Investigation of egg production curve in ostrich using nonlinear functions

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ABSTRACT In most countries, ostrich farming is considered a developing branch of the efficient poultry industry. The profitability of ostrich farm requires specific consideration of productions features such as the female fertility, egg production, hatchability, and growth performance. Hence, this study aimed to fit non-linear functions to describe the ostrich egg production pattern to achieve the most appropriate and recommendable mathematical function for future studies. For this purpose, 14,507 daily records of 184 female ostriches in 5 production seasons (periods) during 2016 to 2021 were used. Five nonlinear functions including Incomplete gamma (Wood function), Corrected gamma (McNally), nonlinear Logistic (Yang), Logistic (Nelder), and Lokhorst were fitted for modeling the egg

production curve in ostrich. The goodness of fit criteria's including Mean Square Error (**MSE**), Likelihood Ratio Test (**LRT**), Akaike Information Criterion (**AIC**), and Bayesian Information Criterion (**BIC**) were used to evaluate and selection of the best function. The results indicated that the Wood and the McNally functions with a slight difference in all fitting criteria were the best-fitted functions and the Yang function with the highest values of MSE, LRT, AIC, BIC, were the most inappropriate function to describe the ostrich egg production curve. The McNally and the Wood can be recommended as appropriate functions to describe egg production during 5 production seasons in the studied ostrich flock.

Key words: egg production phase, mathematical modeling, nonlinear functions, Struthio camelus

2023 Poultry Science 102:102333 https://doi.org/10.1016/j.psj.2022.102333

INTRODUCTION

Egg production is an important segment of the commercial poultry industry, which is one of the important complex quantitative traits during the laying period in any kind of poultry. Variation in egg production is affected by genetic and environmental differences. The number of eggs in each period can be used to evaluate production performance (Dzoma, egg 2009;Bindya et al., 2010; Ghorbani et al., 2013). The poultry industry is considered to have highlighted role in producing meat and eggs as sustainable animal protein source (Abbas et al., 2018a). Ostrich farming, is a developing part of the poultry industry and serves as an alternative protein producing source supporting human

Accepted October 18, 2022.

health (Al-Khalifa and Al-Naser, 2014; Abbas et al., 2017; Brassó et al., 2021). Even though, paying attention to the ostrich breeding industry in developing countries can provide part of the future food needs of these countries (Abbas et al., 2018b). In contrast to other poultry species, ostrich eggs are usually not consumed as human food, whereas egg production is typically important for chicken production. Therefore, ostrich breeding requires intensive and precise management, so the losses due to the low egg fertility can be compensated by increasing the number of eggs laid (Cooper, 2001).

The egg production curve indicates the relationship between the number of eggs and the time/period of the production (Rahimzadeh et al., 2017; Grossman et al., 2000). The application of mathematical functions is the most valuable approach for evaluating egg production during the laying cycle because through that the production period the production curve can be divided into meaningful biological components (Wolc et al., 2020). Additionally, production curve modeling is a useful approach for monitoring flock performance concerning early detection of any farm-related problems

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Received June 10, 2022.

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(Morales et al., 2016; Ramírez-Morales et al., 2017), quantifying persistency of production (Grossman et al., 2000; Grossman and Koops, 2001; Savegnago et al., 2012), predicting future records and trends (Adams and Bell, 1980; Brand et al., 2012; Faraji-Arough et al., 2019; Jahan et al., 2020), evaluating progress through the selection process (Savegnago et al., 2012), and also estimating deviation from the expected production curve (Alvarez and Hocking, 2007; Johnston and Gous, 2007; Faraji-Arough et al., 2018). Egg production curves represent stages. The first stage is the ascending in the curve from the first egg to the peak of the egg production, the second is the production peak, and the third stage is persistence the descent of the curve from the peak to the end of egg production (Grossman et al., 2000). Researches are mainly focused on whole egg production period (long-term egg production) (Narine et al., 2013), or only a part of egg production period (short-term egg production) (Rahimzadeh et al., 2017).

A growing body of literature fits production curves using a wide range of nonlinear functions. Each nonlinear function has 3 or more parameters, having the potential to summarize or derivatives of production-related traits (Ramos et al., 2013; Ware and Power, 2017; Küçüktopcu and Cemek, 2021; Seifi Moroudi et al., 2021). According to a study conducted for molding egg production in laying hens, the logistic-curvilinear, the compartmental, the Lokhorst, and the Adams-Bell functions were ordered respectively to have the highest goodness of fit (Narushin and Takma, 2003). Furthermore, an investigation of Gamma, McNally, and Adams-Bell functions to monitor long-term egg production in Japanese quail reported that the models performed adequately but the Adams-Bell was slightly better fitted for the percentage of egg production (Narine et al., 2013). Another study that compared the distributed-Delay function vs. the Adams-Bell and Lokhorst functions, recommended the Delay and the Lokhorst as the most efficient functions for predicting the egg production curve in different chicken strains (Galeano-Vasco et al., 2013). Two distinct experiments studying egg production modeling suggested that the Compartmental function was applicable to predict egg production traits in broiler breeders and laying hens (Safari-Aligiarloo et al., 2018; Wolc et al., 2020). Additionally, the results of the assessment of eight mathematical models indicated that the Rational, the Modified Compartmental, the Sinusoidal, and the Polynomial functions can be appropriately applied for modeling the egg production curves in white leghorn laying hens based on different model selection criteria (Sharifi et al., 2022).

Limited information is available about factors affecting the economic traits such as egg laying performance in ostrich production. Moreover, compared to other commercial birds, few studies have been conducted on egg production modeling in ostriches. Therefore, this study aimed to investigate nonlinear functions for modeling ostrich egg production and evaluate the goodness of fit of models to determine the best predictive function.

MATERIALS AND METHODS

Data

The field experiment of this study started in the winter of 2015 at the ostrich breeding farm of the South Khorasan Prisoners' Cooperative Foundation and was continued for 5 production periods until the end of the production season of 2020. In this study, families have consisted of 1 male (rooster) and 2 females (hens) per pen, with each pen including 3 birds. The number of 3 pens was different in each year. They were 19 in the first year of production (2015), while they increased during the subsequent production periods. During the production season, the eggs were collected daily from the nests. The required information including hen ID, pen number, date of laying, and weight at laying were recorded on the surface of the eggs. Each bird's onset of egg laying is variable, so the best way to manage the data is to consider the average number of eggs per month. Therefore, the average number of produced eggs was evaluated across 11 consecutive months during 5 yr. The egg-laying period starts from January of each year and continues until November of the following year. In fact, each production period included 11 mo and the birds naturally or forcibly pause laying eggs during December. However, in the first month, some birds lay few eggs, while in the first month of the next production period (next year), they lay no eggs. Therefore, few eggs were laid in December, which were included in the egg production in January. Consequently, January was considered as the first month of egg production. At the beginning of the formation of the base population, all birds were of the same age. Although in the following yr, new birds entered the population. Therefore, egg-laving ostriches were not of the same age in the periods of 2 to 5 vr, except for the first period of production. In fact, some birds had records in 5 consecutive production periods and some less.

In this study, for egg-laying ostriches, the number of eggs produced per month was preferentially considered because the egg-laying period and clutch period in this species are fundamentally different from other egg-laying birds. This difference is physiologically related to the size of the egg and the laying time of the bird. Unlike other species of egg-laying birds, ostriches are raised outdoors and their production is clearly influenced by the environment. Additionally, the egg production cycle in the ostrich is 48 h, compared to 24 h or less in most other laying birds. Also, the duration of the clutch in ostriches can vary from 2 d to more than 2 wk. Therefore, the ostrich may not have eggs for 2 consecutive weeks, which has an important effect on the pattern of the egg production curve. Therefore, it is not possible to simply consider the production of birds on a weekly or even biweekly basis.

At the end of the production periods, the composition of the diet was changed and birds were fed in limited times to induce a forced egg pause, and a one-month rest period was experienced. Especially, the ration changed

 Table 1. The descriptive statistics of the egg production in the studied ostrich population.

Month	Number of hens	$\mathrm{Mean}^1\pm\mathrm{SD}$	CV	Minimum	Maximum
1	184	8.97 ± 4.37	48.7	1	16
2	177	9.83 ± 4.14	42.1	1	14
3	178	9.11 ± 4.12	45.2	1	12
4	170	8.60 ± 4.14	48.1	1	16
5	165	7.83 ± 4.22	53.8	1	16
6	145	7.64 ± 4.06	83.1	1	16
7	125	6.71 ± 4.16	61.9	1	15
8	74	6.31 ± 4.41	69.8	1	15
9	36	5.11 ± 3.04	49.4	1	15
10	13	5.38 ± 3.88	72.1	1	15
11	6	5.00 ± 4.33	86.6	1	11

 $^1{\rm The}$ mean in Table 1 refers to eggs/hen/month. CV, coefficient of variation. SD, standard deviation.

from October to December (the 2 mo leading to the production stop). However, some birds continued to breed despite the diet change, which could be due to the bird's genetic potential. There was natural mortality in both sexes and also some birds were culled at the end of the production period due to poor performance. Due to the fact that the birds got used to living together, the change of the members of the birds did not happen in all 3 pens. A new bird was introduced to the pen only if a family member dies/culled. The descriptive statistics of the egg production used in this study are presented in Table 1.

Modeling Egg Production

In this study, 5 nonlinear functions including incomplete gamma (Wood), corrected Gamma (McNally), nonlinear Logistic (Yang), Logistic (Nelder), and Lokhorst functions were compared to determine the best function for describing the egg production curve in ostrich.

Incomplete Gamma Function Incomplete gamma or the Wood function was initially proposed to study the lactation curve of dairy cattle (Wood, 1967). The general form of this function is as Equation 1:

$$Y_t = a(t^b)(e^{-ct}), \qquad (1)$$

where Y_t is considered as egg production at time t, e is the base of natural logarithms, and a, b and c are the parameters corresponding to the initial production rate, the slope of increasing phase, and the slope of decreasing phase of the production curve, respectively.

Corrected Gamma Function Corrected gamma or the McNally function is a modified form of the Wood function that has been proposed to describe the egg production curve in poultry. The general form of the McNally function (McNally, 1971), is as Equation 2:

$$Y_t = at^b e^{(-ct+dt1/2)},$$
(2)

where Y_t is egg production at time t, e is the base of natural logarithms, and the a, b, and c parameters are showing the initial production rate, the slope of increasing phase, the slope of decreasing phase of the production curve respectively, and the parameter d represents the additional period which is proportional to the square root of time.

Nonlinear Logistic Function A nonlinear Logistic or the Yang function was presented accounting for any kinds of nonlinear differences such as differences in the age of sexual maturity in the incremental slope of the egg production curve (Yang et al., 1989). This function is as Equation 3:

$$I_{t} = \frac{a(e^{-bt})}{1 + e^{-c(t-d)}},$$
(3)

where Y_t is egg production at time t, e is the base of natural logarithms, a is a scale parameter, b is the rate of decrease in egg production, c is an indicator related to variation in sexual maturity, and d is the average age at sexual maturity.

Logistic Function The Logistic or the Nelder function is the generalized function of the Logistic curve its general form is as Equation 4 (Nelder, 1961):

$$Y_t = a \left[1 + e^{(-ct)} \right]^{-d} e^{-bt}, \qquad (4)$$

In the Nelder function, Y_t is egg production at time t, e is the base of natural logarithms, a is the parameter related to the peak of production, c is the constant coefficient, d is the parameter related to the incremental slope of production, and b is the parameter related to the decreasing slope of production.

Lokhorst Function This function is an appropriate mathematical model to describe the daily production process in the form of this function is as Equation 5 (Lokhorst, 1996):

$$Y_{t} = \frac{100}{1 + ab^{t}} - (c + dt + et^{2}),$$
(5)

where Y_t is egg production at time t, e is the base of natural logarithms, a and c are correction terms for the start value of production, b parameter is the time between the start and peak of egg production, d is the rate of reduction in egg production after the peak, and f is the slope of the final reduction.

For fitting different functions, estimating the parameters of each function, the "nlme" function from "nlme" package (3.1-155 version) with "port" algorithm was used in R software (Pinheiro et al., 2013). The "port" is an alternative algorithm based on an adaptive nonlinear least-squares algorithm from the Port library (Dennis et al., 1977).

Goodness of Fit Criteria

The following goodness of fit criteria were used to select the most appropriate function and the best-fitted model to describe the egg production curve in this ostrich population:

Mean Squared Error Mean squared error (MSE) is a performance measure for describing the quality of models and selecting the best model from a set of potential

models. The mean square error for each function is calculated by dividing the error sum of squares by the degree of freedom from Equation 6 (Otwinowska-Mindur et al., 2016; Pham, 2019):

$$MSE = \frac{SSE}{n-p},$$
(6)

where MSE is the mean square error, SSE is the error sum of the square, n is the number of observations, and p is the number of model parameters.

Likelihood Ratio Test The likelihood ratio test (LRT) is a statistical test of the goodness of fit between 2 models. The higher value of the log-likelihood indicates that the model fitted better to the given dataset. The log-likelihood values can be ranged from negative to positive infinity. The LRT statistic is computed by doubling the result of subtraction of the restricted Log Likelihood of the less complicated model (L_A) from the restricted Log-Likelihood of the more complicated model (L_B) as following of Equation 7 (Lewis et al., 2010):

$$LRT = 2\log(L_B/L_A) = 2(\log L_B - \log L_A),$$
(7)

Akaike Information Criterion The Akaike Information Criterion (**AIC**) was used to evaluate the error compensation of fitted models based on their number of parameters. A lower value of this statistic indicates that the model is fitted well relatively. This coefficient is defined as Equation 8 (Savegnago et al., 2012):

$$AIC = n \ln\left(\frac{SSE}{n}\right) + 2p, \tag{8}$$

where the SSE is the residual sum of squares, n is the number of observations, ln indicates the natural logarithm, and p is the number of model parameters.

Bayesian Information Criterion The Bayesian Information (**BIC**) is a fitting criterion for the selection of the best model among several models, BIC can avoid overfitting resulting by increasing the number of model parameters by introducing a penalty term for the extra number of parameters. The model with the lowest BIC prefers as the best model (Lewis et al., 2010; Wit et al., 2012). BIC can be calculated through Equation 9:

$$BIC = n \ln\left(\frac{SSE}{n}\right) + p \ln(n), \tag{9}$$

where the SSE is the residual sum of squares, n is the number of observations, ln indicates the natural logarithm, and p is the number of model parameters.

RESULTS AND DISCUSSION Description of Observed Egg Production

Egg production in our dataset commenced in the first month of study, rose sharply to the peak in the second month, and then gradually declined until the eleventh month resulting in a pattern of a 3-step curve (Table 1) which was in agreement with other the egg production patterns in chickens and other birds (Grossman et al., 2000; Savegnago et al., 2012). Given this specifically observed pattern using linear models seems not to be appropriate for describing the egg production curve in ostrich. Therefore, nonlinear mathematical functions can be the valid and informative methods for this study. Despite the high variations in the number of eggs produced by ostriches (Ipek and Sahan, 2004), it seems the pattern of the egg production was generally the same (Ahmad, 2011). Therefore, functions with multiple parameters have been suggested since they have been reported to describe flock level egg production to depict flock performance (Morales et al., 2016; Ramírez-Morales et al., 2017). In this study, the average monthly egg production at the initial stage of the egg production period was 8.97 eggs and the peak of production was revealed in the second month with an average of 9.83. After the peak of egg production, monthly egg production encountered a decreasing trend reaching 5 eggs at the end of the production (Table 1).

Fitting Nonlinear Functions

The ostrich is quite different than other avian species and has not been extensionally studied. The current study summarizes egg production data using 5 different mathematical functions using different number of parameters. The estimates of model parameters and the measures of different goodness of fit criteria for each fitted function are presented in Tables 2 and 3, respectively.

The inflection point where an egg production curve changes from sloping up to sloping down indicates the

Table 2. Estimates of model parameters, the peak of egg production (time), and the average number of eggs in the peak phase in various fitted functions.

	Wood	McNally	Yang	Nelder	Lokhorst
N of parameters	3	4	4	4	5
A	10.38 ± 0.29	34.52 ± 46.26	4.00 ± 0.83	12.59 ± 1.54	0.59 ± 0.13
В	0.25 ± 0.07	0.85 ± 0.67	-1.00 ± 0.21	1.00 ± 0.69	1.36 ± 0.10
С	0.13 ± 0.02	-0.06 ± 0.21	-1.15 ± 0.19	0.76 ± 0.26	50.38 ± 0.98
D		-1.40 ± 1.56	1.31 ± 0.19	0.09 ± 0.02	-9.39 ± 2.30
F					0.41 ± 0.18
Number of eggs in peak	9.50	9.66	10.01	9.55	9.53
Time of peak (month)	2	2	3	2	2

The a, b, c, d, and f are the model parameters to be estimated.

Function	MSE^1	LRT	AIC	BIC	$Correlation \pm SE^2$
Incomplete gamma (Wood)	17.31	3,619.08	7,247.61	7,268.20	$0.987 \pm 0.037^{**3}$
Corrected gamma (McNally)	17.31	3,619.04	7,248.82	7,274.56	$0.990 \pm 0.032^{**}$
Nonlinear Logistic (Yang)	18.68	3,667.78	7,345.56	7,371.30	$0.896 \pm 0.107^{**}$
Logistic (Nelder)	17.32	3,619.66	7,249.32	7,275.07	$0.988 \pm 0.035^{**}$
Lokhorst	17.34	$3,\!620.01$	7,252.02	7,283.92	$0.978 \pm 0.049^{**}$

Table 3. Goodness of fit criteria of the five functions for describing the egg production curve in ostrich, and correlations among actual and predicted egg production curves.

¹AIC, Akaike information criterion; BIC, Bayesian information criterion; MSE, Mean square error; LRT, Likelihood ratio test.

 2 SE, standard error of the correlation.

³**: Significance level of correlations (*P*-value < 0.001).

peak of the egg production curve here. As mentioned in Table 1, the average number of produced eggs by the studied flock in the peak phase was 9.83 eggs. The lowest and the highest differences with observed value in peak were found in the McNally and the Wood functions, respectively. However, in none of the fitted functions, the absolute difference in average egg numbers at the peak of the production was not higher than 0.33 eggs (Table 2). The time of peak production in four functions of the Wood, the McNally, the Nelder, and the Lokhorst was similar to the real-time (second month) in the real dataset, although, the time of the peak of the egg production in the Yang function was estimated in the third month. Therefore, all the studied functions except the Yang could estimate the time of the peak in the ostrich egg production curve properly which is in contrast with the results reported by in layers (Oni, et al., 2007; Safari-Aliqiarloo et al., 2018; Emam, 2021). It can be concluded that the Yang function has not had enough predictive ability for the peak of egg production pattern in this ostrich data.

Functions' Performance

The goodness of fit of functions showed in Table 3. Comparing the goodness of fit of the studied functions using the MSE criterion indicated that all functions fitted almost equally but the Yang function with the highest MSE of 18.68 performed weaker to describe the egg production curve in ostrich than other functions. In detail, the most suitable functions for describing the egg production curve are the Wood and McNally functions both with equal MSE values of 17.31. Then the Nelder and the Lokhorst functions described moderate fitting to the available egg production with MSE values of 17.32 and 17.34, respectively. Finally, the Yang function was determined as the worstfitted relative to other studied functions. Differential performance examination according to the LRT fitting criterion ordered the compared functions based on their accuracy (lowest to highest LRT values) as follows: the McNally, the Wood, the Nelder, the Lokhorst, and the Yang function. According to the AIC fitting criterion, the Wood function was the most appropriate function with the lowest AIC value of 7,247.61 and the Yang function was the most inappropriate function to monitor egg production trend in ostrich with the highest value AIC of 7,345.56. Based on

the AIC criterion, the compared functions were ordered regarding their performance as follows (lowest to highest AIC): the Wood, the McNally, the Nelder, the Lokhorst, and the Yang function. The BIC values of studied functions offered the same order as AIC represented according to fitting suitability for describing egg production curve in the studied population of ostrich. The local and final ranks of fitted models based on different model selection criteria are presented in Table 4.

The correlation values of the observed and the predicted egg production curves in all fitted functions were exceeded 0.97, except the Yang function (Table 3), which indicates that the 4 of 5 functions are adequately fitted to the present dataset of the ostrich egg production. The Yong function with the lowest correlation value of 0.896 and the highest standard error of 0.107 represents the least fitting to the egg production curve.

In the light of visualizing all the egg production curves simultaneously in Figure 1, it is differentiable that the Yang function could not be compatible with the observed and even other predicted egg production curves. This lack of congruent can result from underfitting of the initial and final egg production, overfitting of the peak production, and unfitting of the rates of decrease and increase in egg production. All this evidence is functioning as destroyers of the accuracy and goodness of fit. To this end, Gavora et al. (1971) by using a 4-parameter model suggested that 2 parameters of the rate of increase and the rate of decrease in egg production might be the most important in the modeling of poultry egg production.

The features of the observed data on ostrich egg production were precisely described by the Wood function suggesting as the best-fitted model. Also, the McNally,

Table 4. The rank of fitted models in describing the ostrich egg production curve.

Function	MSE	LRT	AIC	BIC	Final rank
Incomplete gamma (Wood)	1	2	1	1	1
Corrected gamma (McNally)	1	1	2	2	2
Nonlinear Logistic (Yang)	4	5	5	5	5
Logistic (Nelder)	2	3	3	3	3
Lokhorst	3	4	4	4	4

Abbreviations: AIC, Akaike information criterion; BIC, Bayesian information criterion; MSE, Mean squared error; LRT, Likelihood ratio test.

Models ranked 1 to 5. The number 1 indicates the best-fitted and the number 5 indicates the worst-fitted model and the numbers in between indicate the intermediate performance of the models in describing the egg production curve in ostriches.



Figure 1. Comparative fitted egg production curves.

the Nelder, and the Lokhorst were ranked as the second, the third, and the fourth best-fitted models. While the Yang function could not befit so that revealed high deviation from the observed egg production curve and determined as the worst-fitted function.

Moreover, because of the simplification issue, the Lokhorst function, one of the complex nonlinear functions having 5 parameters for estimating, was not recommended by the authors. Unfortunately, since no research has been performed on ostrich to evaluate and quantify ostrich's egg production patterns using mathematical modeling, the results of this study were just compared with the findings of previous studies in chickens. The outputs of the present study were not consistent with the performance of the Wood and the McNally functions reported in chicken egg production analysis. Previous studies reported that the Wood and McNally models were not flexible enough to fit the egg production rate at the peak of the curve accurately in chickens (Oni et al., 2007; Savegnago et al., 2012; Emam, 2021). This inconsistency may be due to differences in physiology, laying rates and the number of produced eggs between ostriches and chickens. Anyhow, a suitable mathematical function must describe the entire stages of the egg production to the end of production precisely, as the wood function performed in the current study. Furthermore, the findings of a genome-wide association study on egg production traits introduced that different stages of egg production based on the egg production curve have different heritability and genetic architecture across the whole laying period (Liu et al., 2019). Also, Oni et al. (2007) reported that, selection strategies based on functions of curve parameters of egg production performed more reliable and satisfying (Oni et al., 2007). Taken together, the results of this study can be used to design a selection plan based on a specific stage of the egg production curve or based on specific curve parameters in ostrich.

In conclusion, the McNally and the Wood can be recommended as appropriate functions for monitoring the initial rate of production to peak, the peak time of production, the decline rate of the egg production after the peak using the past experiences for future expectations in monthly records of ostrich flocks.

ACKNOWLEDGMENTS

The authors would like to thank the South Khorasan Prisoners' Cooperative Foundation, especially Mr. Ahmad Tajdar, for their sincere cooperation in conducting the present investigation.

DISCLOSURES

The authors have no conflict of interest.

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