Egg production is an important part of the commercial poultry industry. Use of mathematical models to accurately fit egg production curves is necessary to make economic projections for laying hens (Adams and Bell, 1980). It is also of great importance in practical poultry breeding for making predictions about egg production on an annual or any other chosen period basis, to facilitate early selection of the breeder birds (Bindya et al., 2010).

Nonlinear models are widely used to fit egg production data (Cason and Ware, 1990; Miyoshi et al., 1996; Narushin and Takma, 2003; Savegnago et al., 2011). Mathematically, egg production curves can be divided into 3 phases. The first phase is the increase in the slope from first laying to the peak, the second is the peak, and the third is the decrease in the slope from the peak until the end of egg production (Fialho and Ledur, 1997; Grossman et al., 2000).

Most of the nonlinear models presented in the literature to fit egg production can have curve parameters with a biological interpretation, which makes it possible to summarize in 3 or 4 parameters what the egg production pattern is like. However, some nonlinear models such as the Wood model (Wood, 1967) were found to be inappropriate for fitting egg production curves on the basis of hens’ chronological ages because these models were unable to abruptly change from a positive to a negative slope after an initial steep slope, and there was no inflection point in the initial egg production period, thereby leading to greater prediction errors (Congleton et al., 1981). In addition, Yang et al. (1989) reported that the parameters of the Wood model lacked reasonable biological interpretation.

Use of nonlinear models to fit the egg production of different populations makes it possible to compare egg production between them. In this manner, egg produc-
tion can be compared between selected and nonselected lines of hens to study changes to egg production curves caused by selection processes. Despite the numerous papers in the literature that have used nonlinear models for egg production curve fitting, no papers have used nonlinear models to describe changes to egg production curves caused by selection processes. The objectives of this study were to fit the weekly egg production rate of a selected and a nonselected line of a White Leghorn hen population, using nonlinear and segmented polynomial models, and to study how the selection process changed the egg-laying pattern between these 2 lines.

MATERIALS AND METHODS

Birds

The data set was from a White Leghorn population containing hens of a selected line and its respective nonselected line (control line), defined as CC and CCc, respectively. Both of these had been developed and were being maintained within a selection breeding program by Embrapa Swine and Poultry, Concórdia, Santa Catarina, Brazil. The CC is a female line of White Leghorn that was initially selected in 1989, mainly for egg production and quality of eggs. Both the CC and the CCc line originated from a common founder population. The nonselected line (CCc) was established from the CC line, in accordance with the methodology proposed by Gowé et al. (1959), by randomly mating one male from each sire family with an unrelated female from each dam family. The nonselected line was used as a reference population to compare the effects of selection for egg production in the CC line (Schmidt and Figueiredo, 2005). In this study, the seventh generation of the hens was used. Further details about the CC line can be found in Schmidt and Figueiredo (2005).

All the birds were kept in single cages and they received food and water ad libitum. The metabolizable energy (ME) and CP concentrations varied depending on the birds’ phase of life. A commercial diet containing 2,850 kcal of ME/kg and 20% CP (1 to 6 wk of age), 2,700 kcal of ME/kg and 14% CP (7 to 16 wk of age), and 2,800 kcal of ME/kg and 15% CP (17 to 70 wk of age) was provided.

The weekly egg production records over a 54-wk egg-laying period (from 17 to 70 wk of age) relating to 1,693 hens from the selected line and 282 hens from the nonselected line were used for curve fitting. The birds included were the ones that survived until at least the 70th week of age. The egg production data were gathered on 5 d per week. According to Wheat and Lush (1961), this measurement has a correlation of 0.99 with weekly egg production. The individual egg production was expressed as the weekly egg production rate, where weekly egg production rates of zero, 0.2, 0.4, 0.6, 0.8, and 1 corresponded to the production of zero, 1, 2, 3, 4, and 5 eggs per week for each hen, respectively.

Nonlinear Models

The weekly egg production rate for each hen was used to fit the mean population curve for CC and for CCc by means of the iterative Gauss-Newton least-squares method, as described by Hartley (1961), with a nonlinear regression procedure (NLIN) within the SAS 9.2 software (SAS Institute Inc., 2008). The nonlinear models applied to fit the egg production data were

1. Logistic (Nelder, 1961):
   \[ y_t = a \left[ 1 + e^{-\left( t - c \right)} \right]^{-d} e^{-xt}, \]
   where \( y_t \) = egg production rate at \( t \) weeks of laying; \( a \) = asymptotic value of egg production at the peak of egg-laying; \( c \) = constant; \( d \) = mean egg production week in which egg production reaches its peak; \( x \) = rate of production decrease after the peak (eggs/hen-day decrease per week).

2. Compartmental I (McMillan et al., 1970a,b):
   \[ y_t = a \left[ 1 - e^{-\left( t - d \right)} \right] e^{-xt}, \]
   where \( y_t \) = egg production rate at \( t \) weeks of laying; \( a \) = asymptotic value of egg production at the peak of egg-laying; \( c \) = weekly rate of increase in egg production; \( d \) = mean initial week of egg-laying; \( x \) = rate of production decrease after the peak (eggs/hen-day decrease per week).

   \[ y_t = ab \left[ -ct + dt \right]^{0.5}, \]
   where \( y_t \) = egg production rate at \( t \) weeks of laying; \( a \) = asymptotic value of egg production at the peak of egg-laying; \( b \), \( c \), and \( d \) = constants.

   \[ y_t = a \left( e^{-xt} - e^{-bxt} \right), \]
   where \( y_t \) = egg production rate at \( t \) weeks of laying; \( a \) = asymptotic value of egg production at the peak of egg-laying; \( b \) = instantaneous rate of weekly increase in egg-laying; \( x \) = rate of production decrease after the peak (eggs/hen-day decrease per week).

5. Yang model (Yang et al., 1989):
   \[ y_t = \frac{ae^{-xt}}{1 + e^{-\left( t - d \right)}}, \]
   where \( y_t \) = egg production rate at \( t \) weeks of laying; \( a \) = asymptotic value of egg production at
the peak of egg-laying; $c$ = reciprocal indicator of the variation in week of production of first egg; $d$ = mean week of egg production at sexual maturity; $x$ = rate of production decrease after the peak (eggs/hen-day decrease per week).

6. Segmented polynomial model (Fialho and Ledur, 1997):

$$y_t = \begin{cases} 
0 & \text{for } t < t_p - t_{ip}, \\
Pe - 3 \cdot Pe \cdot \left( \frac{t_p - t}{t_{ip}} \right) + 2 \cdot Pe \cdot \left( \frac{t_p - t}{t_{ip}} \right)^3 & \text{for } t_p - t_{ip} \leq t < t_p, \\
Pe - s(t - t_p) & \text{for } t_p \leq t,
\end{cases}$$

where $y_t$ = egg production rate at $t$ weeks of laying; $Pe$ = peak production level (%egg/hen-day); $t_p$ = age of hens, in weeks, at the peak; $s$ = rate of production decrease after the peak (eggs/hen-day decrease per week); $t_{ip}$ = time interval between start and peak of production.

7. Persistency model (Grossman et al., 2000):

$$y_t = \frac{Pe}{t_p} \cdot t - 0.3 \cdot \frac{Pe}{t_p} \cdot \ln \left( \frac{e^{t_p/0.3} + e^{t_p/0.3}}{1 + e^{t_p/0.3}} \right) + 0.3 \cdot s \cdot \ln \left( \frac{e^{t/0.3} + e^{(t_p + P)/0.3}}{1 + e^{(t_p + P)/0.3}} \right),$$

where $y_t$ = egg production rate at $t$ weeks of laying; $Pe$ = peak production level (%egg/hen-day); $t_p$ = age of hens, in weeks, at the peak; $s$ = rate of production decrease after the peak (eggs/hen-day decrease per week); $P$ = number of weeks during which a constant egg production level is maintained after the peak.

Higher values for parameter $x$ and parameter $s$ indicate shorter persistence of egg laying and vice versa. The Logistic model (Nelder, 1961) used in this study was a reparametrization of the original model described by Brown et al. (1976). The term $e^{-x \cdot t}$, where $e$ is the neperian number, $x$ is the parameter associated with the rate of weekly decrease in production, and $t$ is the week of egg laying, was suggested by Brody et al. (1923, 1924). It was added to the Logistic model by Cason and Ware (1990) to describe the rate of weekly decrease of egg production after the peak egg production, because this model was first developed to fit growth data, which does not have rate of decrease after the asymptotic value, as occurs with egg laying.

Statistical Criteria to Evaluate the Fitted Curves

The goodness of fit of each nonlinear mode was evaluated by means of Akaike’s information criterion (AIC), mean square error (MSE), $R^2$, quantitative error measurements (model error and mean model error), and graphical analysis.

**AIC.** Akaike’s information criterion (Akaike, 1974), that can be approximated to the least mean square method (Motulsky and Christopoulos, 2003), is calculated as follows:

$$\text{AIC} = n \cdot \ln \left( \frac{SS_{Error}}{n} \right) + 2 \cdot k,$$

where $n$ is the number of data points, $k$ is the number of parameters in the model, and $SS_{Error}$ is the sum of the squared error.

**MSE.** The MSE is calculated as follows:

$$\text{MSE} = \frac{\sum_{i=1}^{n} \sum_{t=1}^{m} (y_{it} - \hat{y}_{it})^2}{nm - p},$$

where $y_{it}$ and $\hat{y}_{it}$ are the observed and predicted weekly egg production rates, respectively, of hen $i$ at week $t$ of laying, $n$ is the total number of hens, $m$ is the total number of weeks of egg laying evaluated, $nm$ is the total number of observed values in the data set, and $p$ is the number of model parameters.

**Coefficient of Determination ($R^2$).** The $R^2$ is calculated as follows:

$$R^2 = \left( \frac{SS_{model}}{SS_{total}} \right),$$

where $SS_{model}$ is the sum of the squares of the model and $SS_{total}$ is the total sum of the squares.

**Model Error and Mean Model Error.** The fitted curve may present a good fit, as indicated by statistical measurements; that is, small values of MSE and high values of $R^2$. However, these indicators by themselves do not indicate the trend of the fitted curve. The model error (MER) at $t$ weeks of egg laying is defined as

$$\text{MER}_t = \frac{\hat{y}_t - \overline{y}_t}{\hat{y}_t},$$

where $\hat{y}_t$ is the average predicted egg production rate at week $t$ of laying and $\overline{y}_t$ is the average real egg production rate at week $t$ of laying.

The MER is expressed as the deviation between the average predicted egg production rate minus the average observed egg production rate on the basis of the average observed egg production rate. When $\hat{y}_t$ (predicted) and $\overline{y}_t$ (observed) are equal, the deviation of the adjusted egg production rate at week $t$ is zero. When $\hat{y}_t$ (predicted) is higher than $\overline{y}_t$ (observed), the prediction of egg production at $t$ is underestimated (positive model error). When $\hat{y}_t$ (predicted) is smaller than $\overline{y}_t$ (observed), the prediction of egg production at $t$ is under-
estimated (negative model error). The mean model error (MME) is obtained as the mean of all the model errors (MER).

Graphical Evaluation of Curve Fitting

The fitted curve may present a good fit, as indicated by statistical measurements, but these indicators by themselves do not indicate the trend of the fitted curve. Plots of real and fitted data made it possible to evaluate the flexibility of the model, that is, its capacity to fit at a place where the curve changed slope, and the deviations of the data.

Comparison of Nonlinear Trends Between the Selected and Nonselected Lines of Hens

The test described in Motulsky and Christopoulos (2003), SAS Institute Inc. (2008), and Schabenberger (2009) was used to compare nested nonlinear models. This test ascertained whether there was any difference in the curves fitted for egg production between the CC and CCc hen lines.

The null hypothesis was that there would be no significant difference ($P > 0.05$) between the effects of the selected and nonselected hens on the egg production rate and, consequently, there would be no differences between the curve parameters fitted for the selected and nonselected lines. Thus, if the null hypothesis were true, there would only be one curve with the same parameters, called the reduced model, to fit the egg production rate of both the selected and the nonselected hens, and the differences between the sample means would be due to chance. The alternative hypothesis was that there would be a significant difference ($P < 0.05$) between the effects of the selected and nonselected hens on the egg production rate that would imply the existence of 2 different sets of parameter estimates, called full model: one for each line for curve fitting the weekly egg production rate. This test was carried out using the SAS 9.2 software (SAS Institute Inc., 2008). The ANOVA scheme for this test is shown in Table 1.

The idea of the test was that if the reduced model (null hypothesis) was correct, the relative increase in the sum of the squares would be expected to be greater than the relative increase in degrees of freedom.

An alternative and more common presentation of the ratio ($F$) is

$$ F = \frac{SS_{\text{reduced}} - SS_{\text{full}}}{DF_{\text{reduced}} - DF_{\text{full}}}, $$

and the probability of the $F$-test is given by

$$ \text{Prob} > F = 1 - \text{Prob}_F(DF_{\text{reduced}} - DF_{\text{full}}, DF_{\text{full}}). $$

To calculate the probability of the $F$-test value, the SAS PROBF function (SAS Institute Inc., 2008) was used, which returns the probability of an $F$ distribution with $(DF_{\text{reduced}} - DF_{\text{full}})$ degrees of freedom to the numerator and $DF_{\text{full}}$ degrees of freedom to the denominator.

Genetic Gain

The expected differences in egg production rate for each week between the selected and nonselected lines would be due to the hen selection process for improving egg production. This was defined as the genetic gain, calculated as

$$ \Delta G_t = MS_t - MC_t, $$

where $\Delta G$ is the genetic gain in egg production rate at week $t$ of egg laying, and $MS$ and $MC$ are the observed average egg production rates at $t$ for the selected and nonselected lines, respectively.

A $t$-test was performed to ascertain whether there were any significant differences ($P < 0.05$) in the egg production rate between the selected and nonselected hens in each week of egg production. This test was calculated by means of the TTEST procedure of the SAS 9.2 software (SAS Institute Inc., 2008).

RESULTS AND DISCUSSION

Description of Egg Production, Curve Fitting, and Statistical Criteria for Model Selection

The descriptive analysis on egg production for the selected and nonselected lines is shown in Table 2. The
Table 2. Descriptive analysis on egg production for the selected and nonselected lines

<table>
<thead>
<tr>
<th>Line</th>
<th>Number of birds</th>
<th>Number of data lines</th>
<th>Mean of total egg production rate</th>
<th>SD of total egg production rate</th>
<th>CV (%) of total egg production rate</th>
<th>Weeks of egg production at peak(^2)</th>
<th>Age of hens when egg production reaches the peak(^3)</th>
<th>Egg production rate at peak</th>
<th>Age at first egg (days of age)</th>
<th>Week of egg production at first egg(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Selected hens</td>
<td>1,693</td>
<td>84,726</td>
<td>0.769 (0.003)</td>
<td>0.331</td>
<td>41.110</td>
<td>7 to 10</td>
<td>23 to 26</td>
<td>0.860 (0.023)</td>
<td>138.281 (0.216)</td>
<td>1.133 (0.002)</td>
</tr>
<tr>
<td>Nonselected hens</td>
<td>282</td>
<td>13,770</td>
<td>0.691 (0.009)</td>
<td>0.316</td>
<td>47.927</td>
<td>6 to 10</td>
<td>22 to 26</td>
<td>0.794 (0.034)</td>
<td>133.884 (0.550)</td>
<td>1.097 (0.004)</td>
</tr>
</tbody>
</table>

1Values in brackets are the SEM.
2Week of egg production basis (from 1st to 54th week of egg production).
3Week of age basis (from 17th to 70th week of age).

Table 3. Statistical criteria for evaluating the curve fitting of the models for the weekly egg production rate for the selected and nonselected lines

<table>
<thead>
<tr>
<th>Model</th>
<th>Selected line of hens</th>
<th>Nonselected line of hens</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>AIC</td>
<td>MSE</td>
</tr>
<tr>
<td>1. Nelder (1961)</td>
<td>−225,283.68</td>
<td>0.0700</td>
</tr>
<tr>
<td>2. McMillan et al. (1970a,b)</td>
<td>−224,548.73</td>
<td>0.0706</td>
</tr>
<tr>
<td>3. McNally (1971)</td>
<td>−223,588.06</td>
<td>0.0714</td>
</tr>
<tr>
<td>4. McMillan (1981)</td>
<td>−223,333.72</td>
<td>0.0725</td>
</tr>
<tr>
<td>5. Yang et al. (1989)</td>
<td>−225,086.80</td>
<td>0.0702</td>
</tr>
<tr>
<td>6. Fialho and Ledur (1997)</td>
<td>−225,106.17</td>
<td>0.0702</td>
</tr>
<tr>
<td>7. Grossman et al. (2000)</td>
<td>−224,580.60</td>
<td>0.0706</td>
</tr>
</tbody>
</table>

1AIC = Akaike’s information criterion; MSE = mean square error; \(R^2\) = coefficient of determination; MME = mean model error; Min = minimum mean model error; Max = maximum mean model error.
2Number inside parentheses is the week in which the minimum or maximum MME occurred.
average weekly egg production rate for the selected and nonselected lines over the 54-wk period of egg production is shown in Figure 1. The selected line presented higher total egg production rate, sooner peak of egg production, higher egg production at the peak, and later age at first egg, compared with the nonselected line. Although the nonselected line had fewer birds than the selected line, the standard errors of the mean were low, thus indicating accurate averages.

According to AIC, R², MSE, and MME the Logistic model was the one that best fitted the egg production curves for both the selected and the nonselected lines (Table 3) and the Compartmental II model was the worst, in comparison with the others. However, the differences between the values for the goodness of fit criteria were generally so small that, in practice, the models had the same curve fitting. The MME values indicated that all the models had residual errors close to zero and that the minimum and maximum deviations along the egg production cycle were almost the same for all the nonlinear models.

On the other hand, the graphical analysis showed that Compartmental I, McNally, and Compartmental II models (Figure 2) did not present enough flexibility at the point of inflection to properly fit the egg production rate at the peak. This is the reason why the estimates for parameter $a$ of models Compartmental I and Compartmental II surpassed the maximum egg production, which was 1 (100%) for the selected line (Table 4). The McNally model had the worst estimate for parameter $a$, for both lines, in comparison with the estimates for the other models. Moreover, this model, which is a modification of the Wood model, did not have a good fit after the egg-laying peak: the fitted curve of this model showed further increase after the peak, as the hens got older, which did not occur in the observed data (Figure 2). This result was also reported by Adams and Bell (1980). Despite the values of statistical criteria being similar for all models (Table 3), when the flexibility of inflection point (Figure 2) and asymptotic egg production—parameter $a$—(Table 4) were taken into account in model evaluation, the Compartmental I, McNally, and Compartmental II models were not appropriate to fit the egg production curve, for both lines, in comparison with the other models. The curve fitting of Logistic, Yang, Segmented Polynomial, and Persistency models are shown in Figure 3.

Persistency model (Grossman et al., 2000) presented the estimates for the peak parameter (Peak) that were closest to the observed egg production at the peak (Table 2) for both lines, in comparison with the estimates for the asymptotic value provided by the other models. It was found that the fitted curves for weekly egg production rate for the selected line presented slightly lower estimates for the rate of production decrease after the peak (parameter $x$ of Logistic, Compartmental I, McNally, Compartmental II, and Yang models and parameter $s$ of Segmented Polynomial and Persistency models), in comparison with the nonselected line, thus indicating that there was little improvement in persistence of egg production after the laying peak, especially between the 11th and 27th weeks of egg production in the selected line (Figure 1). The Persistency model had an interesting parameter $P$, which estimated the number of weeks during which the level of constant egg production was maintained after the peak. For the selected line, it was estimated that egg production persisted for 19 wk after the peak, versus 6 wk for the nonselected line. This provided an indication that the selection process was efficient in improving the persistence of egg laying.

The parameter $d$ of Logistic model and parameter $t_p$ of Segmented Polynomial and Persistency models pro-
Figure 2. Fitted curves for weekly egg production rate using Compartmental I (a), McNally (b), and Compartmental II (c) models for the selected and nonselected lines of hens. ● = observed egg production rate for the selected line; — fitted curve for egg production rate for the selected line; ▲ = observed egg production rate for the nonselected line; —— fitted curve for egg production rate for the nonselected line.
vided estimates for the week of egg production in which the hens reach their peak. Logistic model estimated the peak production to be one week ahead of the estimates obtained from Segmented Polynomial and Persistency (Table 4). These estimates were close to the observed week of egg production in which the hens reached their peak (Table 2).

The estimates for parameter \( c \) of Yang model indicated that the average week of production in which the hens laid their first egg were close to what was observed, which was around the first week of production (the hens’ 17th week of age). The parameter \( d \) of Yang model indicated that on average, the age of sexual maturity was reached around 3 wk after the birds laid their first egg. According to Morris (1966), cited by Koops and Grossman (1992), sexual maturity occurs when the hens are able to reproduce (age at sexual maturity), but this is not the same as the age at which the hens are able to produce (age at first egg). It can therefore be expected that the age at first egg will be earlier than the age at sexual maturity, and this was observed as differences between the estimates for parameters \( c \) and \( d \) in Yang model, thus indicating that the age at sexual maturity (parameter \( d \)) occurred on average 3 wk after the age at first egg (parameter \( c \)). However, age at first egg usually is an indication of age at sexual maturity. Therefore, this data set did not have any records of the hens’ real age of sexual maturity. Yang model provided an indication of when the hens reached the age of sexual maturity, based on egg production and age at first egg. Segmented Polynomial model provided the length of time from the beginning of egg production to the peak (\( \text{tip} \)) and the parameter \( tp \), which was the week of peak egg production. The difference between \( tp \) and \( \text{tip} \) can provide an idea of the beginning of egg production (Table 4).

<table>
<thead>
<tr>
<th>Model</th>
<th>Selected line of hens</th>
<th>Nonselected line of hens</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parameter</td>
<td>Estimate</td>
<td>SE</td>
</tr>
<tr>
<td>1. Nelder (1961)</td>
<td>( a )</td>
<td>0.9691</td>
</tr>
<tr>
<td></td>
<td>( c )</td>
<td>0.6723</td>
</tr>
<tr>
<td></td>
<td>( d )</td>
<td>9.6769</td>
</tr>
<tr>
<td></td>
<td>( x )</td>
<td>0.0056</td>
</tr>
<tr>
<td>2. McMillan et al. (1970a,b)</td>
<td>( a )</td>
<td>1.3332</td>
</tr>
<tr>
<td></td>
<td>( c )</td>
<td>0.2753</td>
</tr>
<tr>
<td></td>
<td>( d )</td>
<td>1.2653</td>
</tr>
<tr>
<td></td>
<td>( x )</td>
<td>0.0072</td>
</tr>
<tr>
<td>3. McNally (1971)</td>
<td>( a )</td>
<td>0.5592</td>
</tr>
<tr>
<td></td>
<td>( b )</td>
<td>2.5984</td>
</tr>
<tr>
<td></td>
<td>( c )</td>
<td>-0.0891</td>
</tr>
<tr>
<td></td>
<td>( d )</td>
<td>-2.0271</td>
</tr>
<tr>
<td>4. McMillan (1981)</td>
<td>( a )</td>
<td>1.1151</td>
</tr>
<tr>
<td></td>
<td>( b )</td>
<td>0.1828</td>
</tr>
<tr>
<td></td>
<td>( x )</td>
<td>0.0093</td>
</tr>
<tr>
<td>5. Yang et al. (1989)</td>
<td>( a )</td>
<td>0.6586</td>
</tr>
<tr>
<td></td>
<td>( b )</td>
<td>0.3593</td>
</tr>
<tr>
<td></td>
<td>( d )</td>
<td>3.9453</td>
</tr>
<tr>
<td></td>
<td>( x )</td>
<td>0.0053</td>
</tr>
<tr>
<td>6. Fialho and Ledur (1997)</td>
<td>( \text{Peak} )</td>
<td>0.9156</td>
</tr>
<tr>
<td></td>
<td>( \text{tp} )</td>
<td>7.4254</td>
</tr>
<tr>
<td></td>
<td>( \text{tip} )</td>
<td>7.0326</td>
</tr>
<tr>
<td></td>
<td>( s )</td>
<td>0.0043</td>
</tr>
<tr>
<td>7. Grossman et al. (2000)</td>
<td>( \text{Peak} )</td>
<td>0.8733</td>
</tr>
<tr>
<td></td>
<td>( \text{tp} )</td>
<td>7.3976</td>
</tr>
<tr>
<td></td>
<td>( \text{tip} )</td>
<td>-0.0068</td>
</tr>
<tr>
<td></td>
<td>( P )</td>
<td>19.2339</td>
</tr>
</tbody>
</table>

Table 5. Comparison of nonlinear estimates for curve parameters between the selected and nonselected lines of hens, using the \( F \)-test for nested models\(^1\)

<table>
<thead>
<tr>
<th>Model</th>
<th>( \text{SS}_{\text{reduced}} )</th>
<th>( \text{DF}_{\text{reduced}} )</th>
<th>( \text{SS}_{\text{full}} )</th>
<th>( \text{DF}_{\text{full}} )</th>
<th>( F )-test</th>
<th>( P )-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Nelder (1961)</td>
<td>7,269.2</td>
<td>98,492</td>
<td>7,172.2</td>
<td>98,488</td>
<td>333.01</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>2. McMillan et al. (1970a,b)</td>
<td>7,323.4</td>
<td>98,492</td>
<td>7,227.8</td>
<td>98,488</td>
<td>325.82</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>3. McNally (1971)</td>
<td>7,404.2</td>
<td>98,492</td>
<td>7,308.3</td>
<td>98,488</td>
<td>322.95</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>5. Yang et al. (1989)</td>
<td>7,285.5</td>
<td>98,492</td>
<td>7,188.4</td>
<td>98,488</td>
<td>327.76</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>6. Fialho and Ledur (1997)</td>
<td>7,284.0</td>
<td>98,492</td>
<td>7,188.4</td>
<td>98,488</td>
<td>325.55</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>7. Grossman et al. (2000)</td>
<td>7,325.0</td>
<td>98,492</td>
<td>7,222.4</td>
<td>98,488</td>
<td>420.54</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

\(^1\) \( \text{SS}_{\text{reduced}} \) = sum of squares of the Reduced Model; \( \text{SS}_{\text{full}} \) = sum of squares of the Full Model; \( \text{DF}_{\text{reduced}} \) = degrees of freedom of the Reduced Model; \( \text{DF}_{\text{full}} \) = degrees of freedom of the Full Model.
Figure 3. Fitted curves for weekly egg production rate using Logistic (a), Yang (b), Segmented Polynomial (c), and Persistency (d) models for the selected and nonselected lines of hens. ● = observed egg production rate for the selected line; —— fitted curve for egg production rate for the selected line; ▲ = observed egg production rate for the nonselected line; __ __ fitted curve for egg production rate for the nonselected line.
Comparison of Nonlinear Trends Between the Selected and Nonselected Lines of Hens

There were highly significant differences according to the $F$-test ($P < 0.0001$), between the estimates for the curve parameters fitted in the Full and Reduced models. This indicated that the effect of selection over 7 generations had changed the shape of the egg production curves between the 2 lines (Table 5), especially in relation to the parameter $a$.

Genetic Gain

In this population, the differences in egg production in each week between the 2 lines can be explained by the genetic gain obtained through the selection process (Figure 4). Genetic gain occurred when the average weekly egg production rate was higher in the selected line than in the nonselected line in this population. Genetic gain was observed in this population from the 5th to the 54th week of egg production, thus indicating that the selection had not been effective in improving egg production during the first weeks of the production cycle. The $t$-test was significant for almost all weeks of egg production, except for the 1st, 5th, and 10th weeks of egg production in this population.

Evaluation of the models using statistical criteria (Table 3), graphical criteria (Figures 2 and 3), and biological interpretation of the parameters (Table 4) showed that Logistic, Yang, Segmented Polynomial, and Persistency models were appropriate for egg production curve fitting for the selected and nonselected lines in this population. These models presented parameter estimates with biological interpretations of importance for the poultry industry and for research, like peak egg production, persistence of egg laying after the peak, rate of decrease in egg production after the peak, the week in which egg production reached its peak, the length of time from the start to the peak of egg production, age at first egg, and age at sexual maturity (Table 4). The selection of hens for egg production was efficient in this population for modifying the egg production curve (Table 5), thus resulting in genetic gains after the fourth week of laying consisting of improved peak egg production and persistence of egg production in this population (Figure 4).

ACKNOWLEDGMENTS

Financial support was provided by the Brazilian Agricultural Research Corporation (Embrapa; Empresa Brasileira de Pesquisa Agropecuária). R. P. Savegnago and S. L. Caetano were granted scholarships by the São Paulo Research Foundation (FAPESP; Fundação de Amparo à Pesquisa do Estado de São Paulo). V. A. R. Cruz and S. B. Ramos received scholarships from the Coordination Office for Advancement of University-level Personnel (CAPES; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) in conjunction with the Postgraduate Program on Genetics and Animal Breeding, Faculdade de Ciências Agrárias e Veterinárias, Universidade Estadual Paulista (FCAV - UNESP). D. P. Munari held a productivity research fellowship from the National Council for Scientific and Technological Development (CNPq; Conselho Nacional de Desenvolvimento Científico e Tecnológico).

REFERENCES
