EDUCATION AND PRODUCTION

Effect of Hatch on the Distribution for Failure of an Embryo to Survive Incubation

W. W. Kuurman,* B. A. Bailey,† W. J. Koops,‡,* and M. Grossman*†,2

*Department of Animal Sciences, University of Illinois, Urbana, Illinois 61801;
†Department of Statistics, University of Illinois, Champaign, Illinois 61820;
‡Department of Animal Sciences, Animal Production Systems Group, Wageningen University and Research Centre, P.O. Box 338, 6700 AH Wageningen, The Netherlands

ABSTRACT The objectives of this paper were to validate an improved model to describe failure to hatch by using data obtained from two hatches of a line of chickens and to examine the effect of hatch on the distribution for time of failure of an embryo to survive incubation. Breakout analysis of 11,254 eggs that failed to hatch was used to characterize the distribution for time of failure to survive and the probability of failure to hatch. The distribution for time of failure to survive was modeled by a biphasic Weibull distribution, corresponding to the two phases of increased embryonic mortality during incubation. Distribution parameters for time of failure to survive were estimated by maximum likelihood and minimum Hellinger distance. Goodness-of-fit statistics validated the appropriateness of the biphasic Weibull distribution. Overall, the proportion of infertility was 0.213, and the proportion of embryonic mortality by the end of incubation was 0.086. Among embryos that suffered mortality during incubation, the proportion that died during Phase 1 was 0.77; therefore, 0.23 died during Phase 2. For Phase 1, mean time of mortality was 2.6 d, and standard deviation was 3.3 d. For Phase 2, mean time was 17.4 d, and standard deviation was 2.0 d. Time of mortality was distributed differently in the two hatches; this difference occurred mostly during Phase 1. Failure rates of the two hatches were different during the first 3 d of incubation. The model is useful to assess probability of failure to hatch and the distribution for time of failure to survive during incubation.

(Key words: chicken, embryonic mortality, infertility, hatchability, mathematical modeling)

INTRODUCTION

Failure of an egg to hatch reduces reproductive efficiency and therefore is of economic interest to the poultry industry (Etches, 1996). An egg that fails to hatch is infertile or it is fertile but the embryo suffers mortality prior to or during incubation. During the 3 wk of incubation, embryonic mortality is most frequent during the first week, least frequent during the second week, and intermediate during the third week (Payne, 1919; Byerly, 1930; Moseley and Landauer, 1949). Time of mortality during incubation, therefore, is distributed primarily over two phases, the first phase during the first week and the second phase during the third week (Jassim et al., 1996), during which physiological and development functioning of the embryo changes at relatively high rates (Rolnik, 1970).

Increased mortality occurs, for example, early in embryonic development during vascular formation (Etches, 1996). Increased mortality also occurs late in embryonic development with changes in nourishment and in the respiratory system (Payne, 1919). Embryonic mortality can be due to genetic or environmental causes (Byerly, 1930; Moseley and Landauer, 1949; Etches, 1996), for example, chromosomal abnormalities early in embryonic development (Thorne et al., 1991) or inability of the egg shell to exchange sufficient respiratory gases and water (Rahn et al., 1979).

Embryonic mortality is analyzed, generally, by computing the proportion of mortality among fertile eggs incubated during each discrete period of incubation, either daily (Payne, 1919; Byerly, 1930) or weekly (Whitehead et al., 1985; Yoo and Wientjes, 1991; Scott and Mackenzie, 1993), and by comparing these proportions within or across hatches.

Embryonic mortality, however, is a continuous process throughout incubation, and, therefore, is more appropri-
ately modeled by a continuous model. The first continuous model to describe failure to hatch was developed by Jassim et al. (1996), who modeled empirically probabilities of infertility and total embryonic mortality and the cumulative distribution of the two phases for time of embryonic mortality during incubation, using a sum of two logistic distributions. This diphasic logistic model was improved upon by Kuurman et al. (2000), using data from Jassim et al. (1996), so that the model could be interpreted more readily biologically, and statistical inferences on model parameters could be made more appropriately. Four aspects of improvement were suggested: 1) probabilities of infertility and total embryonic mortality should be computed directly from observed proportions, not be estimated as model parameters; 2) time of embryonic mortality during incubation should be modeled by a diphasic Weibull distribution, not by a diphasic logistic distribution; 3) distribution parameters should be estimated from noncumulative proportions of mortality, not from cumulative proportions; and 4) parameters should be estimated by maximum likelihood (ML) or minimum Hellinger distance (MHD), not by least squares. The method of MHD is similar to ML but is less sensitive to outliers than ML and, therefore, is a good alternative to ML and by MHD from observed times of mortality.

Time of failure to survive occurs continuously during incubation. In this study, however, similar to Jassim et al. (1996), time of failure to survive was not observed on a continuous time scale \( t \) (\( 0 \leq t \leq 21 \)), rather, it was observed on a discrete time scale \( T \) (\( T = 1, 2, \ldots, 21 \) days). Let \( n_T \) denote the number of embryos that died during Day \( T \) so that the total number of embryos that died during incubation is \( n = \sum_{T=1}^{21} n_T \). The observed proportion of embryos that failed to survive during each Day \( T \) therefore, is \( \text{prop}_T = n_T/n \). To estimate parameters of the distribution for time of failure to survive requires the predicted probability of failure to survive during Day \( T \) (\( T = 1 \leq t \leq T \)). This predicted probability is (Kuurman et al., 2000)

\[
\int_{T-1}^{T} p(\text{fail}; t; \text{mort}) \, dt = \left[ P(\text{fail}; T; \text{mort}) - P(\text{fail}; T - 1; \text{mort}) \right],
\]

which is the difference between cdf for failure to survive evaluated by Day \( T \), \( P(\text{fail}; T; \text{mort}) \), and by Day \( T - 1 \), \( P(\text{fail}; T - 1; \text{mort}) \).

An appropriate cdf for failure to survive is the diphasic Weibull cdf (Kuurman et al., 2000). The Weibull distribution is based on the “weakest link” theory, i.e., an embryo dies if one of its vital functions fails. The Weibull distribution was considered to be more appropriate than the logistic and Log-logistic distributions to model time of failure to survive (Kuurman et al., 2000), because the logistic distribution is greater than zero for time \( t \) \( < 0 \), and goodness-of-fit statistics for the Log-logistic distribution were less favorable. Cumulative probability of failure to survive by time \( t \) therefore, was modeled by

\[
P(\text{fail}; t; \text{mort}) = m_1 W_1(t) + (1 - m_1) W_2(t)
\]

where \( m_1 \) is the proportion of total embryonic mortality in the first phase, and \( 1 - m_1 \) is the proportion in the second phase. For each Phase \( i = 1, 2 \), we assumed that failure to survive by time \( t \) was distributed according to the Weibull cdf

\[W_i(t) = 1 - e^{-\left[\ln(t) - \ln(\gamma_i)\right]^{\lambda_i}}\]

where \( \gamma_i \) and \( \lambda_i \) are parameters to be estimated, and e is the base of the natural logarithm ln. For \( t \leq 0 \), \( W_i(t) \) is
defined to be zero, whereas for \( t > 0 \), \( W_i(t) \) approaches zero asymptotically as \( t \to 0 \) positively or approaches unity as \( t \to +\infty \). Parameter \( \gamma_i \) is a scale parameter and is sometimes called the “characteristic life” because by time \( \gamma_i \) for each Phase \( i \), approximately 63.2% of the embryos have failed to survive (Nelson, 1982). Parameter \( \lambda_i \) is a shape parameter and determines if the probability of failure to survive at time \( t \) for a live embryo, which is not going to survive Phase \( i \), is increasing (\( \lambda_i < e \)), constant (\( \lambda_i = e \)), or decreasing (\( \lambda_i > e \)) as time \( t \) increases (Nelson, 1982).

For each Phase \( i = 1, 2 \), the mean (\( \mu_i \)) and standard deviation (\( \sigma_i \)) are (Kuurman et al., 2000)

\[
\mu_i = \gamma_i \Gamma[\ln(\lambda_i) + 1] \\
\sigma_i = \gamma_i \sqrt{\Gamma[2 \ln(\lambda_i) + 1] - \Gamma[\ln(\lambda_i) + 1]^2}
\]

where \( \Gamma \) denotes the gamma function. These expressions are equivalent, in an alternative form, to those by Nelson (1982).

### Failure Rate

In the study of systems reliability, the reliability function, or survival function, and the hazard function, or failure rate, are important (Hahn and Shapiro, 1967; Nelson, 1982). In general, if the probability that an object has failed by time \( t \) is described by a failure function \( F(t) \), then the probability that the object has not failed by time \( t \) is described by the survival function \([1 - F(t)]\). The probability that the object has failed over a short time given it has not failed by the start of this period is proportional to the failure rate

\[
Z(t) = \frac{f(t)}{1 - F(t)}
\]

where \( f(t) \) is the first derivative of \( F(t) \) with respect to \( t \) (Hahn and Shapiro, 1967; Nelson, 1982).

In this study, interest is in modeling the distribution of failure to survive during incubation, which can be used to predict the probability of failure to hatch. The failure function of an incubated egg is \( P(fail; t) \), which is the cumulative probability of failure to hatch by time \( t \) of incubation. The survival function, therefore, is \( 1 - P(fail; t) \), which is the probability that an incubated egg contains a live embryo by time \( t \) of incubation.

Proportion of failure to hatch by the end of incubation (\( t = 21 \)), among all eggs incubated or among only fertile eggs, is used often to evaluate a hatch. In addition to this proportion, which is observed by the end of incubation, the rate at which a live embryo fails to survive at time \( t \) during incubation also can be of interest. Probability of failure to hatch at time \( t \) of incubation \( p(fail; t) \) is the first derivative of \( P(fail; t) \) with respect to \( t \), thus the failure rate of a live embryo at time \( t \) of incubation is

\[
Z(t) = \frac{p(fail; t)}{1 - P(fail; t)}
\]

which is proportional to the probability that a live embryo dies at time \( t \).

### Data

Data for this experiment were from eggs that were produced by a commercial layer line of chickens. The experiment comprised 110 sires and 110 groups of about 16 dams each. The 16 dams in each group were paternal half-sibs and were housed two per cage. Each group of dams was artificially inseminated twice a week throughout the experiment with semen from the same sire. There were two hatches: Hatch 1 and Hatch 2. Starting 1 wk after the first insemination of the experiment, eggs for Hatch 1 were collected and accumulated in storage from 2 through 18 d. Starting the day after egg collection was completed for Hatch 1, eggs for Hatch 2 were collected and accumulated in storage from 2 through 14 d.

Within each hatch, eggs were stored at 12.8 to 14.4 C with 85% RH; eggs stored for 1 wk or less were large end up, and eggs stored longer than 1 wk were small end up. After storage, eggs within each hatch were prewarmed at 24.4 C for 8 h, and then incubated at 37.5 C with 85% RH for 21 d. Eggs from Hatch 1 were in a different incubator than eggs from Hatch 2; a total of 37,651 eggs was incubated. On Day 18 of incubation, eggs were transferred to a hatcher, and on Day 21, 25,881 eggs hatched, and 516 piped. Of the piped eggs one contained blood, and for analytical purposes the remaining 515 were live pips, assumed to have hatched. The total number of incubated eggs, therefore, was 37,650, of which 26,396 hatched. The distribution of numbers and proportions of eggs that were incubated and that hatched are in Table 1, by hatch and overall. Among eggs incubated overall, the proportion that hatched was 0.70 and so the proportion that failed to hatch was 0.30.

Eggs were candled on Day 6 for Hatch 1 and on Day 9 for Hatch 2 to determine if an egg was clear, i.e., if the egg was infertile or if the embryo failed to survive preincubation or early incubation. Breakout analysis on a total of 11,254 eggs was performed visually, without the aid of a microscope, on eggs that were clear at candling and on eggs that failed to hatch on Day 21 to determine if an egg was infertile or to determine the day of embryonic mortality during incubation. The 8,027 eggs determined to be infertile were truly infertile or had suffered preincubation embryonic mortality. [Microscopic investigation of infertile eggs would have provided more accurate information about actual infertility and pre-incubation mortality.] Each of the 3,227 eggs with a visible dead embryo was assigned a value from 1 through 21, corresponding to the day during which the embryo died.

The distribution of numbers and proportions of eggs that were infertile and that were fertile but suffered embryonic mortality by the end of incubation are in Table 1, by hatch and overall. Among eggs incubated overall,
TABLE 1. Distribution of numbers and proportions of eggs incubated, hatched, infertile, and fertile but suffered embryonic mortality by the end of incubation, by hatch and overall

<table>
<thead>
<tr>
<th></th>
<th>Hatch 1</th>
<th></th>
<th>Hatch 2</th>
<th></th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number</td>
<td>Proportion</td>
<td>Number</td>
<td>Proportion</td>
<td>Number</td>
</tr>
<tr>
<td>Incubated</td>
<td>21,547</td>
<td>1.000</td>
<td>16,103</td>
<td>1.000</td>
<td>37,650</td>
</tr>
<tr>
<td>Hatched</td>
<td>15,477</td>
<td>0.718</td>
<td>10,919</td>
<td>0.678</td>
<td>26,396</td>
</tr>
<tr>
<td>Infertile</td>
<td>3,900</td>
<td>0.181</td>
<td>4,127</td>
<td>0.256</td>
<td>8,027</td>
</tr>
<tr>
<td>Mortality</td>
<td>2,170</td>
<td>0.101</td>
<td>1,057</td>
<td>0.066</td>
<td>3,227</td>
</tr>
</tbody>
</table>

A larger proportion failed to hatch because of infertility (0.21) than because of mortality (0.09). Infertility was lower for Hatch 1 (0.18) than for Hatch 2 (0.26), but mortality was higher for Hatch 1 (0.10) than for Hatch 2 (0.07). Observed numbers $n_T$ and proportions $\text{prop}_T$ of embryos that failed to survive during Day $T$ of incubation are in Table 2, by hatch and overall.

**Estimation of Parameters**

The set of five parameters $\theta = (m_1, \gamma_1, \lambda_1, \gamma_2, \lambda_2)$ for the diphasic Weibull distribution was estimated by ML and by MHD for each hatch and overall. The method of ML is sensitive to outliers in the data (Beran, 1977; Cutler and Cordero-Braña, 1996; He and Fung, 1999), i.e., ML parameter estimates are not robust; the method of MHD in contrast is more robust (Beran, 1977; Simpson, 1987; Cutler and Cordero-Braña, 1996).

The right-hand side of Equation [2] was used to estimate parameters of the probability of failure to survive during Day $T$ by maximizing, with respect to parameters $\theta$, the Log-likelihood function

$$L(\theta) = \sum_{T=1}^{21} n_T \ln [P(\text{fail}; T|\text{mort}) - P(\text{fail}; T-1|\text{mort})]$$

and the Hellinger distance function (Kuurman et al., 2000)

$$H(\theta) = \sum_{T=1}^{21} \sqrt{\text{prop}_T [P(\text{fail}; T|\text{mort}) - P(\text{fail}; T-1|\text{mort})]}.$$
Four goodness-of-fit criteria were used to validate the appropriateness of the diphasic Weibull distribution to model probability of failure to survive during Day T. The first was the coefficient of determination ($R^2$), computed as the square of the correlation between observed and predicted values. The second was the first-order autocorrelation ($\phi$) among residuals ($r_T$) (Miller and Wichern, 1997), computed as

$$\phi = \frac{\sum_{T=1}^{21} (r_T - \bar{r})(r_{T+1} - \bar{r})}{\sum_{T=1}^{21} (r_T - \bar{r})^2}$$

with variance $\sigma^2 = \sum_{T=1}^{21} (r_T - \bar{r})^2/21$ (Miller and Wichern, 1977), where $\bar{r}$ is the average residual and residual $r_T$ is computed as

$$r_T = \text{prop}_T - [P(\text{fail}; T|\text{mort}) - P(\text{fail}; T - 1|\text{mort})]$$

The third was the ML estimate of the SD of residuals ($\sigma_R$), computed as

$$\sigma_R = \sqrt{\frac{1}{21}\sum_{T=1}^{21} (r_T - \bar{r})^2}.$$

Note that the expected average residual is zero. In practice, however, the computed average residual $\bar{r}$ might not be zero. To compute $\phi$ and $\sigma_R$, therefore, each residual $r_T$ was corrected for $\bar{r}$.

The fourth was the value of the cumulative probability of failure to survive by time $t = 21 P(t = 21)$, computed by substituting estimates for parameters in $P(\text{fail}; t = 21|\text{mort})$. This value is an indication of the total proportion of mortality during incubation described by the distribution for time of failure to survive.

Recall that eggs for Hatch 1 were not treated exactly the same as eggs for Hatch 2, i.e., some eggs in Hatch 1 were stored longer than some eggs in Hatch 2; Hatches 1 and 2 were in different incubators; and eggs in Hatch 2 were laid after those in Hatch 1. One or more of these differences could have affected time of embryonic mortality so that time of failure to survive, hypothetically, might have been distributed differently for each hatch. To test this hypothesis a two-sided test was performed on each of the five diphasic Weibull distribution parameter estimates within method of estimation. Difference between hatch results was tested using a Z test, based on the standard normal distribution, because the number of observations in this study was relatively high (2,170 for Hatch 1 and 1,057 for Hatch 2). Note that the Z test is approximate because variances of parameters might not be the same (Hogg and Tanis, 1997). To obtain an overall significance level of $\alpha = 0.05$ for the two-sided hypothesis test, the significance level for each of the five individual tests was set to $0.05/5 = 0.01$, based on the Bonferroni inequality (Miller, 1966).

**RESULTS AND DISCUSSION**

Goodness-of-fit criteria for the distribution for time of failure to survive fitted by ML and by MHD are in Table 3, by hatch and overall. Coefficients of determination ($R^2$) for overall were similar for ML and MHD (0.95). The $R^2$ was higher for Hatch 1 (0.97) than for Hatch 2 (0.72), probably because variances of the observed proportions $\text{prop}_T$ were lower for Hatch 1 than for Hatch 2 as a result of the number of observations for Hatch 1 (2,170) being twice that for Hatch 2 (1,057).

First-order autocorrelation ($\phi$) for overall was slightly closer to zero for ML (–0.30) than for MHD (–0.33). The $\phi$ was slightly closer to zero for Hatch 1 (–0.34) than for Hatch 2 (about –0.37). The negative value for $\phi$ indicates that if an observation were greater than its predicted value on Day T, then it tended to be less than its predicted value on Day $T + 1$ and visa versa. A negative value for $\phi$, therefore, might be considered to be more favorable than a positive value.

The SD of residuals ($\sigma_R$) for overall were the same for ML and MHD (0.015). The $\sigma_R$ for Hatch 1 (0.014) was half that for Hatch 2 (0.028), as expected, because the number of observations for Hatch 1 was twice that for Hatch 2. Predicted cumulative probabilities of failure to survive by time $t = 21 P(t = 21)$ for each hatch and for overall were about the same for ML and MHD (about 0.99). These cumulative probabilities were less than unity, as expected, but they showed that more than 99% of the cumulative probability of failure to survive by time $t = 21$ was predicted by the diphasic Weibull model.

For the diphasic Weibull distribution, goodness-of-fit statistics were more favorable in this study than for those found by Kuurman et al. (2000), probably because this study contained more observations (3,227) than the study of Kuurman et al. (2000), which used data from Jassim et al. (1996) that contained only 43 observations. These results indicate that the diphasic Weibull distribution is appropriate to model time of failure to survive in chickens and, therefore, validates the use of the diphasic Weibull distribution.

Maximum likelihood (ML) and MHD estimates and SE for model parameters and estimates for derived parameters for each phase of embryonic mortality are in Table 4, by hatch and overall. Results for ML and MHD estimates were similar. Overall proportion of embryonic mortality in the first phase ($m_1$) was 0.77; therefore, proportion in the second phase was 0.23. Among embryos that failed to survive during Phase 1, about 63.2% failed to survive by about 2.3 $d$ ($\gamma_1$). For those still alive at time $t$, the probability that they would die decreased as time $t$ increased, because $\lambda_1$ (about 3.5) was greater than $e$. Among embryos that failed to survive during Phase 2, about 63.2% failed to survive by about 18.3 $d$ ($\gamma_2$). For those still alive at time $t$, the probability that they would
die increased as time t increased, because \( \lambda_2 \) (about 1.1) was less than e. For each Phase \( i = 1, 2 \), estimates for \( \gamma_i \) and \( \lambda_i \) were used to compute the derived parameters mean (\( \mu_i \)) and SD (\( \sigma_i \)). For Phase 1 overall, mean time of mortality (\( \mu_1 \)) was about 2.6 d and SD (\( \sigma_1 \)) was about 3.3 d. For Phase 2 overall, mean time of mortality (\( \mu_2 \)) was about 17.4 d and SD (\( \sigma_2 \)) was about 2.0 d. Results for Hatches 1 and 2 have similar interpretations.

Hatches 1 and 2 were not different for \( \gamma_2 \) or \( \lambda_2 \) (\( P > 0.03 \)), whereas they were different for \( m_1, \gamma_1, \) and \( \lambda_1 \) (\( P < 0.001 \)). Time of failure to survive, therefore, was distributed differently (\( P \leq 0.05 \)) in each hatch. To estimate parameters of the diphasic Weibull distribution for data from Jassim et al. (1996), for example, MHD was preferred to ML because the number of observations was relatively small (43), and outliers could have influenced parameter estimates (Kurman et al., 2000).

Observed and predicted probabilities of failure of an embryo to survive during Day T of incubation are in Figure 1 for overall and in Figure 2 for Hatches 1 and 2. Figures 1 and 2 depict the two phases of increased embryonic mortality during early and late incubation. Probabilities of failure to survive during Day T were predicted using ML estimates and could not be distinguished.

Parameter estimates for ML and MHD are asymptotically equivalent as number of observations \( n \rightarrow \infty \) (Beran, 1977; Simpson, 1987). The number of observations was relatively large in this study so that ML is appropriate to estimate parameters. When the number of observations is relatively small, however, MHD is more appropriate to estimate parameters. To estimate parameters of the diphasic Weibull distribution for data from Jassim et al. (1996), for example, MHD was preferred to ML because the number of observations was relatively small (43), and outliers could have influenced parameter estimates (Kurman et al., 2000).

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### Table 3. Goodness-of-fit criteria for the distribution for time of failure to survive fitted by maximum likelihood (ML) and by minimum Hellinger distance (MHD)

<table>
<thead>
<tr>
<th>Goodness-of-fit criterion</th>
<th>Hatch 1</th>
<th>Hatch 2</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ML</td>
<td>MHD</td>
<td>ML</td>
</tr>
<tr>
<td>( R^2 )</td>
<td>0.970</td>
<td>0.970</td>
<td>0.721</td>
</tr>
<tr>
<td>( \phi )</td>
<td>-0.338</td>
<td>-0.336</td>
<td>-0.368</td>
</tr>
<tr>
<td>( \sigma_\phi )</td>
<td>0.074</td>
<td>0.073</td>
<td>0.088</td>
</tr>
<tr>
<td>( \sigma_R )</td>
<td>0.014</td>
<td>0.014</td>
<td>0.028</td>
</tr>
<tr>
<td>( P(t = 21) )</td>
<td>0.993</td>
<td>0.996</td>
<td>0.992</td>
</tr>
</tbody>
</table>

1Coefficient of determination (\( R^2 \)), first-order autocorrelation (\( \phi \)) and its SE (\( \sigma_\phi \)), maximum likelihood estimate of residual SD (\( \sigma_R \)), and cumulative probability of failure to survive by time \( t = 21 \) [\( P(t = 21) \)], by hatch and overall.

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### Table 4. Maximum likelihood (ML) and minimum Hellinger distance (MHD) estimates and SE for model parameters and estimates for derived parameters for each Phase \( i = 1, 2 \) of the distribution for time of failure to survive incubation, by hatch and overall

<table>
<thead>
<tr>
<th>Parameter1</th>
<th>Method</th>
<th>Estimate</th>
<th>SE</th>
<th>SE</th>
<th>SE</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Hatch 1</td>
<td></td>
<td>Hatch 2</td>
<td></td>
<td>Overall</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ML</td>
<td>0.79</td>
<td>0.010</td>
<td>0.72</td>
<td>0.017</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MHD</td>
<td>0.80</td>
<td>0.009</td>
<td>0.73</td>
<td>0.016</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ML</td>
<td>1.97</td>
<td>0.082</td>
<td>3.39</td>
<td>0.176</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MHD</td>
<td>1.81</td>
<td>0.069</td>
<td>3.30</td>
<td>0.167</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ML</td>
<td>3.95</td>
<td>0.153</td>
<td>2.75</td>
<td>0.103</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MHD</td>
<td>3.86</td>
<td>0.136</td>
<td>2.74</td>
<td>0.102</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ML</td>
<td>18.32</td>
<td>0.104</td>
<td>18.22</td>
<td>0.150</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MHD</td>
<td>18.37</td>
<td>0.093</td>
<td>18.04</td>
<td>0.154</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ML</td>
<td>1.10</td>
<td>0.006</td>
<td>1.11</td>
<td>0.009</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MHD</td>
<td>1.09</td>
<td>0.004</td>
<td>1.11</td>
<td>0.008</td>
</tr>
</tbody>
</table>

Parameter estimates for ML and MHD are asymptotically equivalent as number of observations \( n \rightarrow \infty \) (Beran, 1977; Simpson, 1987). The number of observations was relatively large in this study so that ML is appropriate to estimate parameters. When the number of observations is relatively small, however, MHD is more appropriate to estimate parameters. To estimate parameters of the diphasic Weibull distribution for data from Jassim et al. (1996), for example, MHD was preferred to ML because the number of observations was relatively small (43), and outliers could have influenced parameter estimates (Kurman et al., 2000).

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Within a row for Hatches 1 and 2, parameter estimates with the same superscript are not different (\( P > 0.01 \)); those with different superscripts are different (\( P \leq 0.01 \)).

1In days, except \( m_1 \).
FIGURE 1. Overall observed (○) and predicted (——) probabilities of failure of an embryo to survive during Day T of incubation.

Visualized from probabilities predicted using MHD estimates.

Observed and predicted cumulative probability of failure to hatch by time t of incubation \( P(fail; t) \) are in Figure 3 for Hatches 1 and 2. Predicted probabilities for Hatches 1 and 2 were computed by substituting into Equation [1] the observed proportions of infertility and mortality (Table 1) and the model parameters estimated by ML (Table 4). Predicted cumulative probability of failure to hatch increased to 0.28 for Hatch 1 and 0.32 for Hatch 2 by the end of incubation.

Predicted failure rates of a live embryo at time t of incubation \( Z(t) \) are in Figure 4 for Hatches 1 and 2. Predicted failure rates were computed by substituting into Equation [5] the observed proportions of infertility and mortality (Table 1) and the model parameters estimated by ML (Table 4). Failure rate was relatively high at the start and at the end of incubation, corresponding to the two phases of increased embryonic mortality. During the first 3 d of incubation, failure rate for Hatch 1 was higher than for Hatch 2. During the remaining days of incubation, however, failure rates for Hatches 1 and 2 were about the same. The difference between Hatches 1 and 2 for failure rate was due to differences in the distribution for time of failure to survive and in the proportions of infertility and mortality, probably caused by environmental effects and not by genetic effects.

Failure rates can be useful to assess conditions during incubation that can be changed, e.g., temperature or relative humidity. Different failure rates show how conditions during incubation differed in sustaining life at time t of incubation. A high failure rate shows that conditions are not favorable to sustain life, whereas a low failure rate shows that conditions are favorable. Application of the condition that has the lowest failure rate on a particular day of incubation to a future incubation might help to increase hatchability.

The objective of this paper was to validate an improved model to describe failure to hatch on an independent data.
set obtained from two hatches of chickens and to examine
the effect of hatch on the distribution for failure of an
embryo to survive incubation. The diphasic Weibull dis-
btribution appropriately assessed failure of an embryo to
survive during incubation. Maximum likelihood (ML)
and MHD were used to estimate distribution parameters,
based on noncumulative observed proportions of failure
to survive during incubation. The method of MHD is
useful if data contain outliers, because MHD is more
robust than ML to estimate distribution parameters. The
diphasic Weibull distribution can be used to analyze ef-
fects of management and genetics on the distribution of
embryonic mortality during incubation. Failure rate can
be used to indicate on which days during incubation the
probability that a live embryo dies is different between
hatches.

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REFERENCES

Beran, R., 1977. Minimum Hellinger distance estimates for para-
Byerly, T. C., 1930. Time of occurrence and probable causes
Proceedings of the 4th World’s Poultry Congress. H.M. Sta-
tionary Office, London, UK.
Assoc. 91:1716–1723.
Wallingford, UK.
Hahn, G. J., and S. S. Shapiro, 1967. Statistical Models in Engi-
Inference. Prentice Hall, Upper Saddle River, NJ.
Jassim, E. W., M. Grossman, W. J. Koops, and R.A.J. Luykx,
1996. Multiphasic analysis of embryonic mortality in chick-
Kuurman, W. W., B. A. Bailey, W. J. Koops, and M. Grossman,
2000. A model for failure of a chicken embryo to survive
incubation. Technical Report 77. Department of Statistics,
University of Illinois, Champaign, IL.
John Wiley and Sons, New York, NY.
Miller, B., and D. W. Wichern, 1977. Intermediate Business Sta-
of embryonic development. Pages 244–337 in: Fertility and
Hatchability of Chicken and Turkey Eggs. L. W. Taylor, ed.
John Wiley and Sons, New York, NY.
Sons, New York, NY.
Payne, L. F., 1919. Distribution of mortality during the period
Rahn, H., A. Ar, and C. V. Paganelli, 1979. How bird eggs
Israel.
Scott, T. A., and C. J. Mackenzie, 1993. Incidence and classifica-
tion of early embryonic mortality in broiler breeder chickens.
some analysis of early embryonic mortality in layer and
Whitehead, C. C., M. H. Maxwell, R. A. Pearson, and K. M.
Herron, 1985. Influence of egg storage on hatchability, em-
byronic development and vitamin status in hatching broiler
Media/Cambridge University Press, Cambridge, UK.
Yoo, B. H., and E. Wientjes, 1991. Rate of decline in hatchability
with preincubation storage of chicken eggs depends on ge-