Animal Reproduction Science 203 (2019) 10–24

Contents lists available at ScienceDirect

Animal Reproduction Science

journal homepage: www.elsevier.com/locate/anireprosci

Analyses of mathematical models for Yangzhou geese egg-laying curves

Binbin Guo[a], Sanqin Zhao[a], Xibing Shao[b], Weimin Ding[a,*], Zhendan Shi[b,*], Zhongliang Tang[a]

[a] College of Engineering, Nanjing Agricultural University, Nanjing, 210031, China
[b] Key Laboratory of Protected Agriculture Engineering in the Middle and Lower Yangtze Reaches, Ministry of Agriculture, Institute of Animal Science, Jiangsu Academy of Agricultural Sciences, Nanjing, 210014, China

ARTICLE INFO

Keywords:
Mathematical model
Egg-laying curve
Yangzhou goose
Photoperiod
Age

ABSTRACT

Mathematical models of the egg-laying curves for Yangzhou geese exposed to both natural and artificial photoperiods were established to optimise the parameters for maximising geese reproductive performance and for the development of precision feeding methods. With the natural photoperiod, egg-laying starts in autumn when daily photoperiod decreases, but accelerates after the winter solstice, and reaches the peak in spring when photoperiod increases. An accumulating model was constructed based on the hypothesis that the egg-laying capacity of geese was determined by two components of the photoperiod: photo-stimulation and photo-inhibition. In addition, a second segmented model was constructed based on the hypothesis that the photo-stimulation only occurred with lengthening photoperiods after the winter solstice, and the lesser laying rate in autumn could be attributed to the non-photo-dependent animal-husbandry technologies. This model consists of a logistic model before the winter solstice, and an accumulating model after this solstice. The use of the logistic and accumulating resulted in more precise predictions that occurred with use of Model 1 with a greater R^2 and lesser RMSE, AIC and BIC. Likewise, the egg-laying curves when there was consideration of artificial photoperiods could also be constructed with consideration of stimulatory and inhibitory photoperiodic effects. The model consists of an initial logistic and subsequently a quadratic polynomial model. With use of this model, there is consideration of changes in egg-laying patterns when there is a fixed photoperiod, with the model parameters reflecting the effects by photoperiod control-programs and age of the geese. In conclusion, new mathematical models have been developed to best fit egg-laying curves when there are both natural and artificial photoperiods. These models can contribute to development of precision-feeding technologies for breeding geese in future.

1. Introduction

The reproduction of geese, like those of most avians, has a distinct seasonality that is mostly entrained by the photoperiod (Wang et al., 2002). With artificial lighting conditions, the breeding season of geese can be substantially modified, and the egg-laying curves can be changed into entirely different shapes compared to that with natural photoperiods. Such egg-laying curves may be expressed in equations or mathematical models (Cason and Britton, 1988; Lokhorst, 1996; Narushin and Takma, 2003) similar to other

* Corresponding authors.
E-mail addresses: wmding@njau.edu.cn (W. Ding), zdshi@jaas.ac.cn (Z. Shi).

https://doi.org/10.1016/j.anireprosci.2019.02.003
Received 8 August 2018; Received in revised form 24 January 2019; Accepted 6 February 2019
Available online 08 February 2019
0378-4320/

controlled systems, so that the egg or gosling production can be more predictable and the precision feeding can be realised for the efficient management of geese breeding. The reproductive functions of birds are regulated by stimulatory and inhibitory factors, which are both affected by photoperiod (Dawson, 2015). Geese egg-laying patterns or curves when there are both natural and artificial photoperiods, however, were described only qualitatively in association with the physiological or endocrine status brought about by photoperiodic changes (Huang et al., 2008; Zhu et al., 2017).

Numerous mathematical models have been developed for modelling the egg-laying rate of poultry (Mcnally, 1971; Adams and Bell, 1980; McMillan, 1981; Yang et al., 1989; Fialho and Ledur, 1997). In these models, either segmented or elementary functions were used to formulate the egg-laying curve of flocks. The segmented models are more flexible, dividing the laying curves into two or more stages according to the curve shape, and describing these separately. Linear equations and polynomial functions are widely used. The segmented polynomial model (Fialho and Ledur, 1997), for example, uses three types of mathematical functions (constant-cubic-linear) to describe the three egg-laying stages of hens. The Adams-Bell model (Adams and Bell, 1980) exploits a growth curve to describe the pre-peak increase and a linear function to mimic the post-peak decrease of the egg-laying rate. These models, however, did not correlate the model parameters to the physiological regulation of the fowl reproductive status. In contrast, the Wood (Mcnally, 1971), McMillan (McMillan, 1981), and YangNing (Yang et al., 1989) models provided for more precise physiological interpretations and have had greater application. These models have been applied to describe the flock egg-laying curves of chickens (McMillan et al., 1986; Shi, 1993; Li et al., 2013; Agnieszka et al., 2016) and ducks (Lü et al., 2014) that were bred when there were artificial lighting conditions. The R^2 is generally used to evaluate the goodness of curve fit, which was considered as an inadequate measure for nonlinear models (Spiess, 2010). Further improvements with more precise models are needed to improve predictive data for bird egg-laying curves.

There have been no mathematical models developed for simulating the egg-laying performances of geese that were bred when there was natural photoperiod. The objective of the present study, therefore, was to develop mathematical models for the egg-laying curves of geese that were exposed to either natural or artificial photoperiods for the development of precision feeding technologies. In addition, the model parameters were analysed with the goal of predicting quantitatively, rather than qualitatively as has previously occurred, the stimulatory and inhibitory regulation of the reproductive functions of geese by the photoperiod, as well as variations in the egg-laying performances due to age differences.

2. Materials and methods

2.1. Experiments and data collection

Data (listed in Table 1) used in this study were obtained from a series of experiments of geese breeding flocks that were conducted on Sunlake Swan Farm (32.4 °N, 119.42 °E) in Changzhou, China. In Experiment 1, there was recording of the data for egg-laying from a flock of 520 2-year old geese that were exposed to a natural photoperiod. Experiment 2 was conducted to evaluate the egg-laying performances when there were three different artificial photoperiod programs (Zhu et al., 2017). The basal program consisted of an 8 h short photoperiod for 2 months followed by a 12 h long photoperiod to induce out-of-season breeding in geese (Buckland and Guy, 2001). The 8 h short photoperiod treatment usually started from January each year. With the second program, there was use of an additional 18 h long photoperiod treatment for 1 month prior to the short 8 h photoperiod to improve the egg-laying performance. The reduction of the 12 h photoperiod in the second program to 11 h in the laying phase gave rise to the third program. In Experiments 3 and 4, there were comparisons of the egg-laying curves of geese of different ages when there was consideration of imposing the second and third photo-program, respectively. In Experiment 5, there was comparison of the stimulatory effect of different lengths of photoperiod on initiation of geese' egg-laying. There were totally four groups, with each group having 1120 breeding geese and there were three replications of the groups. The first and second phase photoperiod for the four groups of geese were the same as those previously described in this manuscript for the third photo-program, but the third phase photoperiod increased to 13.5 (group E1 and E2) and 15 (group E3 and E4) h respectively, and lasted for 50 days.

Table 1
Detailed information of the egg-laying data used in this study.

Experiment No.	Group No.	Geese age (year)	Number of goose (female:male = 4:1)	Photo-programs
1	A	2	520	Production flock exposed to the natural photoperiod of Changzhou (32.4°N, 119.42°E)
2	B1	1	375	Experimental flock treated with the photo-program of 8h-12h
	B2	1	375	Experimental flock treated with the photo-program of 18-8-12 h
3	C1, C2	1	1100	Production flocks treated with the photo-program of 18-8-12 h
	C3, C4	2	1030	
	C5, C6	3	1100	
4	D1, D2	1	1100	Production flocks treated with the photo-program of 18-8-11 h
	D3, D4	2	1030	
	D5, D6	3	1100	
5	E1, E2	1	1120	Experimental flock treated with the photo-program of 18-8-13.5 h
	E3, E4	1	1120	Experimental flock treated with the photo-program of 18-8-15 h

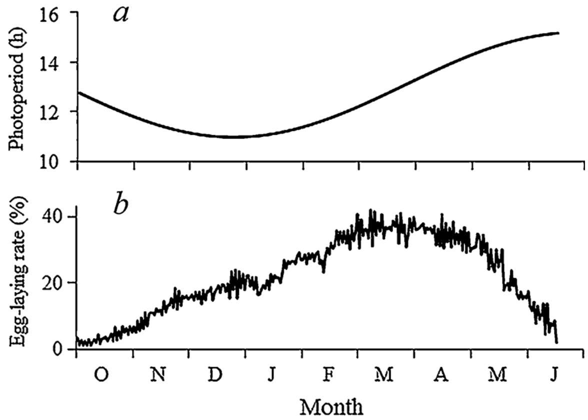

Fig. 1. Daily egg-laying rate curve (a) of Yangzhou geese when there was a natural photoperiod in Changzhou, China (b, 32.4 °N, 119.42 °E).

In these five experiments, there was management of the geese flocks in standard husbandry conditions with free access to feed and drinking water, and in houses where photoperiod, temperature and ventilation were controlled. There was daily recording of the number of eggs produced throughout the experimental periods and number of eggs was divided by the number of geese in the study on the same day to calculate the daily egg-laying rate.

2.2. Modelling egg-laying curves when there was a natural photoperiod

2.2.1. Model 1

When there was a natural photoperiod, Yangzhou geese started to lay eggs in the autumn when the daily photoperiod was decreasing (Shi et al., 2008). Though increasing, the egg-laying rate was relatively less when the decreasing photoperiod prevailed before the winter solstice. The egg-laying rate increased further as the daily photoperiod increased after the winter solstice, and reached a peak in spring (March to April), after which it rapidly decreased to zero in June (Fig. 1). According to a hypothesis regarding the photo-regulation of seasonal reproductive activities, two factors, stimulatory (S) and inhibitory (I) effects that are both regulated by photoperiod, act in tandem to regulate the seasonal egg-laying pattern (Dawson, 2015). Results of previous studies (Farner and Lewis, 1971; Follet and Maung, 1978) indicate photoperiodic effects modulate reproductive performance to the greatest extent in the early stages of reproduction. To quantify the relationship between the photoperiod and photo-stimulation, the slopes of the initial egg-laying rate when there were different long photoperiods (11 h, 12 h, 13.5 h, 15 h) were calculated with the data recorded from Experiments 2, 3, 4 and 5. Egg-laying rate curve data from these experiments are depicted in Fig. 2. The initial increase in rate of egg-laying was proportional to the effects of the long photoperiod (Fig. 3). The regression between the photo-stimulation (S) and photoperiod (p) was determined by using Equation 1. The standard errors for the slope (0.3767) and the intercept (3.5101) were 0.0325 and 0.4218, respectively.

$$S = 0.3767p - 3.5101 \quad (1)$$

During the laying period, the daily egg-laying rate was the sum of the difference between the values attributed to photo-

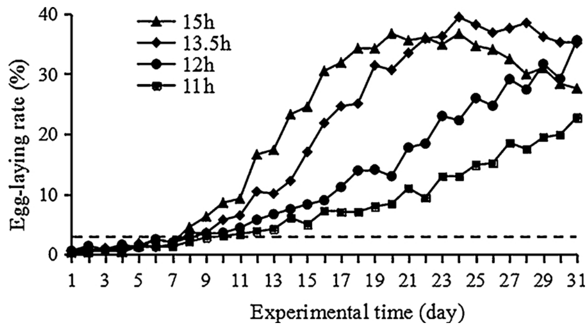

Fig. 2. Egg-laying rate curve for geese in their first year of egg production when there was a change from ab 8 h short photoperiod to different longer photoperiods; Egg-laying data when there was 13.5 (E1, E2) and 15 (E3, E4) h photoperiods were from Experiment 5 to compare variation in egg-laying curves with imposition of different long photoperiods; 13.5 h and 15 h photoperiods lasted for 50 days rather than the whole laying period, but it was enough to calculate initial increase of the egg-laying; Egg-laying data with a 12 h photoperiod were from Experiments 2 (B2) and 3 (C1, C2); Experiment 2 was conducted to induce geese out-of-season breeding and Experiment 3 was the pevailing production practice; Egg-laying data with use of a 11 h photoperiod were from Experiment 4 (D1, D2); In each experiment, the increase in egg-laying did not change until laying rate exceeded 3% (the dotted black line above).

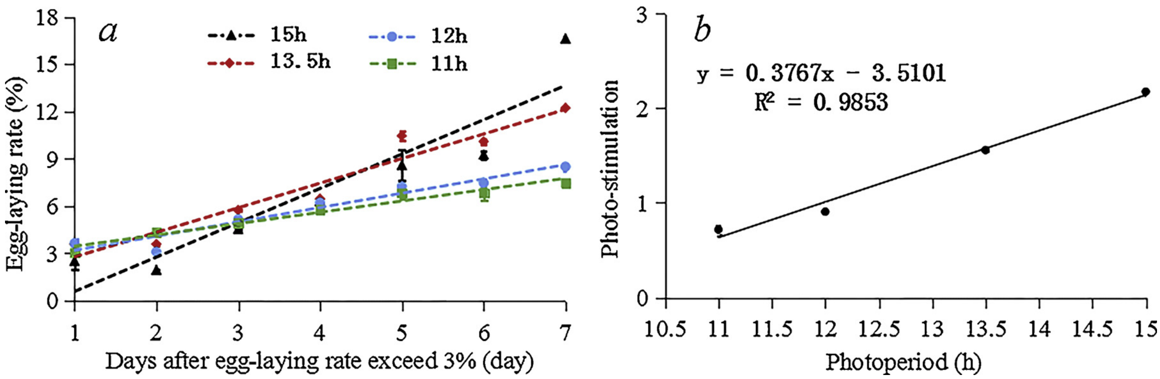

Fig. 3. Initial increase of egg-laying (a, mean ± S.D.) following an acute change in photoperiod from 8 to 15, 13.5, 12, and 11 h photoperiods; Data for seven consecutive days after laying rate exceeded 3% were used to calculate the initial increase rate 3% was selected according to Fig. 2, because there were no differences in egg-laying rate between the groups under different photoperiod before egg-laying exceeded 3%; Fig. b depicts the liner relationship between increase egg-laying rate and photoperiod.

stimulation and photo-inhibition. Thus, the photo-inhibition could be calculated by subtracting the daily egg-laying increment from the values attributed to photo-stimulation. The regression between the photo-inhibition (I) and photoperiod (p) was calculated using Eq. (2). The standard errors for the multiplier (0.002) and the rate constant (0.492) were 0.0006 and 0.0189, respectively.

$$I = 0.002 \cdot \exp\ (0.492p) \tag{2}$$

This output from use of this equation indicated the photo-inhibition was less when there was a shorter photoperiod, but the effects of photo-inhibition became greater in an exponential form as the photoperiod increased, especially when approaching the summer solstice. As a result, the egg-laying rate could be expressed as follows:

$$y(p) = \sum a \cdot p_i + b - c \cdot \exp(k \cdot p_i) \tag{3}$$

where $y(p)$ is the egg-laying rate corresponding to photoperiod p; $a{\cdot}p + b$ and $c{\cdot}\exp(k{\cdot}p)$ are the photo-stimulation and photo-inhibition effects on the egg-laying, respectively, a and k are the two photo-responsive parameters; b and c are constant coefficients.

2.2.2. Model 2

For the actual egg-laying rate curve, there was a slight decrease around the winter solstice before there was a further increase to the peak (Fig. 1, b). This slight decrease was similar to a lengthened medium level plateau until the winter solstice in geese that became sexually mature and started laying in early September (Zhao et al., 2004). This slight decline in the egg-laying curve or delay in the laying rate increase in the autumn is consistent with the theory that the shortening days in autumn lead to a decrease in response to photorefractoriness to the previously inhibitory long photoperiod. This photoperiodic pattern is non-stimulatory to reproduction, and other factors such as genetics and nutrition intake affect the basal reproductive functions during this period of the year (Shi et al., 2008). A segmented model was proposed to incorporate this physiological regulation theory when modelling the egg-laying curve for geese. In the first pre-winter solstice period, a logistic model was proposed to simulate the curve for the initiation and rate of egg-laying, which was hypothesised to be determined by the genetic potential and animal-husbandry technologies such as the nutrition intake, rather than the prevailing decrease in the photoperiod. The second post-winter solstice part was an accumulating curve based on the photo-simulation and inhibition effects, as described with Model 1. In the pre-winter solstice phase, the egg-laying rate changed to a plateau over time t, which essentially followed a logistic model:

$$y(t) = f \cdot s \cdot \exp(r \cdot t)/(f + s \cdot (\exp(r \cdot t) - 1)) \tag{4}$$

where f is the theoretical maximum egg-laying rate (the asymptote), s is the initial egg-laying rate, and r is an increase parameter determined by the genetic potential and animal-husbandry technologies. After the winter solstice, the egg-laying rate increased from the previous level to a peak through the spring and finally decreased in early summer as the photo-inhibition effects exceeded those of photo-stimulation. Thus, in the second post winter solstice phase, starting at the initial laying rate of $y(t_0)$ at the winter solstice, the curve can be fitted the same as in Model 1 by

$$y(t_i) = y(t_0) + \sum a \cdot p(t_i) + b - c \cdot exp(k \cdot p(t_i)) \tag{5}$$

Then, the combined model can be expressed by the following segmented function:

$$y(t) = \begin{cases} f \cdot s \cdot \exp(rt) \big/ f + s \cdot (\exp(rt) - 1) & t \le t_0 \\ y(t_0) + \sum a \cdot p(t_i) + b - c \cdot exp(k \cdot p(t_i)) & t > t_0 \end{cases} \tag{6}$$

2.3. Modelling of egg-laying curves when there is imposing of artificial photo-programs

Modern geese breeding utilises an artificial photo-program to control egg-laying at the desired times and improve the egg-laying performance (Huang et al., 2008; Shi et al., 2008; Zhu et al., 2017). The common photo-programs used in production consist of three segments: an initial 18 h long photoperiod lasting for 1 month, followed by 2 months of a short 8 h photoperiod, and a final 12 or 11 h photoperiod to induce egg-laying. Following treatment with such a photo-program, the egg-laying curves of Yangzhou geese change in an asymmetric pattern. The egg-laying starts slowly and rapidly increases to the peak, followed by a more or less stable laying plateau and then there is a nonlinear decrease in egg-laying rate. To model such a curve, the following assumptions were made.

Before the peak egg-laying rate, the amount of geese that start laying eggs were assumed to follow a normal distribution when there is an increase from a shorter to a moderately long photoperiod. A logistic model, therefore, could be used to describe the egg-laying rate as described by Lokhorst (1996). The mathematical expression was the same as that for Eq. (4), where f is the theoretical maximum egg-laying rate (the asymptote), s is the initial egg-laying rate, and r is the increase parameter determined by the photoperiod (or the photo-stimulatory parameter). The second assumption is that there will be a delay in initiation of photo-inhibitory effects when there are 11 to 12 h photoperiods for several days. This effect is greatest in inducing the decreasing phase of the egg-laying rate curve. According to the observed egg-laying data, use of a quadratic polynomial is justified to describe the gradual decrease in egg-laying. Comprehensively, the egg-laying rate y corresponding to time t during the entire laying period can be expressed as follows:

$$y(t)=\begin{cases} f\cdot s\cdot \exp(r\cdot t)\big/ f+s\cdot(\exp(r\cdot t)-1) & t\le t_0\\ a\cdot(t-t_0)^2+b\cdot(t-t_0)+y(t_0) & t>t_0\end{cases} \tag{7}$$

where $y(t_0)$ is the practical maximum egg-laying rate, t_0 is the time when egg-laying rate starts to decrease, a and b are the photo-inhibitory parameters, which reflect the acceleration in rate of decrease and initial decrease in rate of egg-laying.

To prove the validity of use of Model 7 in describing geese egg-laying curves, a comparison was made of Model 7 and other two commonly used models, the Wood Model ($y(t)=A\cdot t^{t0}\cdot\exp(-kt)$) and the Yang Ning Model ($y(t)=A\cdot\exp(-kt)/1+\exp(-b\cdot(t-t_0))$). In the Wood model, the A, t_0 and k are parameters to be estimated and these have no biological significance. In the Yang Ning Model, A is the theoretical maximum egg-laying rate, k is the rate of decrease in laying ability, b is the reciprocal indicator of the variation in sexual maturity, and t_0 is the mean age of sexual maturity of the birds.

2.4. Statistical analysis

Testing of Model 1 proposed for Yangzhou geese when there is a natural photoperiod was done in Excel 2007 using the automatic accumulation function. Testing of Models 7 and 2 (the pre-winter solstice phase) was accomplished by using R 3.3.3 with the nonlinear least square method. The performance and comparison of all the models were assessed using goodness-of-fit, including R^2, RMSE, residual plots, AIC and BIC (Spiess, 2010). Differences of model parameters considering the three photo-programs were analysed with one-way analyses of variance (ANOVA). Effects of the age of geese on model parameters were analysed using a two-way analyses of variance (two-way ANOVA) with age and the two photo-programs as the main fixed effects. The significance level was set to probability or P-value less than 0.05. The statistical analyses of model parameters were performed with SPSS statistics 17.0.

3. Results

3.1. Models of egg-laying curve when there is a natural photoperiod

3.1.1. Model 1

In the model $y(p)=\sum a\cdot p_i+b-c\cdot\exp(k\cdot p_i)$, it was assumed that both photo-stimulation and photo-inhibition occurred simultaneously, but that there were differential relative responses to these two factors that regulated changes in the laying curve, as is depicted in Fig. 4 a. In September of each year, the stimulatory effect of the photoperiod became greater than the inhibitory effect. Consequently, egg-laying began approximately 20 days later and gradually increased to a maximum in April. After April, the effects on egg-laying of photo-inhibition became much greater than the photo-stimulation because of photo-refractoriness, which rapidly led to the termination of egg-laying. The high value of R^2 (0.930) and the low value of RMSE (3.796) depicted in Fig. 4 c indicate that this model could well explain the changes of egg-laying rate when there is a natural photoperiod. Most of the residuals were within -5% to ˜5% and residuals at the peak egg-laying were relatively large, with the maximum value being ± 10% (Fig. 4 d). The AIC and BIC values for Model 1 were 1417.47 and 1431.65, respectively.

3.1.2. Model 2

Model 2 was a segmented model that consisted of a logistic model $y(t)=f\cdot s\cdot\exp(rt)/(f+s\cdot(\exp(rt)-1))$ before the winter solstice, and afterwards an accumulating model $y(t_i)=y(t_0)+\sum a\cdot p(t_i)+b-c\cdot\exp(k\cdot p(t_i))$, which was similar to Model 1. In Fig. 5 there is a depiction of the fitted results. Before the winter solstice, egg-laying was slowly initiated being 1.147 ± 0.054% (parameter s) from 1 October and gradually increasing to a theoretical plateau value of 19.23 ± 0.68% (parameter f) at an infinite time (Fig. 5 b). This moderate egg-laying when there was a decreasing photoperiod in the autumn was hypothesised to be a result of the genetic potential and animal-husbandry technologies such as the nutrition intake rather than the prevailing reduction in photoperiod.

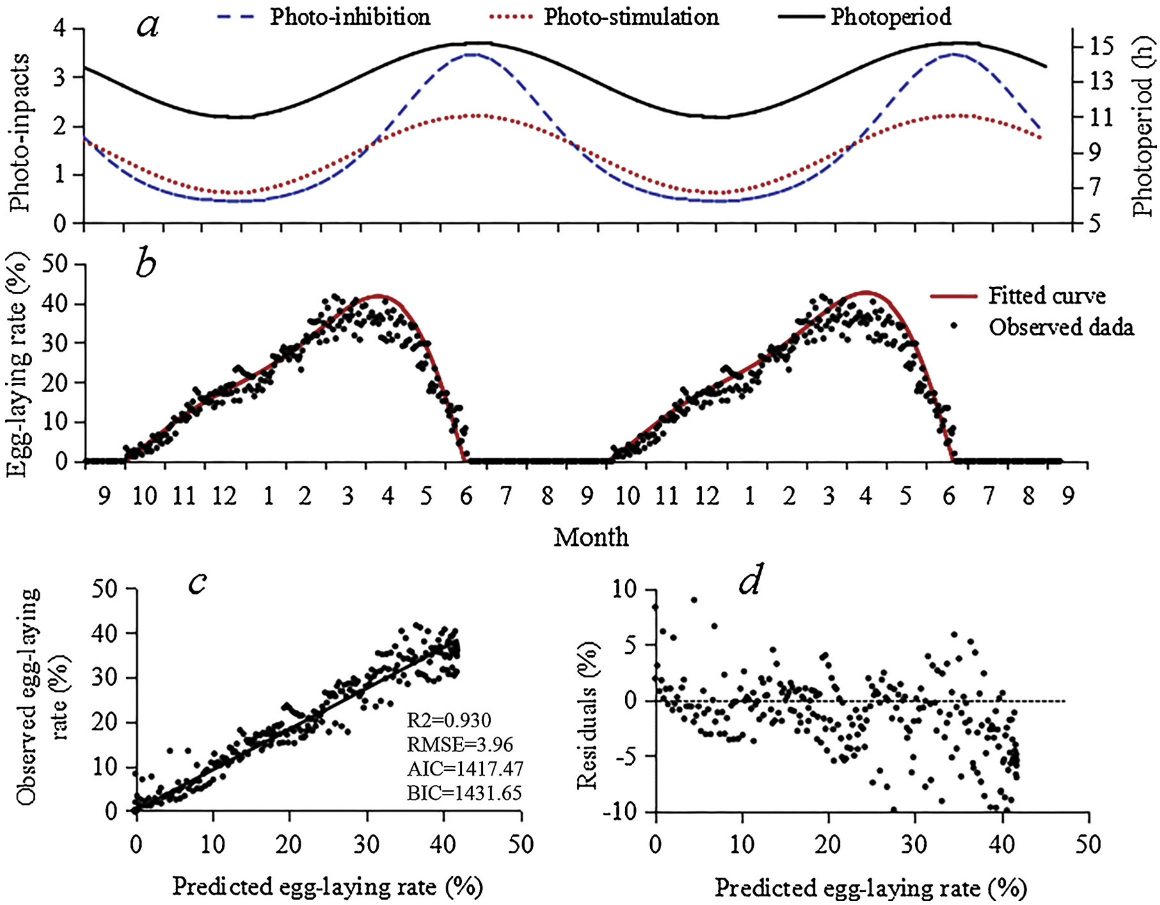

Fig. 4. Fitting results of Model 1; Photo-stimulation (a, dotted line) was calculated using Equation 1 ($S = 0.3767p - 3.5101$) and the photo-inhibition (a, dashed line) was calculated using Equation 2 ($I = 0.002 \cdot e^{0.492p}$);Daily increment (positive or negative) in the egg-laying rate was the difference between the photo-stimulation and photo-inhibition; Egg-laying began approximately 20 days later after the photo-stimulation exceeded photo-inhibition and decreased when the photo-inhibition exceeded photo-stimulation (b, solid line); Model 1 described well the geese egg-laying data with high R^2, low RMSE (c) and residuals (d).

Parameter r (0.0699 ± 0.0059) reflected the increase rate of the egg-laying to the peak values. After the winter solstice, the egg-laying rate was determined by the sum of the difference between the photo-stimulation ($S = 0.3767p - 3.5101$) and photo-inhibition ($I = 0.002 \cdot \exp(0.492p)$) effects based on $y(t_0)$ (18.36%), which served as the end point of the first segment and starting point of the second segment. In early April, the egg-laying rate peaked at 40% and subsequently decreased as the photo-inhibition effects became greater than the photo-stimulation effects. The rate of decrease in the egg-laying was much greater than the increase, because the effects of photo-stimulation were proportional to the photoperiod while the inhibition changed based on an exponential function with photoperiod. Thus, the model parameter k (0.492) was greater than parameter a (0.3767). The negative value of parameter b (-3.5101) in the equation for the photo-stimulation indicated that a completely dark environment inhibited egg production in geese. As Fig. 5 c depicts, the values for RMSE (3.459), AIC (1375.85) and BIC (1400.67) were less than those when Model 1 (RMSE, AIC and BIC were 3.796, 1417.47, and 1431.65, respectively) was utilised for these estimations. Most of the residuals were within -5% to ˜5% and the values at the greater egg-laying rate were relatively large, with the maximum value being ± 10% (Fig. 5 d).

3.2. Models of egg-laying curve when there was imposing of artificial photo-programs

3.2.1. Fitting and comparison results

There is depiction of the fitted results with use of the Model 7, Wood Model and Yang Ning Model of three sets of egg-laying data (group B2, C3 and C5 in Table 1) in Figs. 6–8. Estimated model parameters and goodness-of-fit (AIC and BIC) are listed in Table 2.

Overall, R^2 for the all the model fittings was greater than 0.9 (Fig. 7). There was the minimum value with use of the Wood Model, with this value was 0.912 (Fig. 7 g). With use of Model 7, most of the residuals were within -5% to +5% ranges and were randomly distributed (Fig. 8 a–c). By contrast, the use of the Yang Ning and the Wood Models resulted in residuals distributed in certain relationships with the predicted values (Fig. 8, e–i). Such lack of fit effects were evident especially at the onset and end of egg-laying (Fig. 6 e–i). The average values of AIC and BIC with use of Model 7 (848.6 and 864.9) were less than with use of the Yang Ning (971.4

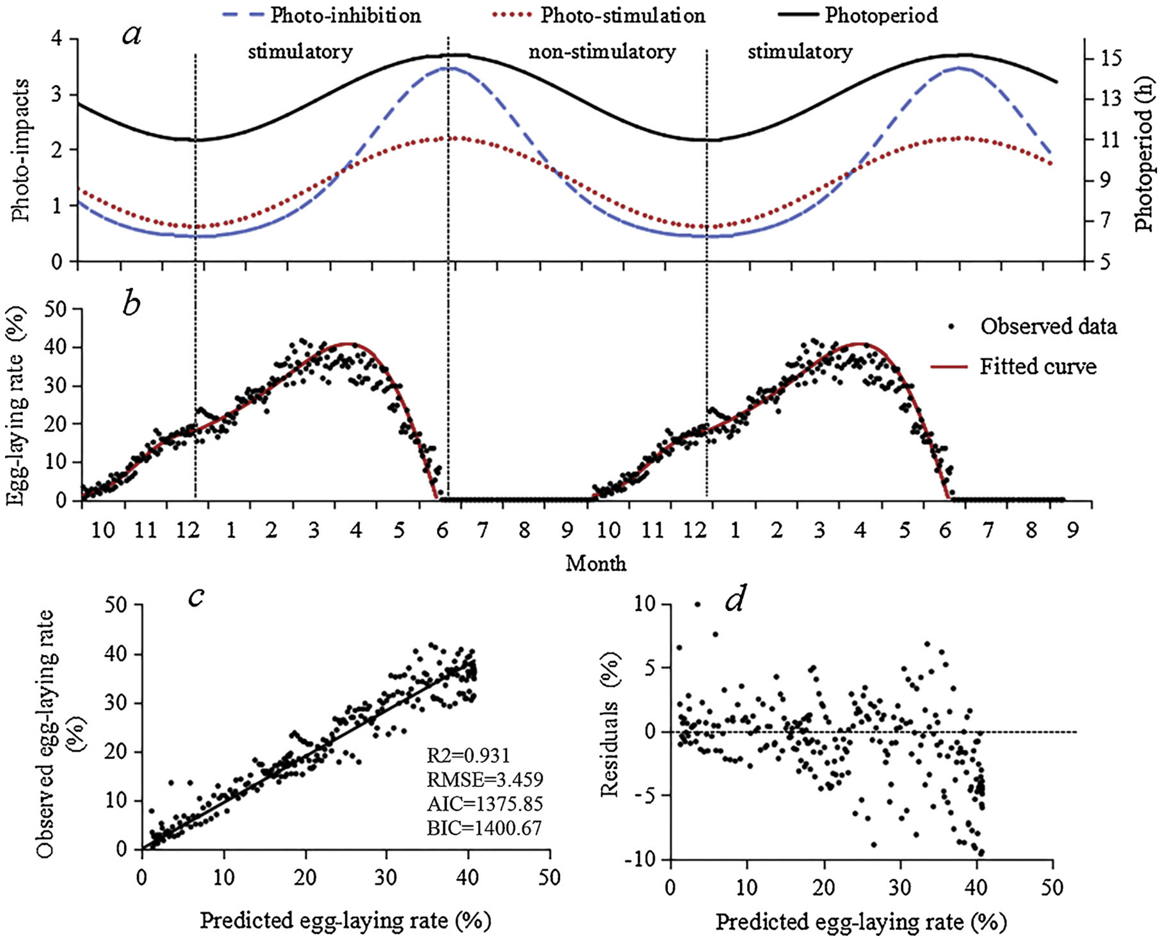

Fig. 5. Fitted results of Model 2; Modelled annual photo-stimulation (a, dotted line) and photo-inhibition (a, dashed line) were the same as in Fig. 4; From the onset of laying to the winter solstice, the egg-laying rate curve (b, solid line) was fitted using logistic Eq. (4); During this period, photoperiod was non-stimulatory to the egg-laying; The egg-laying curve, after the winter solstice, was modelled using Eq. (5); During this period, the daily increment (positive or negative) in egg-laying was the difference between the photo-stimulation and photo-inhibition; Use of Model 2 resulted in a better fitting performance than Model 1 with a greater R^2 and lesser RMSE (c) and residuals (d).

and 984.5) and Wood (970.3 and 980.0) Models, which indicated there was a better fit with use of Model 7 (Table 2).

The estimated parameters with use of Model 7 are included in Table 2 and there were indications that the geese started egg-laying slowly (s = 1.074 ± 0.150%) and there was a rapid increase to the theoretical maximum level f (41.78 ± 0.43%). Parameter r (0.154 ± 0.006) reflected the rate of increase of egg-laying. After about 70 to 120 days (parameter t_0), the egg-laying rate began to decrease from the maximum $y(t_0)$ (41.71%), with parameter b (-0.1510 ± 0.00146) reflecting the initial decreasing rate and parameter a (-0.00139 ± 0.00018) the acceleration in rate of decrease in egg-laying. Values of model parameters were consistent with the biological significance of the parameter.

3.2.2. Effect of artificial photo-programs on model parameters

Photo-programs had significant effects on the shapes of egg-laying curves. The estimated parameters of egg-laying curves when there are different artificial photo-programs are included in Table 3.

Treatment with an 18 h long photoperiod for 1 month prior to imposition of the 8 h short photoperiod resulted in an accelerated rate of increase in egg-laying (parameter r) and enhanced maximum egg-laying rate (parameter f), but there was no effect on the decreasing rate as a result of this photoperiodic regimen. Rate of increase in egg-laying without the prior 18 h long photoperiod treatment (0.132 ± 0.007) was slower than that (0.167 ± 0.007) with use of the three-phase photoperiodic (18 h-8 h–12 h) regimen. Egg-laying rate of the two groups both peaked around the 70th day of egg production, but the theoretical maximum egg-laying rate increased from 38.40 ± 0.69% to 44.20 ± 0.38%, with an increment of 5.86 percentage points. After the peak egg-laying rate, there was a decreasing trajectory for both of the two curves with the rate of decrease being similar (Fig. 9).

The photoperiod during the laying phase also affected the shapes of the egg-laying curves. Parameter r for geese when there was imposition of the 12 h photoperiod was 0.167 ± 0.007, while with imposition of the 11 h photoperiod it was 0.127 ± 0.003. The value for parameter r, however, was greater for the third phase when there was the longer (12 h) photoperiod. As a result, egg-laying

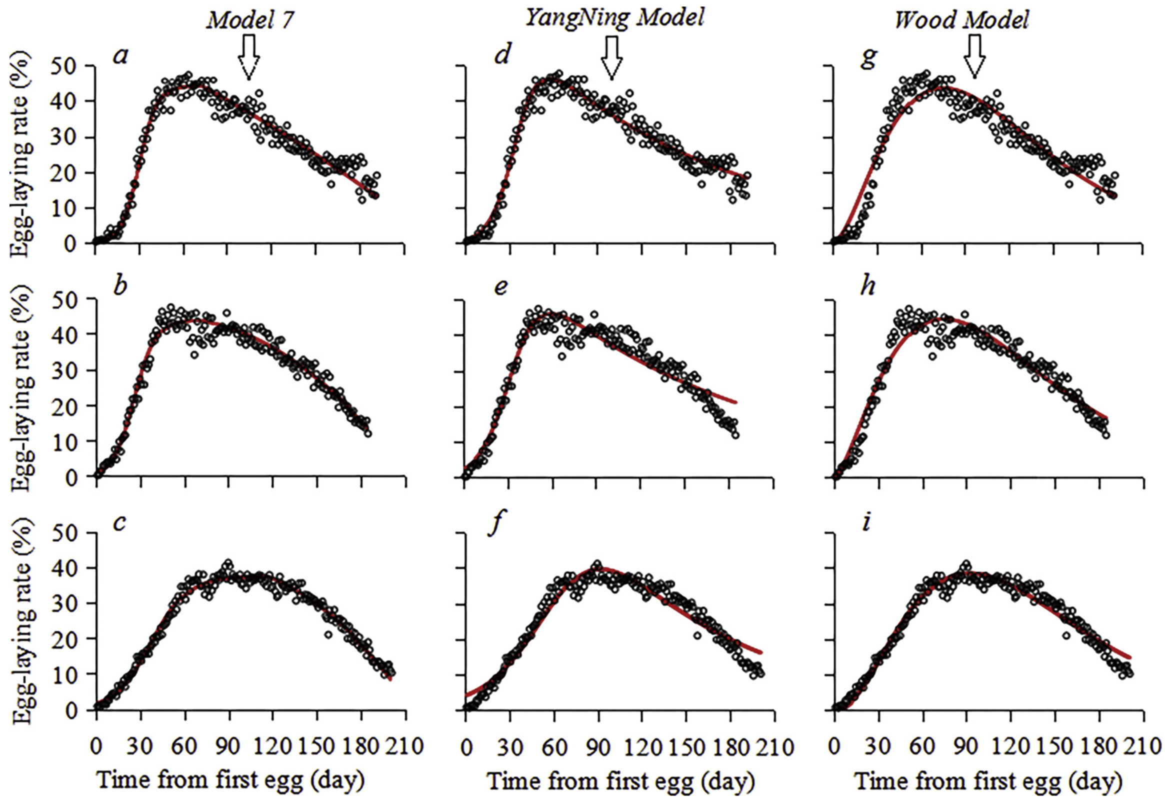

Fig. 6. Fitted egg-laying curves of geese with different artificial photo-programs and of different ages using Model 7 (a, b, c), Yang Ning Model (d, e, f) and Wood Model (g, h, i).

rate increased more rapidly, though there were no significant differences on the maximum egg-laying rate (41.44 ± 0.17% and 44.20 ± 0.38%%, respectively). With the 11 h photoperiod, there was a more consistent egg-laying performance with the post peak laying rate decreasing very slowly (Fig. 9). This was associated with a much lesser decreasing rate parameter $|b|$ at 0.0313 ± 0.0061 as compared with the 0.2252 ± 0.0103 when there was a 12 h photoperiod.

3.2.3. Effects of age on model parameters

The egg-laying performances of geese of different ages differed considerably. Estimates of model parameters are listed in Table 4. The variance in model parameters can well describe the shape differences of egg-laying curves caused by age difference.

There were no significant differences in parameter f between the geese in their first (41.06 ± 0.34) and second (43.18 ± 0.56) year of egg production, but it was less ($P < 0.05$; 38.59 ± 0.32) for geese in their third year of egg production. As a result, the maximum egg-laying rate of the third year geese was the least. Different values of parameters r, a and b indicated that geese of different ages had different sensitivities to a given photo-program. A greater value of r reflected a more rapid increase in the egg-laying rate to the laying peak, and a larger value of $|a|$ or $|b|$ implied that the egg-laying rate would decrease more rapidly. Results in Table 3 indicate egg-laying rate of the geese during their second year of egg production peaked the earliest as indicated by the greater ($P < 0.05$) value for parameter r (0.214 ± 0.012) than the geese in their first (0.132 ± 0.005) and third year (0.112 ± 0.004) of egg production. The value (-11.5 ± 2.2) of parameter $|a|$ for geese in their third year of egg production was slightly less than for the other age groups, however, the greater value for parameter $|b|$ (0.1950 ± 0.0136) resulted in a more rapid decrease in egg production (Fig. 10 a) for the post peak egg-laying rate. Besides, for geese of three ages, the model parameters r and $|b|$ with imposition of a 12 h photoperiod were greater than that with imposition of a 11 h photoperiod (Table 4 and Fig. 10 b).

4. Discussion

In the present study, mathematical models of the egg-laying curves of geese exposed to both natural and artificial photoperiods were developed for Yangzhou geese that bred when there was both natural and artificial photoperiods. Two effects of photoperidic regulation, photo-stimulation and photo- inhibition, were considered in construction of the models. The models were improved from the original single equation model into segmented models, and by inclusion of RMSE, AIC and BIC values as evaluation measures apart from consideration of the R^2 alone. These improvements not only illustrated the biological significances of photo-stimulation and photo-refractoriness that affect reproductive or egg-laying cycles of birds, but also indicated quantitatively the subtle effects on

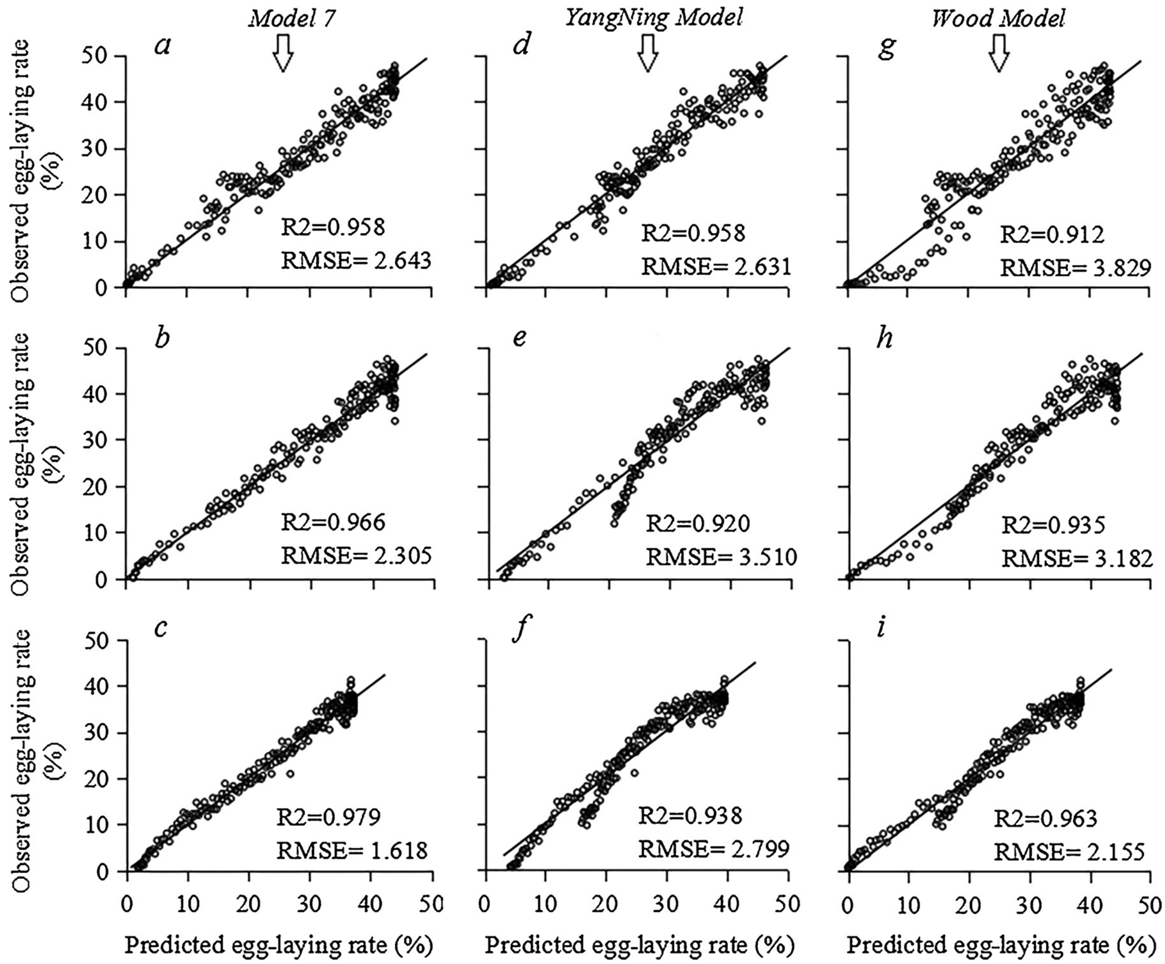

Fig. 7. Predicted compared with observed egg-laying rate using Model 7 (a, b, c), Yang Ning Model (d, e, f) and Wood Model (g, h, i).

egg-laying rate changes and laying performance as affected by different photoperiods or ages of geese.

Model 1 for geese egg-laying curves when there is a natural photoperiod was proposed based on the previous photoperiod regulation theories (Sharp and Blache, 2003; Dawson, 2015). Construction of Model 1 was based on the two independent but interacting components of the photoperiodic effects, namely the photo-stimulation and photo-inhibition (Fig. 4 a). In this way, representation of the two photoperiodic effects by mathematic parameters aided in the enhanced understanding of regulation of seasonal egg-laying in geese. This approach also conforms to the theory of Dawson (Dawson, 2015) regarding the annual cycle in the testicular size of quail and starlings. The egg-laying rate was the sum of the difference in effects because of photo-stimulation and photo-inhibition. A decrease in the photoperiod in late summer and early autumn suppressed the photo-refractoriness effects caused by the long days in summer (Sharp and Blache, 2003). Subsequently, the positive net stimulation of the photoperiod induced egg-laying approximately 20 days later because it took approximately 20 days for large ovarian follicles to develop to the extent that ovulation occurred (Huang et al., 2008; Qin et al., 2013). This also explained the necessity of using an increasing long artificial photoperiod approximately 1 month before the expected time of egg-laying in some out-of-season breeding experiments (Huang et al., 2008; Wang et al., 2008; Zhu et al., 2017).

For the actual egg-laying curves of geese, there is a slight suppression in egg-laying rate around the winter solstice before there is a further increase to a peak. This period of suppression corresponds to a prolonged medium plateau in egg-laying in the autumn in geese that were produced from hatchings that occurred in January with these animals becoming sexually mature and initiating egg-laying earlier (i.e., September; Zhao et al., 2004). Results of previous studies indicate that poultry egg production is affected by many factors, both intrinsic genetic traits of the bird itself (Tůmová et al., 2017) and extrinsic effects of the environment, such as temperature (Sebastian et al., 2014) and nutrition intake (Ding et al., 2016). Thus, it could be assumed that the moderate egg-laying before the winter solstice could be regulated by animal-husbandry technologies other than the photoperiod, which was not considered to be stimulatory to the reproductive system (Sharp, 1993; Sharp and Blache., 2003). Thus, Model 2, a segmented model that consists of a logistic model before the winter solstice and subsequently as an accumulative model, was proposed based on the previous single equation model. This use of this model resulted in a greater fitting performance than with use of Model 1 in describing the characteristics of the egg-laying curves with a lesser value of RMSE, AIC, and BIC. This segmented Model 2 is especially useful for

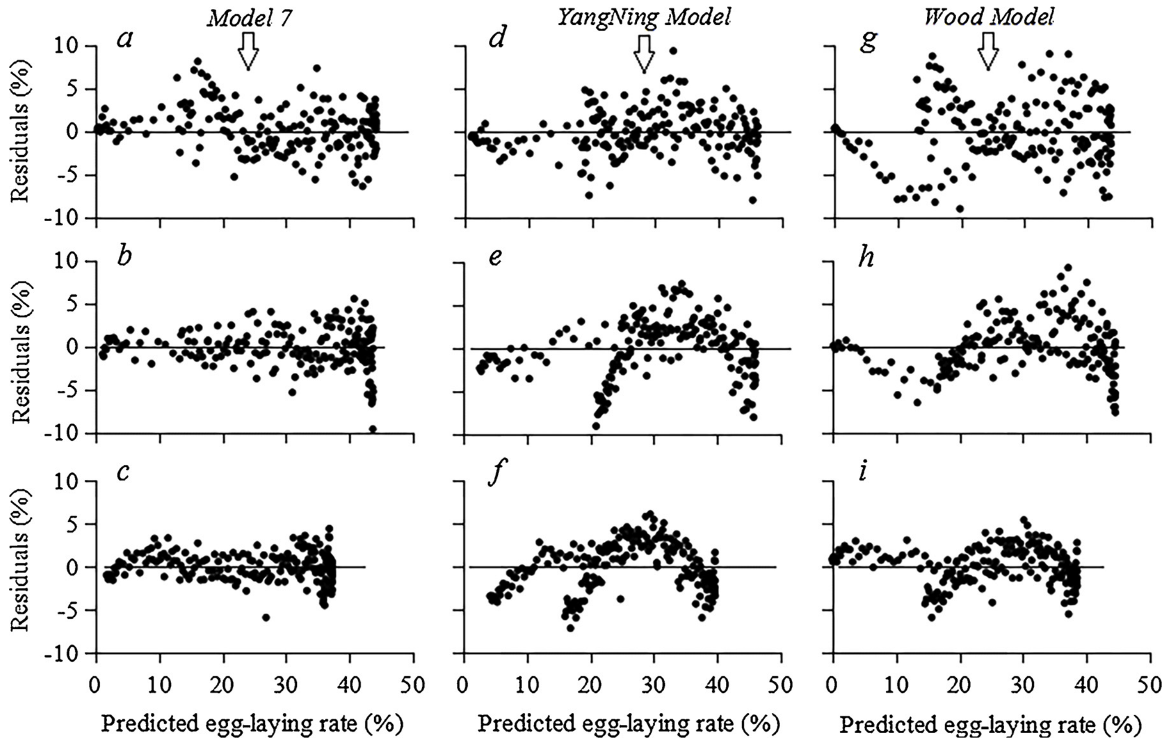

Fig. 8. Residuals compared with predicted egg-laying rate using Model 7 (a, b, c), Yang Ning Model (d, e, f) and Wood Model (g, h, i).

describing the egg-laying curves of geese that were hatched in January and became sexually mature and started laying earlier (i.e., early September), for the laying curve provided evidence for a lengthened medium level plateau until the winter solstice (Zhao et al., 2004).

There was development of Model 1 and Model 2 based on the photo-stimulation and photo-inhibition theory without considering any other factors. For example, geese egg-laying rates were influenced by animal-husbandry technologies such as temperature and nutrition intake in addition to photoperiod (Shi et al., 2015). Further, that's why some residuals were large in Figs. 4 b and Fig. 5b. Unlike the 24-hour oviposition cycle in chicken hens (Johnston and Gous, 2007), the interval between oviposition of two eggs for geese is approximately 46 h (Qin et al., 2013), which could lead to greater fluctuations in egg-laying rate for two consecutive days, reducing the uniformity of egg-laying rate, especially during the peak production period. This could lead to the fitting residues to the observed egg-laying data to enlarge to as great as 10%.

The geese egg-laying curves when there are artificial photo-programs had a similar pattern as observed in hens (McNally, 1971; Yang et al., 1989; Alvarez and Hocking, 2007). The mathematical models for laying hens, however, were not suitable for geese because of the inconsistencies of the model parameters to the actual geese egg-laying curve, as well as the lack of predictive capacity, such as the greater estimated maximum egg-laying rate *A* with use of the Yang Ning Model and the larger value for AIC and BIC with use of both the Yang Ning and Wood Models (Table 2). For a group of laying hens, the theoretical maximum egg-laying rate was usually assumed to be 100% (Adams and Bell, 1980; McMillan, 1981) or 80% (Yang et al., 1989) dependent on genetic potential and animal-husbandry technologies. For Yangzhou geese, however, the maximum egg-laying rate reported is approximately 50% (Zhao et al., 2004; Zhu et al., 2017). The estimated maximum egg-laying rate of 90% with use of the Yang Ning Model in Table 2 was impossible to achieve for geese. Although the R^2 values with use of both the Yang Ning and Wood Models were greater than 0.9, which were generally considered good fits. Values of AIC and BIC, as well as the special relationship between residuals and the predicted values, however, indicated that use of the R^2 value alone was an inadequate criterion for assessing nonlinear models (Spiess, 2010). By contrast, the use of a modified segmented model, which consists of an initial logistic and subsequently a quadratic polynomial model, allows for the capacity to predict geese egg-laying curves and the shape difference caused by photoperiod and age differences. The larger residuals at high predicted egg-laying rates could be attributed to the effect of the relatively greater temperatures in the summer (Shi et al., 2015) and the intervals between oviposition of two eggs (Qin et al., 2013).

Imposition of an additional 18 h long photoperiod treatment for 1 month prior to the imposition of the basal programme of 8 to 12 h enhanced the maximum egg-laying rate (parameter *f*) and enhanced the rate of increase (parameter *r*) in egg-laying for geese. Consequently, laying performance of the geese improved by approximately 32% (Zhu et al., 2017). These photoperiod induced changes in the curve parameters that explained the enhanced reproductive functions or performances, which resulted from greater FSH and LH gene expressions which led to an enhanced ovarian follicle development (Zhu et al., 2017). Enhanced reproductive functions by imposing a long photoperiod prior to the short photoperiod was also evident in both European starlings (Sockman et al., 2004) and house finches (Salvante et al., 2013).

Table 2
Estimated model parameters and goodness-of-fit of three different models.

Model	Group No.	Parameter estimates												Goodness-of-fit	
		f	*S.E.*	*s*	*S.E.*	*r*	*S.E.*	*a*	*S.E.*	*b*	*S.E.*	t_0	$y(t_0)$	AIC	BIC
Model 7	B2	44.20	0.38	0.286	0.063	0.167	0.007	−0.00031	0.00003	−0.2252	0.0103	72	44.15	928.10	944.39
	D3	43.79	0.60	1.136	0.222	0.141	0.008	−0.00169	0.00016	−0.0702	0.0144	64	43.69	843.92	860.02
	D5	37.35	0.31	1.800	0.164	0.081	0.003	−0.00216	0.00034	−0.1577	0.0192	112	37.28	773.81	790.33
Average		41.78 ± 0.43		1.074 ± 0.150		0.154 ± 0.006		−0.00139 ± 0.00018		−0.1510 ± 0.0.0146		83	41.71	848.61	864.91
		A	*S.E.*	*b*	*S.E.*	*k*	*S.E.*	t_0	*S.E.*	–	–	–	–	AIC	BIC
Yang Ning	B2	74.51	3.52	0.1235	0.0102	0.0074	0.0004	34.38	0.98	–	–	–	–	924.37	937.40
	D3	73.28	4.96	0.1019	0.0108	0.0068	0.0006	32.39	1.58	–	–	–	–	997.62	1010.51
	D5	124.70	17.5	0.0526	0.0033	0.0103	0.0009	63.68	3.76	–	–	–	–	992.24	1005..45
Average		90.83 ± 8.66		0.0927 ± 0.0081		0.0082 ± 0.0006		43.48 ± 2.11		–	–	–	–	971.41	973.96
		A	*S.E.*	*k*	*S.E.*	t_0	*S.E.*	–	–	–	–	–	–	AIC	BIC
Wood	B2	0.0699	0.0331	0.0259	0.0017	1.94	0.14	–	–	–	–	–	–	1066.45	1076.22
	D3	0.1548	0.0549	0.0231	0.0013	1.71	0.11	–	–	–	–	–	–	959.339	969.00
	D5	0.0080	0.0031	0.0262	0.0011	2.41	0.11	–	–	–	–	–	–	885.01	894.92
Average		0.0776 ± 0.0304		0.0251 ± 0.0014		2.02 ± 0.12		–	–	–	–	–	–	970.26	980.05

Table 3
Estimates of model parameters of egg-laying rate of geese of the same age when there were different artificial photo-programs.

Photo- programs	Group No.	Parameter estimates											
		f	*S.E.*	*s*	*S.E.*	*r*	*S.E.*	*a* (*10^3)	*S.E.*(*10^3)	*b*	*S.E.*	t_0	$y(t_0)$
8h-12	B1	38.40[b]	0.69	1.920	0.306	0.133[b]	0.007	−0.42	0.03	−0.2558	0.0129	69	38.01
18-8-12h	B2	44.20[a]	0.38	0.286	0.063	0.167 [a]	0.007	−0.31	0.03	−0.2252	0.0103	72	44.15
18-8-11h	D	41.44 [a]	0.17	1.302	0.116	0.127 [c]	0.003	−2.21	0.38	−0.0313	0.0061	110	41.44

Values in the same column with different superscript letters (a–c) are different (P < 0.05); Parameter estimates for group D were average values of group D1 and D2.

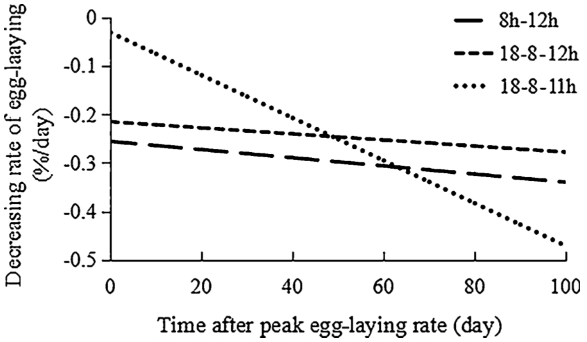

Fig. 9. Decreasing rate of egg-laying rate for geese when there are three different photoperiod programs; There were no significant differences between 8 h–12 h and 18-8-12 h group, however, egg-laying rate of 18-8-11 h group decreased less rapidly for about 50 days after the peak rate of egg-laying.

On the basis of the second photo-program, the reduction in the photoperiod from 12 h to 11 h during the laying phase also resulted in a changed shape of the egg-laying curve of geese. The results of the present study indicate that imposition of different photoperiods resulted in changed shapes of the egg-laying curve by affecting model parameters *r*, *a* and *b*. When there were greater values for parameters $|a|$ and $|b|$, there was a reduction in geese egg-laying performance as a result of the acceleration in the decrease of egg-laying rate, while there was a comparatively greater value for parameter *r* for enhanced laying performance as a result of shortening the time for the egg-laying rate to reach its peak. The egg-laying of geese exposed to a 12 h photoperiod increased more rapidly but was less persistent than in geese where there was imposing of the 11 h photoperiod, which resulted in reduction in egg production during the entire laying period. This was because exposure to a longer photoperiod, though more stimulatory to gonadotropin secretion by the anterior pituitary (Lewis and Gous, 2006; Lewis et al., 2010), also induced a more rapid development of photo-refractoriness and cessation of egg-laying (Dawson, 1987). For example, transferring starlings from an 8 to 18 h photoperiod induced testis regression in 3 weeks compared with 5 weeks when there was a 13 h photoperiod (Sharp, 1993). In Hungarian White geese, the peak in egg-laying rate was on day 33 when there was a 14 h photoperiod as compared with the peak on day 53 when there was a 11 h photoperiod. An increase from shorter (8 h) to a relatively longer photoperiods (11 h) resulted in a stimulation of the neuroendocrine system and led to an enhancement in reproductive functions being sustained for a longer period (lesser values of $|a|$ and $|b|$), which resulted in a greater egg-laying performance (Zhu et al., 2019).

Age of the geese also affects egg-laying curves. The egg-laying performance decreased with increases in age. For example, in the third year of production of geese there was the least laying performance as indicated by the least *r* and *f* values, which indicated there was a comparatively long period before the laying peak occurred, and the maximum egg-laying rate was the least for these older geese. The greater value of $|a|$ and $|b|$ for geese in the third year of egg production meant that the egg-laying rate would decrease more rapidly in geese of this age. Thus, the laying performance was the least in the geese that were in their third year of egg production in the present study. Compared to the geese in their first year of egg production, the total egg production of the geese in their second year of production decreased markedly as described by Zhao et al. (2004). Model parameters can well explain this phenomenon, such as the basically the same value in parameter *f* and *b*, but a relatively greater value of *r* and $|a|$ for geese in their second year of egg production. There were no differences in the maximum egg-laying rate and the time when the decreasing rate of egg-laying started for geese in their first and second year of egg production, but there was a slightly greater value of $|a|$ in geese in their second year of egg production the led to a more rapid decrease in egg-laying rate. There were similar outcomes in both laying hens and broiler breeders where aged birds had a lesser egg-laying rate (Johnston and Gous, 2003). The underlying mechanisms causing the reduction in egg-laying rate of older geese could be changes in the ovulation and oviposition intervals, which could lead to increases in the number of days between ovipositions (Zakaria et al., 1983; Zakaria, 1999). In addition, the egg-laying rate of geese in their second year of egg production increased more than that of geese in their first year of egg production. This may have been the result of the effect of the prior photo-experience, rather than age *per se*, because the previous photo-experience can sensitise the neuroendocrine system to the photoperiod, and enhance some aspects of early photo-induced reproductive development (Salvante

Table 4
Estimates of model parameters of egg-laying rate of geese of different ages and when there were two different artificial photo-programs.

Photoperiod	Age (year)	GroupNo.	Parameter estimates											
			f	S.E.	s	S.E.	r	S.E.	a (*10^4)	S.E. (*10^4)	b	S.E.	t_0	$y(t_0)$
12 h	1	C1	39.40	0.41	1.287	0.159	0.148	0.006	−9.9	0.9	−0.1495	0.0009	66	39.33
		C2	40.89	0.35	1.356	0.195	0.161	0.007	−9.8	0.9	−0.1382	0.0009	63	40.86
11 h	1	D1	41.93	0.30	1.508	0.187	0.123	0.004	−17.1	1.6	−0.0140	0.0114	97	41.91
		D2	42.02	0.29	1.942	0.207	0.116	0.004	−18.3	2.3	−0.0240	0.0153	99	42.00
	Average		41.06 ± 0.34 [a]		1.533 ± 0.187		0.132 ± 0.005 [b]		−13.8 ± 1.4		−0.0814 ± 0.0071 [b]		81 [b]	41.03 [a]
12 h	2	C3	42.50	0.38	0.068	0.021	0.309	0.015	−12.7	0.8	−0.0979	0.0082	49	42.50
		C4	45.23	0.63	0.048	0.018	0.260	0.015	−13.7	1.1	−0.1200	0.0112	51	44.11
11 h	2	D3	43.79	0.60	1.136	0.222	0.141	0.008	−16.9	1.6	−0.0702	0.0144	64	43.69
		D4	41.20	0.63	1.191	0.270	0.145	0.010	−18.5	1.5	−0.0330	0.0129	61	41.14
	Average		43.18 ± 0.56 [a]		0.611 ± 0.133		0.214 ± 0.012 [a]		−15.5 ± 1.3		−0.0803 ± 0.0117 [b]		57 [c]	42.86 [a]
12 h	3	C5	39.81	0.33	0.246	0.045	0.133	0.005	−1.8	0.9	−0.2719	0.0084	87	39.76
		C6	39.92	0.37	0.289	0.049	0.116	0.004	−1.9	1.1	−0.2405	0.0103	91	39.75
11 h	3	D5	37.35	0.31	1.800	0.164	0.081	0.003	−21.6	3.4	−0.1577	0.0192	112	37.28
		D6	37.27	0.25	1.557	0.143	0.086	0.003	−20.6	3.2	−0.1097	0.0166	113	37.22
	Average		38.59 ± 0.32 [b]		0.973 ± 0.100		0.104 ± 0.004 [c]		−11.5 ± 2.2		−0.1950 ± 0.0136 [a]		101 [a]	38.50 [b]

Average values in the same column with different superscript letters (a–c) are different ($P < 0.05$).

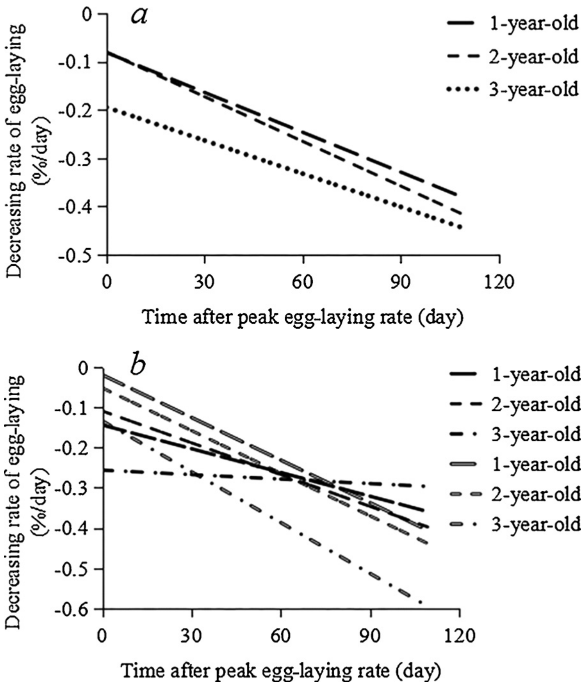

Fig. 10. Decreasing rate of egg-laying rate of geese at different ages and with two different photo-programs; Figure a is the mean decreasing rate of each age; There were no significant differences in decreasing rate between the geese in the first and second year of egg production, but those in the third year of egg production had a more rapid decrease in production after peak rate of egg-laying (Fig. a); For geese of the three ages in egg production, the decreasing rates with 12 h photoperiod (b, single deshed line) were more rapid than that with the 11 h photoperiod (b, double deshed line).

et al., 2013).

In conclusion, the proposed models in the present study could well describe the egg-laying curve of Yangzhou geese, revealing the two effects of photoperiod on the egg-laying capacity when there are natural and artificial photoperiods, as well as the physiological significance of the model parameters. In addition, the results of the proposed model also provide for quantitative, rather than qualitative estimations of egg-laying as compared with that of previously-developed models with the effects of changes in egg-laying changing tendencies being exerted by both photoperiod programs that were imposed and ages of the geese. Practically, such models can also be used to provide a mathematical controlling system for the future development of precision feeding technologies.

Conflict of interest

The authors declare that they have no conflict of interest.

Acknowledgments

This study was supported by the National Natural Science Foundation of China (grant no. 31372314), China Agriculture Research System (CARS-42-20), Technology Research and Development Program of Jiangsu Province (BE2012392).

I also thank an anonymous reviewer for helpful suggestions that greatly perfected our models.

References

Adams, C.J., Bell, D.D., 1980. Predicting poultry egg production. Poult. Sci. 59, 937–938.
Agnieszka, O.M., Małgorzata, G., Joanna, K.G., 2016. Mathematical models for egg production in broiler breeder hens. Ann. Anim. Sci. 16, 1185–1198.
Alvarez, R., Hocking, P.M., 2007. Stochastic model of egg production in broiler breeders. Poult. Sci. 86, 1445–1452.
Buckland, R., Guy, G., 2001. Goose production. FAO Anim. Prod. Health Pap. 154.
Cason, J.A., Britton, W.M., 1988. Comparison of compartmental and Adams-Bell models of poultry egg production. Poult. Sci. 67, 213–218.
Dawson, A., 1987. Photorefractoriness in European starlings: critical daylength is not affected by photoperiodic history. Physiol. Zool. 60, 722–729.
Dawson, A., 2015. Annual gonadal cycles in birds: modeling the effects of photoperiod on seasonal changes in GnRH-1 secretion. Front. Neuroendocrinol. 37, 52–64.
Ding, Y., Bu, X.C., Zhang, N.N., Li, L.L., Zou, X.T., 2016. Effects of metabolizable energy and crude protein levels on laying performance, egg quality and serum biochemical indices of Fengda-1 layers. Anim. Nutr. 2, 93–98.
Farner, D.S., Lewis, R.A., 1971. Photoperiodism and reproductive cycles in birds. In: Giese, A.C. (Ed.), Photophysiology. Academic Press, London.
Fialho, F.B., Ledur, M.C., 1997. Segmented polynomial model for estimation of egg production curves in laying hens. Br. Poult. Sci. 38, 66–73.
Follet, B.K., Maung, S.L., 1978. Rate of testicular maturation, in relation to gonadotrophin and testtosterone levels, in quail exposed to variouse artificial photoperiods and to natural daylengths. J. Endocrinol. 78, 267–280.

Huang, Y.M., Shi, Z.D., Liu, Z., Liu, Y., Li, X.W., 2008. Endocrine regulations of reproductive seasonality, follicular development and incubation in Magang geese. Anim. Reprod. Sci. 104, 344–358.
Johnston, S.A., Gous, R.M., 2003. An improved mathematical model of the ovulatory cycle of the laying hen. Br. Poult. Sci. 44, 752–760.
Johnston, S.A., Gous, R.M., 2007. A mechanistic, stochastic, population model of egg production. Br. Poult. Sci. 48, 224–232.
Lewis, P.D., Gous, R.M., 2006. Effect of final photoperiod and twenty-week body weight on sexual maturity and early egg production in broiler breeders. Poult. Sci. 85, 377–383.
Lewis, P.D., Danisman, R., Gous, R.M., 2010. Photoperiods for broiler breeder females during the laying period. Poult. Sci. 89, 108–114.
Li, J.Y., Zhan, K., Liu, W., Han, T., 2013. Mathematical models for egg production curves of caged Huainan partrige chicken. Fujian J. Agric. Sci. 12, 1204–1207.
Lokhorst, C., 1996. Mathematical curves for the description of input and output variables of the daily production process in aviary housing systems for laying hens. Poult. Sci. 75, 838–848.
Lü, M.Z., Luo, L.H., Feng, Y.Y., Zhao, J.R., Huang, D.C., Chen, J.L., 2014. Study on mathematical models of egg performance curves in Xianhu ducks. China Poult. 36, 6–12.
McMillan, I., 1981. Compartmental model analysis of poultry egg production curves. Poult. Sci. 60, 1549–1551.
McMillan, I., Gowe, I.S., Gavora, J.S., Fairfull, R.W., 1986. Prediction of annual production from part record egg production in chickens by three mathematical models. Poult. Sci. 65, 817–822.
McNally, D.H., 1971. Mathematical model for poultry egg production. Biometrics 27, 735–738.
Narushin, V.G., Takma, C., 2003. Sigmoid model for the evaluation of growth and production curves in laying hens. Biosyst. Eng. 84, 343–348.
Qin, Q.M., Sun, A.D., Guo, R.H., Lei, M.M., Ying, S.J., Shi, Z.D., 2013. The characteristics of oviposition and hormonal and gene regulation of ovarian follicle development in Magang geese. Reprod. Biol. Endocrinol. 11, e65.
Salvante, K.G., Dawson, A., Aldredge, R.A., Sharp, P.J., Sockman, K.W., 2013. Prior experience with photostimulation enhances photo-induced reproductive response in female house finches. J. Biol. Rhythms 28, 38–50.
Sebastian, D., Claudia, A.F., Wascher, E.M., 2014. Ambient temperature and air pressure modulate hormones and behaviour in Grey-lag geese (Anser anser) and Northern bald ibis(Geronticus eremita). Behav. Processes 108, 27–35.
Sharp, P.J., 1993. Photoperiodic control of reproduction in the domestic hen. Poult. Sci. 72, 897–905.
Sharp, P.J., Blache, D., 2003. A neuroendocrine model for prolactin as the key mediator of seasonal breeding in birds under long- and short-day photoperiods. Can. J. Physiol. Pharmacol. 81, 350–358.
Shi, X.W., 1993. Research on the mathematical models of egg production curves in chicken. J. Yunnan Agric. Univ. 8, 31–36.
Shi, Z.D., Tian, Y.B., Wu, W., Wang, Z.Y., 2008. Controlling reproductive seasonality in the geese: a review. Worlds Poult. Sci. J. 64, 343–355.
Shi, Z.D., Sun, A.D., Shao, X.B., Chen, Zhe, Zhu, H.X., 2015. Boosting the economic returns of goose breeding and developing the industry by controlled photoperiod for out-of-season reproduction. Proc. Int. Symp. Anim. Environ. Welfare 357–363.
Sockman, K.W., Williams, T.D., Dawson, A., Ball, G.F., 2004. Prior experience with photostimulation enhances photo-induced reproductive development in female European starlings: a possible basis for the age-related increase in avian reproductive performance. Biol. Reprod. 71, 979–986.
Spiess, Neumeyer, 2010. An evaluation of R^2 as an inadequate measure for nonlinear models in pharmacological and biochemical research: a Monte Carlo approach. BMC Pharmacol. 2010 (10), 6.
Tůmová, E., Uhlířová, L., Tůma, R., Chodová, D., Máchal, L., 2017. Age related changes in laying pattern and egg weight of different laying hen genotypes. Anim. Reprod. Sci. 183, 21–26.
Wang, S.D., Jan, D.F., Yeh, L.T., Wu, G.C., Chen, L.R., 2002. Effect of exposure to long photoperiod during the rearing period on the age at first egg and the subsequent reproductive performance in geese. Anim. Reprod. Sci. 73, 227–234.
Wang, B.W., Ge, W.H., Zhang, M.A., Yü, S.H., Yue, B., Guo, H.Y., Sun, B.H., 2008. Reproduction technique of meat goose breeders in non-breeding season. China Poult. 30, 13–16.
Yang, N., Wu, C., McMillan, I., 1989. New mathematical model of poultry egg production. Poult. Sci. 68, 476–481.
Zakaria, A.H., 1999. Ovarian follicular growth in laying hens in relation to sequence length and egg position in various sequence lengths. Archiv für Geflugelkunde 63, 264–269.
Zakaria, A.H., Miyaki, T., Imai, K., 1983. The effect of aging on the ovarian follicular growth in laying hens. Poult. Sci. 62, 670–674.
Zhao, W.L., Wang, Z.Y., Gong, D.Q., Zhang, J., Dai, G.J., Xie, K.Z., Jü, J.G., Jü, Y., Duan, B.F., Wen, G.B., Wu, H.J., Ding, T., Tian, Y., 2004. Primary study on laying-egg rule of Yangzhou geese. China Poult. 26, 12–13.
Zhu, H.X., Shao, X.B., Chen, Z., Wei, C.K., Lei, M.M., Ying, S.J., Yü, J.N., Shi, Z.D., 2017. Induction of out-of-season egg-laying by artificial photoperiod in Yangzhou geese and the associated endocrineand molecular regulation mechanisms. Anim. Reprod. Sci. 180, 5560–5569.
Zhu, H.X., Liu, X.Q., Hu, M.D., Lei, M.M., Chen, Z., Ying, S.J., Yu, J.N., Dai, Z.C., Shi, Z.D., 2019. Endocrine and molecular regulation mechanisms of the reproductive system of Hungarian White geese investigated under two artificial photoperiodic programs. Theriogenology 123, 167–176.