functions that encompass simpler functions for particular values of certain additional parameters (Darmani-Kuhi et al., 2010). Darmani-Kuhi et al. (2003) showed that description of growth in broilers by fixed-shape sigmoid functions such as Logistic or Gompertz curves may not be adequate because of the failure of the assumption that a constant curve shape holds across selected lines. Tabatabai et al. (2005) introduced the Hyperbolastic growth functions in 3 types including H1 (generalizes Logistic growth function); H2 (stand-alone); and H3 (generalizes Weibull growth function).

The results of other experiments showed that choosing the growth functions were species-specific, strain-specific and even line-specific (Ricklefs, 1979; Anthony et al., 1996). Hyánková et al. (2001) found that the shape of growth curve was not affected by short-term divergent selection in Japanese quail.

The aim of present study was to fit the best predictive function to describe the growth curve of divergently selected
Experimental Birds

feed contain 28g CP/kg and 2900 ME/kg) and arti-
culled equally into 3 groups and allowed to reproduce. Then birds were divergently selected (phenotypic selection) for higher (HW) and lower (LW) 4-wk BW. No selection was carried out in the third group as the control line (C line).

In the selected lines, selection pressure in males was 10% and in females was 20%. The cumulative response to selection over 7 generations for HW line was 19.88 g (males: 22.15, females: 18.95 g) and for the LW line was −25.15 g (males: −22.15 g, females: −28.15 g).

For this experiment, 135 birds from the HW line, 239 birds from the LW line and 201 birds from the C line were weighted at hatch and placed into separate pens. Allquails were supplied with balanced feed (i.e., standard commercial feed contain 28 g CP/kg and 2900 MEJ ME/kg) and artificially lighted housing for 24 hours/day. Birds were kept in a room maintained at about 35°C during the first week, 28°C during the second week, and at 20~24°C from the 3rd week onwards. Food and water were available ad libitum. Until three weeks of age, the body weights were measured daily on all chicks, and thereafter chicks were weighted at 24, 28, 32 and 42 days of age.

Material and Method

Experimental Birds

The experimental population was originated from a com-
mmercial Japanese quail farming center in Yazd, Iran. Around 1,000 birds were transported to the animal research station of Tehran University. At first a number of birds were randomly selected from the base random bred population and distributed equally into 3 groups and allowed to reproduce. Then birds were divergently selected (phenotypic selection) for higher (HW) and lower (LW) 4-wk BW. No selection was carried out in the third group as the control line (C line).

Table 1. Equation for seven growth curve functions and their time to inflection, used in this study

<table>
<thead>
<tr>
<th>Function</th>
<th>Expression</th>
<th>Time to inflection</th>
</tr>
</thead>
<tbody>
<tr>
<td>H1</td>
<td>( w(t) = \frac{M}{1 + \exp \left( -M \frac{\beta t - \arcsin(h(t))}{\theta} \right)} )</td>
<td>( t^* = \frac{1}{\beta} \ln \left( \frac{M - \overline{w}}{\overline{w}} \right) )</td>
</tr>
<tr>
<td>H2</td>
<td>( w(t) = \frac{M}{1 + \frac{\theta t}{\theta - 1 - \theta \arcsinh \left( \frac{\theta t}{\theta - 1} \right)}} )</td>
<td>( t^* = \frac{-1}{\beta} \ln \left( \frac{\theta t}{\theta - 1} \right) )</td>
</tr>
<tr>
<td>H3</td>
<td>( w(t) = \frac{M}{w_0 \left( \frac{M}{w_0} \right) \exp \left( -\beta t \right)} )</td>
<td>( t^* = \frac{1}{\beta} \ln \left( \frac{M}{\overline{w}} \right) )</td>
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<tr>
<td>Logistic</td>
<td>( w(t) = \frac{M}{w_0 \left( \frac{M}{w_0} \right) \exp \left( -\beta t \right)} )</td>
<td>( t^* = \frac{-1}{\beta} \ln \left( \frac{\theta t}{\theta - 1} \right) )</td>
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<tr>
<td>Richards</td>
<td>( w(t) = M(1 \pm \theta \exp(-\beta t))^{-\frac{1}{\theta}} )</td>
<td>( t^* = \frac{1}{\beta} \ln \left( \frac{M}{\overline{w}} \right) )</td>
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<tr>
<td>Gompertz</td>
<td>( w(t) = \frac{M}{w_0 \left( \frac{M}{w_0} \right) \left( 1 - \exp \left( -\beta t \right) \right)} )</td>
<td>( t^* = \frac{1}{\beta} \ln \left( \frac{M}{\overline{w}} \right) )</td>
</tr>
<tr>
<td>Von bertalanffy</td>
<td>( w(t) = \frac{M}{w_0 \left( \frac{M}{w_0} \right) \exp \left( -\beta t \right)} )</td>
<td>( t^* = \frac{1}{\beta} \ln \left( \frac{M}{\overline{w}} \right) )</td>
</tr>
</tbody>
</table>

\( (\overline{w}) = \) live weight (g) at age \( t \), \( \beta \) =relative intensity of growth rate, \( \theta \) and \( \gamma \) =models parameters, \( M \) =asymptotic body weight. In Hyperbolastic growth functions (H1 (generalizes Logistic growth function), H2 (stand-alone) and H3 (generalizes Weibull growth function)), \( (\alpha) \) =defined as a function of the other parameters \( M, \beta \) and initial observed value \( w_0 \) at time \( t_0 \). \( (t^*) \) =time at inflection. (References) =Hyperbolastic growth functions (Tabatabai et al., 2005), Richards (Hyánková et al., 2001), Von bertalanffy (Darmani-Kuhi et al., 2010), Gompertz (Sakomura et al., 2005), Logistic (Strathe et al., 2010).
served and predicted body weights.

Relative error standard deviation \( SD_{RE} = SD(\text{RE}) \), where \( SD \); standard deviation.

Mean square error \( MSE = SSE/(n-k) \), Where \( n \); the number of observations, \( SSE \); sum of square of errors, \( k \); the number of parameters.

Akaike’s information criteria \( AIC = n \ln(SSE/n) + 2k \), where \( n \); the number of observations, \( SSE \); sum of square of errors, \( k \); the number of parameters, (Akaike, 1974).

Schwarz Bayesian information criteria \( BIC = n \ln(SSE/n) + k \ln(n) \), where \( n \); the number of observations, \( SSE \); sum of square of errors, \( k \); the number of parameters, (Schwarz, 1978).

Smaller Akaike or Bayesian information criteria or \( MSE \) (Aggrey et al., 2003) values for any model indicate the model fitted to the data better than other models (Dogan et al., 2010).

In the previous study of this authorship group (Beiki et al., 2011) no sexual dimorphism was observed in three investigated lines. Similar results have been reported by Oguz et al. (1996). Therefore the growth data in all three lines were analyzed without considering the sexual dimorphism. The obtained information’s from the best function fitted to the data were analyzed by the following equation:

\[
y_{ij} = \mu + L_i + e_{ij}
\]

Where \( y_{ij} \) = an observation of the jth bird from the ith line, \( \mu \) = the population mean, \( L_i \) = the effect of ith line and \( e_{ij} \) the random error. Data were analyzed by SAS v.9.1.3 (SAS institute, 2005). In Hyperbolastic growth functions, time at inflection point was obtained using Microsoft Excel 2007 by numerical solution in Goal Seek procedure.

**Results**

The estimated parameters and goodness of fit criteria for all three lines are presented in Tables 2 and 3, respectively. The behavior of each function for HW line was illustrated in Fig. 1 as an example for all three lines. The results indicated that all growth functions were fitted to the data obtained from different lines without any difficulty by nonlinear regression.

Based on function behavior, the Gompertz and Logistic functions were not able to show a suitable fit to all three lines, while other growth functions provided an excellent fit (e.g., Fig. 1). Contrary to Rickles (1985), who stated that the fitted parameters using the Richards function are difficult to interpret biologically, the current study showed that fitting the Richards function can lead to meaningful biological indicators. The results for goodness of fit in different lines are as follow:

**The HW Line**

Determination and adjusted determination coefficients obtained from Richards, Von bertalanffy and H3 functions were the highest values. It must be noted that models with better fitting to the data will led to lower \( MSE \) values. When the functions ranked based on \( MSE \), the Richards function showed the lowest \( MSE \) value and H3 function with \( MSE \) equal to 13.50 was superior than Von bertalanffy function with \( MSE \) equal to 15.29. In term of relative error means (\( \text{RE} \)), Richards function with \( \text{RE} \) equal to 0.035, H3 with \( \text{RE} \) equal to 0.037 and Von bertalanffy with \( \text{RE} \) equal to 0.057 provided the best fit to the collected data set, respectively. The relative error standard deviation \( SD_{RE} \) was lowest for Richards, H3 and H2 equations respectively.

Based on \( AIC \) and \( BIC \) values, the results indicated that data for HW line are better described by Richards function than any other equation. Fitting the growth functions to the data led to the lowest \( AIC \) and \( BIC \) values for H3 followed by H2 and Richards functions respectively.

The overall goodness of fit statistics in HW line indicated that the Richards function has the best fitting to the data followed by H3, H2, H1, Von bertalanffy, Gompertz and Logistic functions, respectively.

**The LW Line**

The models comparison based on determination coefficients showed that Richards, H3 and Von bertalanffy function led to better fit to the data than any other functions. The functions ranking based the goodness of fit by adjusted determination coefficients \( Adj. R^2 \) were different from those of determination coefficients. The best functions from \( Adj. R^2 \) criteria point of view were Richards, Von bertalanffy and H2, respectively.

Fitting the growth functions led to the lowest \( MSE, \overline{R}, \overline{SD_{RE}}, AIC \) and \( BIC \) values for Richards, H3 and H2 functions respectively. In compare to the HW line, results for the LW line indicated that the Richards function described data better than any other functions.

All estimated statistic values in the LW line showed that Richards function provide the higher accuracy of fitness followed by H3, H2, H1, Von bertalanffy, Logistic and Gompertz functions, respectively.

**The C Line**

Based on determination coefficients, results indicated that Richards, H3 and H2 functions provide the best fit to the data, respectively. However when the best functions ranked based on adjusted determination coefficients, Richards, H2 and Von bertalanffy provided the best fit to data respectively. The lowest values for \( MSE \) and \( \overline{R} \) obtained from Richards H3 and H2. Moreover, fitting the growth functions led to the lowest \( SD_{RE}, AIC \) and \( BIC \) for Richards and H2 functions respectively.

The overall rank of the functions based on estimated statistic values in this line was the same as those reported in the LW line. In total, Richards function could be fitted best to the profile for all three lines. For this reason the Richards function parameters were used to assess the effect of divergent selection on the shape of growth curve. In Table 4 the Richards function parameters were presented for all three lines.

The \( \beta \) parameter (Table 4) is expressed the maturation rate of the curve (i.e. the relative rate at which asymptotic body weight is reached) (Knížetová, 1995). In HW line, the low value of \( \beta \) expressed lower maturation rate, compared to LW and C lines \( P<0.05 \). The age at maximum growth was occurred in the same age all three lines approximately (Table 2). Compared to the C line, the shape parameter value, \( \gamma \),
Fig. 1. Live weight and growth functions predicted BW vs. age (predicted values using 7 growth functions, namely include: H1, H2 and H3, Richards, Vonbertalanffy, Logistic, Gompertz) from HW line.
Table 2. Criteria that used to verifying of the fit of the predictive functions in divergent and control lines of Japanese quail

<table>
<thead>
<tr>
<th>Criteria</th>
<th>Function</th>
<th>Line</th>
<th>( M )</th>
<th>( \beta )</th>
<th>( \theta )</th>
<th>( \gamma )</th>
<th>( \delta )</th>
<th>( t^* )</th>
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<td>Mean ( \pm SE )</td>
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<td>( BIC )</td>
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</table>

(HW)=selected for increased 4-wk BW, (LW)=selected for decreased 4-wk BW, (C)=unselected random bred. \( MSE \)=mean square error, \( R^2 \) and \( Adj.R^2 \)=determination and adjusted determination coefficient, respectively, \( RE \)=mean relative error, \( SDRE \)=relative error standard deviation, \( AIC \)=Akaike’s information criteria, \( BIC \)=Schwarz Bayesian information criteria.

Table 3. Growth curve parameters and time to inflection point for divergent and a control lines of Japanese quail using different growth functions

<table>
<thead>
<tr>
<th>Function</th>
<th>Line</th>
<th>( M )</th>
<th>( \beta )</th>
<th>( \theta )</th>
<th>( \gamma )</th>
<th>( \delta )</th>
<th>( t^* )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean ( \pm SE )</td>
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</table>

(HW)=selected for increased 4-wk BW, (LW)=selected for decreased 4-wk BW, (C)=unselected random bred. \( M \)=asymptotic body weight, \( \beta \)=relative intensity of growth rate, \( \delta \)=models parameters, \( t^* \)=time at inflection.
increased in the LW line and decreased in the HW line \((P<0.05)\). Thus it can be concluded that divergent selection for 4-wk BW altered the shape of growth curve. The HW and LW lines have significantly higher and lower asymptotic body weight compared to the C line, respectively \((P<0.05)\). These results suggested that changes in the asymptotic weights were the output of changes in the relative intensity of growth and shape parameter during divergent selection for 4-wk BW.

Discussion

Many functions have been developed to deal with sigmoid growth (Zeide et al., 1993) and new ones are continuously being proposed. However no function could accurately describe every biological phenomenon that researchers encounter in their practice (Tabatabai et al., 2005).

The Logistic model is symmetric around the point of inflection. Wright (1926) and Winsor (1932) stated that the log equation could describe the growth functions of individual organisms which displayed an asymmetrical S-shape better than Logistic functions. The Richards function which is a log function is more flexible than other functions and it can fit asymmetric growth patterns (Zhu et al., 1988; Yin et al., 2003). However, Richards function has more parameters than the Logistic function. Its flexibility, due to its shape parameter, \(\gamma\) (dimensionless), makes it a generalized alternative to other models (e.g. monomolecular, Gompertz, Logistic, Von bertalanffy) (Thornley and France, 2007). The Gompertz and Logistic functions, have fixed growth shapes with inflection points at 37 and 50\% of the asymptote, respectively. The Gompertz function has the same number of parameters as the Logistic function and the same as Von bertalanffy function (with flexible inflection point) can fit asymmetric growth, but they are not very flexible (Yin et al., 2003).

The H1 function has one parameter more than the Logistic and Gompertz functions, but it is more flexible and can fit asymmetric growth patterns as well as increasing and decreasing growth pattern. The H2 function has the same number of parameters as H1 and can fit asymmetric curves, but it can’t fit decreasing growth patterns, so it is less flexible. The H3 function has the same flexibility as H1 function at the expense of one more parameter, similar to the Richards equations. Some of the flexibility of the H1, H2 and H3 functions were illustrated by Tabatabai et al. (2005).

Generally, statistics criteria were used in the current research confirmed that flexible growth functions such as Richards and Hyperbolic (H1, H2 and H3) as an alternative to simpler equations (with a fixed point of inflection), provided higher accuracy of fitness (smaller \(MSE, \bar{R}E, SD_{\bar{R}E}, AIC\) and \(BIC\) for quail growth data. Similar results have been reported in the meat and egg chicken strains by Darmani-Kuhi et al. (2003). These results were in disagreement with the previous theory that stated Gompertz equation was the best fit for galiforms (Tzeng and Becker, 1981; Ricklefs, 1985; Anthony et al., 1991; Akbas and Oguz, 1998; Dogan et al., 2010). Brisbin et al. (1986), Knizetová et al. (1991a, 1991b), Darmani-Kuhi et al. (2003), Balcioğlu et al. (2005), Sezer and Tarhan (2005) and Darmani-Kuhi et al. (2010) successfully fitted Richards function to the poultry growth data. Further, in unselected quail population, Dogan et al. (2010) were compared different growth functions and reported that Gompertz was the best function followed by Richards, and H3. Ahmadi and Mottaghitalab (2007), Golian and Ahmadi (2008) reported that more flexibility of H3 and Richards function may lead to more accurate prediction and better fit to the broiler growth data than H1, H2 and Gompertz-growth functions. Although the results of current study indicated that Richards growth function provided the best descriptions for Japanese quail growth data, it must be noted that this equation can sometimes lead to optimization problems and the process can fail to converge, primarily due to difficulty in estimating initial weight \(w_0\) values (Darmani-Kuhi et al., 2010). However, Darmani-Kuhi et al. (2010) reported that if \(w_0\) is known and does not need to be estimated, fixing \(w_0\) might solve non-convergence problem with the Richards function (as in present study).

Use of Richards function to assess the effect of divergent selection on the shape of growth curve indicated that selection for higher 4-wk BW has resulted in a correlated increase in asymptotic body weight, and a correlated decrease in the shape parameter of Richards function. The reverse was true when the birds were selected for lower 4-wk BW which is in agreement with previous results reported by Barbato (1992),

<table>
<thead>
<tr>
<th>Growth parameters</th>
<th>HW</th>
<th>C</th>
<th>LW</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asymptotic weight, (M) (g)</td>
<td>305.111±6.997</td>
<td>240.347±5.679</td>
<td>215.277±5.429</td>
</tr>
<tr>
<td>Shape parameter, (\gamma)</td>
<td>-0.227±0.032</td>
<td>0.005±0.026</td>
<td>0.086±0.025</td>
</tr>
<tr>
<td>Relative intensity of growth, (\beta)</td>
<td>0.064±0.003</td>
<td>0.087±0.002</td>
<td>0.087±0.002</td>
</tr>
<tr>
<td>Age at maximum growth, (t) (day)</td>
<td>17.060±0.343</td>
<td>16.793±0.278</td>
<td>17.513±0.266</td>
</tr>
</tbody>
</table>

(HW)=selected for increased 4-wk BW, (LW)=selected for decreased 4-wk BW, (C)=unselected random bred. Growth parameters with no common superscript \(a, b, c\) are significantly different \((P<0.05)\). \((\beta/d)=\ln(\phi)\), \((\phi)=w'/w\), \((w)=\)body weight, \((\gamma)=\)shape parameter, \((d)=\)day. This ratio estimates the maturation rate of the curve (i.e. the relative rate at which \(M\) is reached (Knizetová, 1995).

In conclusion, the comparison of seven growth functions in terms of the goodness of fit criteria revealed that flexible growth functions (especially Richards function) were the most appropriate functions to describe the age-related changes of body weight in different Japanese quail lines. This result is especially important when the behavior of a particular data set is not defined previously (Darmani-Kuhi *et al.*, 2003). Nevertheless, selection of the best function requires special attention to characterize the growth patterns of animals in different environmental condition (Dogan *et al.*, 2010). Therefore it should be reasonable to compare different functions to fit before to select the more accurate one.

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