Multiphasic Analysis of Embryonic Mortality in Chickens

E. W. JASSIM,* M. GROSSMAN,* W. J. KOOPS,† and R.A.J. LUYKX‡

*Department of Animal Sciences, University of Illinois, Urbana, Illinois 61801, †Department of Animal Husbandry, Wageningen Agricultural University, P.O. Box 338, 6700 AH Wageningen, The Netherlands, and ‡Hybro R&D, Euribrid B.V., 5830 AA Boxmeer, The Netherlands

ABSTRACT Infertility and embryonic mortality are economically important for the commercial broiler industry because they are components of hatchability. Embryonic mortality in chickens is not uniformly distributed over the course of incubation; two phases of embryonic mortality are characteristic of chicken development.

The objective of this paper was to develop a mathematical model to assess infertility and to characterize the distribution over time of embryonic mortality in chickens. A model was constructed based on evidence in the literature for multiple phases of embryonic mortality before and during incubation. A multiphasic model, with two phases, included parameters for the proportion of eggs that were infertile and the proportion that were fertile but the embryo died before or during incubation. For those eggs that were fertile but the embryo died, the model included the proportion of embryonic mortality during each phase, day of peak mortality, and duration of phase.

Data on embryonic mortality for white Cornish chickens were used to illustrate the multiphasic model. Model parameters could be estimated easily and interpreted with clear biological meaning. Estimates of parameters, in general, were reasonably precise and consistent with the literature. With multiphasic analysis, one can assess infertility and characterize the distribution of embryonic mortality in chickens, which can lead to a useful understanding of management and genetic aspects of these components of hatchability.

(Key words: multiphasic analysis, infertility, embryonic mortality, hatchability, chicken)

1996 Poultry Science 75:464-471

INTRODUCTION

Infertility and embryonic mortality are of great economic importance for the commercial broiler industry because they are components of hatchability. Embryonic mortality in chickens is influenced by nutrition (Beer, 1969), management (Byerly, 1938; Lundy, 1969), and genetic factors (Byerly et al., 1934; Landauer, 1951; Cole, 1969; Hutt, 1969). Embryonic mortality at early (0 to 11 d) and late (12 to 22 d) periods of development has been shown to be lowly heritable (Brah et al., 1991), as expected for dichotomous traits with one class at low frequency.

Embryonic mortality in chickens is not uniformly distributed over the course of incubation. About 65% of embryonic mortality occurs in two phases: an early phase, with a peak at about Day 4 of incubation, and a late phase, with a peak at about Day 19 of incubation (Payne, 1919). Two phases of embryonic mortality are characteristic of avian development (e.g., Byerly, 1931; Bronkhorst, 1933; Insko and Martin, 1935; Romanoff, 1949; Moseley and Landauer, 1949; Landauer, 1951).

Phases of embryonic mortality are associated with major changes in embryo metabolism. The first phase coincides with the period of peak lactic acid production (Romanoff, 1949), and occurs during a change in carbon dioxide elimination (Landauer, 1951) and during the time that the mesonephros, part of the embryonic kidney, first functions (Byerly, 1931). The second phase coincides with the period when the demand for oxygen increases significantly (Rol’nik, 1970). Events associated with the second phase of embryonic mortality may even cause death for several days after hatching (Otrygan’eva, 1963).

Multiphasic models have been used to study several biological phenomena, including growth (Grossman and Koops, 1988) and egg production (Koops and Grossman, 1992) in chickens and, most recently, nonreturn rates in dairy bulls (Koops et al., 1995; Grossman et al., 1995). In general, a multiphasic model assumes that a biological process occurs in phases, usually over the course of time. In this study, the model assumes that embryonic mortality occurs in several phases before and during the period of incubation.
MULTIPHASIC ANALYSIS OF EMBRYONIC MORTALITY

Day of incubation

FIGURE 1. For eggs that failed to hatch (• • •) with probability f, the course of probability for groups: G1 (--; ), eggs that were infertile with probability g; and G2 (--; --), eggs that were fertile but the embryo died with probability (f - g).

Using a multiphasic analysis to study the components of hatchability, infertility, and embryonic mortality, can lead to a useful understanding of management and genetic aspects. The objective of this paper, therefore, was to develop a mathematical model to assess infertility and to characterize the distribution over time of embryonic mortality in chickens. Data on embryonic mortality provided by Euribrid B.V., the Netherlands, were used to illustrate the model.

MATERIALS AND METHODS

Mathematical Model

All eggs set and incubated can be divided into those that failed to hatch, with probability f, and those that hatched, with probability (1 - f). Those eggs that failed to hatch can be divided further into two groups (Figure 1): Group 1 (G1), those that were infertile, with probability P(G1) = g; and Group 2 (G2), those that were fertile but the embryo died either before incubation (before oviposition or during storage) or during incubation, with probability P(G2) = (f - g).

Those eggs in Group 1 have a constant probability (g) of being infertile. Those eggs in Group 2, however, have a probability (f - g) of embryonic mortality that is not constant, but can be distributed over phases. With two phases, for example, there may be an early phase, in which the embryo died before incubation or during the early part of incubation, and a late phase, in which the embryo died during the late part of incubation or soon after hatching (Figure 1).

To assess infertility and to characterize the distribution of embryonic mortality, we will consider only those eggs that failed to hatch: those that were infertile (Group 1) and those that were fertile but the embryo died before or during incubation (Group 2). Probability of failure to hatch, therefore, is the probability of infertility or embryonic mortality by time t, P(t), which can be written as:

\[ P(t) = \sum_{i=1}^{2} P(t \mid G_i)P(G_i) \]  

[1]

where \( P(t \mid G_i) \) is the conditional probability of infertility or embryonic mortality by time t, given Group i (i = 1, 2). The conditional probability for each group will be examined separately.

Group 1: Given that eggs are infertile (Figure 1), the conditional probability of infertility is unity:

\[ P(t \mid G_1) = 1 \]  

[2]

Group 2: Given that eggs are fertile but the embryo died before or during incubation (Figure 1), the conditional probability of embryonic mortality by time t can be expressed in general as a sum of n logistic functions:

\[ P(t \mid G_2) = \sum_{i=1}^{n} \frac{m_i}{1 + e^{(t - q_i)/d_i}} \]  

[3]

where n is the number of phases; e is the base of the natural logarithms; and, for phase i, \( m_i \) is the proportion of embryonic mortality during that phase, subject to the constraint that \( \sum_{i=1}^{n} m_i = 1 \), so that \( m_n = 1 - \sum_{i=1}^{n-1} m_i \); \( q_i \) is the day of peak mortality; and \( 4d_i \) is a measure in days of duration of the phase, and includes about 96% of mortality during that phase (Koops and Grossman, 1991). Such a function has the property of constraining probabilities within each phase to a lower asymptote of zero for \( t < q_i \) and an upper asymptote of \( m_i \) for \( t > q_i \). Because of the possibility that the embryo died before incubation (\( t < 0 \)), \( P(t \mid G_2) \) may not equal zero at \( t = 0 \) (Figure 1).

Finally, probability of infertility or embryonic mortality by time t, \( P(t) \), is modeled by substituting [2] and [3] into [1] to yield the multiphasic model:

\[ P(t) = g + (f - g) \left[ \sum_{i=1}^{n} \frac{m_i}{1 + e^{(t - q_i)/d_i}} \right] \]  

[4]

Data

White Cornish parents used to produce eggs for this study were hatched on 23 March 1994. Between 30 and 33 wk of age, each of four males was allowed to mate in a pen with seven females. For each of two hatches, eggs were collected and stored at 16 C and 75% relative humidity. For Hatch 1, eggs were collected and stored between 18
October through 31 October; incubation began on 1 November 1994. For Hatch 2, eggs were collected and stored between 1 November through 14 November; incubation began on 15 November 1994.

Temperature of the incubator was 37.6°C and relative humidity was 56%. On Day 18 of incubation, eggs were transferred to the hatcher, where temperature was 37.4°C and relative humidity was 57%. On Day 19, relative humidity was increased to 80%.

A total of 428 eggs was set, and eggs were candled individually on Days 6, 9, 18, and 21 of incubation. The hatchery manager determined infertility or day of death by breakout analysis of those eggs that were suspected of being infertile or of having suffered embryonic death. Number of infertile eggs and number of eggs containing a dead embryo were recorded by dam, sire, and hatch, for each day of incubation. An egg that was determined to be infertile or that was fertile but the embryo died before incubation was recorded as infertile on Day 0 (Table 1).

For an egg that is candled at 7 d or earlier, it is difficult to distinguish with certainty between one that is infertile and one that is fertile but the embryo died before incubation (Munro and Kosin, 1945; Hutt, 1969; North and Bell, 1990).

For Day 0 and for each day of incubation, from Day 1 through Day 21, number of eggs that were infertile or that contained a dead embryo was cumulated to obtain the cumulative number (Table 1). Each cumulative number was then divided by total number of eggs set to obtain the relative cumulative number, or cumulative proportion (Table 1).

Seven eggs recorded as "pipped" survived through incubation but did not hatch; therefore, they were not included in the analysis. Such eggs were counted as if they hatched, thus causing the estimate of failure to hatch (f) to be biased downward. Infertile eggs that may have developed pathogenetically and died during incubation, however, were included in the analysis. Such eggs, although low in frequency, would be counted as if they were fertile, thus causing the estimate of infertility (g) to be biased downward.

Estimation of Parameters

Results from the literature indicate that embryonic mortality in chickens is distributed over two phases. For [4], therefore, we assumed a diphasic (n = 2) model

\[
P(t) = g + (f - g) \left\{ \frac{m_1}{1 + e^{\frac{t - c_1}{d_1}}} + \frac{1 - m_1}{1 + e^{\frac{t - c_2}{d_2}}} \right\}
\]

where parameters were defined for [4], and where \( m_1 \) is the proportion of embryonic mortality during Phase 1 and \( 1 - m_1 \) is the proportion of embryonic mortality during Phase 2.

To assess infertility and to characterize the distribution of embryonic mortality over time, Equation [5] was fitted to cumulative proportion (Table 1), first overall, for a general interpretation, then for each of the two hatches, for a view of the difference between hatches, and finally for each of the four sires, for a view of differences among sires. Parameters were estimated by nonlinear regression, using an adaptive nonlinear least squares algorithm (Sherrod, 1992). A default value of \( 1 \times 10^{-10} \) was used for the tolerance factor, which specifies the convergence criterion for the iterative estimation procedure. Goodness of fit for the model was measured by residual standard error.

RESULTS AND DISCUSSION

Estimates and standard errors for proportion of eggs that failed to hatch (f), proportion of eggs that were infertile (g), proportion of embryonic mortality in Phase 1 (m1), day of peak mortality for Phase 1 (c1), days of duration of Phase 1 (d1), day of peak mortality for Phase 2 (c2), and days of duration of Phase 2 (d2), and the residual standard error are in Table 2, overall, by hatch, and by sire. Each estimate was statistically significant (P < 0.001), except as noted in the table.

Cumulative proportion and predicted course for probability of failure to hatch are in Figure 2 for overall (---) and predicted probability for failure to hatch for Phase 1 overall (-----) and for Phase 2 overall (-----), at each day of incubation.

FIGURE 2. Cumulative proportion for failure to hatch for overall (•) and predicted course of probability for failure to hatch for overall (-----). Actual proportion for failure to hatch for overall (○) and predicted probability for failure to hatch for Phase 1 overall (-----) and for Phase 2 overall (-----), at each day of incubation.
TABLE 1. Number of eggs set, number of infertile eggs (Inf. eggs), number of dead embryos for each day of incubation, by sire, by hatch, and overall; and cumulative number (CN) and cumulative proportion (CP), by hatch and overall.

<table>
<thead>
<tr>
<th>Sire</th>
<th>Eggs set (n)</th>
<th>Inf. eggs</th>
<th>Day of incubation</th>
<th>(Hatch 1)</th>
<th>Hatch 2</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>55</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>36</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>6</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>7</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>3</td>
<td>48</td>
<td>4</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>9</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>10</td>
<td>2</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>4</td>
<td>76</td>
<td>21</td>
<td>11</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>12</td>
<td>2</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>13</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>215</td>
<td>25</td>
<td>14</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>CN</td>
<td>25</td>
<td>29</td>
<td>15</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>CP</td>
<td>0.116</td>
<td>0.135</td>
<td>16</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.149</td>
<td>17</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.191</td>
<td>18</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.205</td>
<td>19</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.205</td>
<td>20</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.205</td>
<td>21</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Overall:

| CN | 55 | 61 | 66 | 77 | 79 | 81 | 84 | 84 | 84 | 85 | 85 | 85 | 85 | 86 | 86 | 87 | 92 | 93 | 97 | 98 |
| CP | 0.128 | 0.142 | 0.154 | 0.180 | 0.185 | 0.189 | 0.196 | 0.196 | 0.196 | 0.199 | 0.199 | 0.199 | 0.199 | 0.201 | 0.201 | 0.203 | 0.215 | 0.217 | 0.227 | 0.229 |
probability results in the predicted course of probability for failure to hatch.

**Overall**

Overall (Table 2 and Figure 2), proportion of eggs that failed to hatch ($f$) was about 0.23, which means that about 77% of eggs hatched. Proportion of eggs that were infertile ($g$) was about 0.12, which means that about 88% of eggs were fertile.

An estimate for proportion of eggs that were infertile (0.115, Table 2) is a measure of the "true" proportion of infertile eggs and not a measure of the observed proportion of "infertile" eggs (0.128, Table 1), because the observed proportion includes those eggs that were infertile as well as those that were fertile but the embryo died before incubation. Thus, the difference (0.013) between the observed and the estimated proportion of infertile eggs is a measure of the proportion of eggs that were fertile but the embryo died before incubation.

Proportion of eggs that were fertile but the embryo died before or during incubation ($f - g$) was 0.11. For those eggs (Figure 2), about 0.70 ($m_1$) of the embryos died during Phase 1, the early phase, which means that about 0.30 ($1 - m_1$) died during Phase 2, the late phase. Peak mortality was at 1.9 d ($c_1$) for the early phase and at 18.4 d ($c_2$) for the late phase. Duration was about the same for each phase: 4.6 d ($4d_1$) for the early phase and about 4.8 d ($4d_2$) for the late phase.

**Hatches**

Proportion of eggs that failed to hatch ($f$) was about 0.25 for Hatch 1 and about 0.22 for Hatch 2 (Table 2 and Figure 3). Proportion of eggs that were infertile ($g$) was about 0.10 for Hatch 1 and about 0.14 for Hatch 2. The difference between the observed (Table 1) and the estimated (Table 2) proportion of infertile eggs was 0.02 for Hatch 1 and 0.005 for Hatch 2. Although the difference between hatches is fourfold, it is of little practical importance.

Proportion of eggs that were fertile but failed to hatch ($f - g$) was about 0.15 for Hatch 1 and about half of that (0.08) for Hatch 2. For those eggs (Figure 3), the proportion of embryos that died during the early phase of incubation ($m_1$) was about 0.73 for Hatch 1 but only about 0.63 for Hatch 2. Consequently, the proportion of embryos that died during the late phase ($1 - m_1$) was about 0.27 for Hatch 1 and about 0.37 for Hatch 2. Thus, most embryonic mortality occurred during the early phase compared with the late phase, but more so for Hatch 1 than for Hatch 2.
MULTIPHASIC ANALYSIS OF EMBRYONIC MORTALITY

TABLE 2. Estimates (Est) and standard errors (SE) for proportion of eggs that failed to hatch (f), proportion of eggs that were infertile (g), proportion of embryonic mortality in phase 1 (m1), day of peak mortality for phase 1 (c1), days of duration of phase 1 (4d1), day of peak mortality for phase 2 (c2), and days of duration of phase 2 (4d2), and the residual standard error, overall, by hatch, and by sire.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Hatch</th>
<th>Sire</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Overall</td>
<td>1</td>
</tr>
<tr>
<td>f</td>
<td>Est</td>
<td>0.233</td>
</tr>
<tr>
<td></td>
<td>SE</td>
<td>0.005</td>
</tr>
<tr>
<td>g</td>
<td>Est</td>
<td>0.115</td>
</tr>
<tr>
<td></td>
<td>SE</td>
<td>0.008</td>
</tr>
<tr>
<td>m1</td>
<td>Est</td>
<td>0.696</td>
</tr>
<tr>
<td></td>
<td>SE</td>
<td>0.044</td>
</tr>
<tr>
<td>c1</td>
<td>Est</td>
<td>1.90</td>
</tr>
<tr>
<td></td>
<td>SE</td>
<td>0.29</td>
</tr>
<tr>
<td>4d1</td>
<td>Est</td>
<td>4.60</td>
</tr>
<tr>
<td></td>
<td>SE</td>
<td>0.66</td>
</tr>
<tr>
<td>c2</td>
<td>Est</td>
<td>18.44</td>
</tr>
<tr>
<td></td>
<td>SE</td>
<td>0.51</td>
</tr>
<tr>
<td>4d2</td>
<td>Est</td>
<td>4.82**</td>
</tr>
<tr>
<td></td>
<td>SE</td>
<td>1.35</td>
</tr>
<tr>
<td>Residual</td>
<td>SE</td>
<td>0.0024</td>
</tr>
</tbody>
</table>

1 Each estimate is statistically significant at the 0.001 level of probability, except as noted.

*P ≤ 0.10.

*P ≤ 0.05.

**P ≤ 0.01.

Peak mortality during the early phase (c1) was about 1.8 d for Hatch 1 and 2.0 d for Hatch 2. Peak mortality during the late phase (c2) was at about 17.8 d for Hatch 1 and about 18.9 d for Hatch 2.

Duration of the early phase (4d1) was about 5 d for Hatch 1 and about 3.7 d for Hatch 2. Duration of the late phase (4d2) was about 6.7 d for Hatch 1, but about 2.7 d for Hatch 2. Note that the standard error for duration of the late phase for Hatch 1 is larger than those for other durations. This relatively large standard error may be due to a smaller proportion of embryonic deaths in the late phase of Hatch 1 distributed over a longer period of time (Figure 3).

The model fitted Hatch 2 better (residual SE = 0.0021) than Hatch 1 (residual SE = 0.0036).

**Sires**

For infertility and for many characteristics of embryonic mortality, results for Sire 4 deviated from results for the other three sires (Tables 1 and 2); thus, results for Sire 4 will be discussed in comparison with average results for the other sires. Results for Sires 1, 2, and 3 are in Figure 4, whereas results for Sire 4 are in Figure 5.

Proportion of eggs that failed to hatch (f) averaged about 0.15 for Sires 1, 2, and 3 (Table 2 and Figure 4) and was about 0.43 for Sire 4 (Table 2 and Figure 5). Proportion of eggs that were infertile (g) averaged about 0.05 and was about 0.03 for Sire 4, which was not significantly different from zero. The difference between the observed (computed from Table 1) and the estimated (Table 2) proportion of infertile eggs averaged 0.001 and was 0.284 for Sire 4. There were almost no eggs that were fertile but the embryo died before incubation for Sires 1, 2, and 3, whereas this proportion was almost 30% for Sire 4.

For the proposed model, the high estimate for Sire 4 may be due to the high number of dead embryos observed on Day 1 relative to the number observed on Day 2 (Table 1 and Figure 5), in contrast to the numbers observed for Sires 1, 2, and 3 (Table 1 and Figure 4). This means that the slope of the curve at Day 1 is steeper for Sire 4 than for the other sires, which results in a higher estimate of the proportion of dead embryos before incubation for Sire 4 than for the other sires. The higher number of dead embryos observed on Day 1 for Sire 4 may be due, in part, to the difficulty in determining whether an embryo died before incubation, on Day 1, or on Day 2.

Proportion of eggs that were fertile but failed to hatch (f - g) averaged about 0.1 for Sires 1, 2, and 3 (Table 2 and Figure 4), but was about 0.4 for Sire 4 (Table 2 and Figure 5). For those eggs, the proportion of embryos that died during the early phase of incubation (m1) averaged about 0.58, but was about 0.92 for Sire 4. Consequently, the proportion that died during the late phase (1 - m1) averaged about 0.42, but was only about 0.08 for Sire 4.

Again, most embryonic mortality occurred during the early phase compared with the late phase, but more so for Sire 4 than for the other sires.

Peak mortality during the early phase (c1) was on average at about 2.5 d for Sires 1, 2, and 3 (Table 2 and Figure 4), but at -3.0 d with a high standard error for Sire 4 (Table 2 and Figure 5). The reason for this negative
The objective of this paper was to develop a mathematical model to assess infertility and to characterize the distribution over time of embryonic mortality in chickens. A model was constructed based on evidence in the literature for multiple phases of embryonic mortality before and during incubation. A multiphasic model, with two phases, included parameters for the proportion of eggs that failed to hatch and the proportion that were infertile. For those eggs that were fertile but the embryo died before or during incubation, the model included the proportion of embryonic mortality during each phase, day of peak mortality, and duration of phase.

Data on embryonic mortality for white Cornish chickens were used to illustrate the multiphasic model. Model parameters could be estimated easily and interpreted with clear biological meaning. Estimates of parameters, in general, were reasonably precise and consistent. Low numbers of observations for embryonic mortality increases the risk that observed distribution of embryonic mortality, between and within phases, will deviate from the expected distribution under the proposed model. For example, it is impossible to fit the late phase if embryonic mortality occurs only during the early phase.

With multiphasic analysis, one can assess infertility and characterize the distribution of embryonic mortality in chickens, which can lead to a useful understanding of the management and genetic aspects of these components of hatchability.

ACKNOWLEDGMENTS

Cor Aldenzee, Euribrid B. V., collected the data for this study, and Rohan L. Fernando, University of Illinois, provided helpful discussions. Students in a course on scientific writing taught at Wageningen Agricultural University, the Netherlands, provided useful suggestions to improve the first draft of the manuscript.

This paper is dedicated to the memory of B. B. Bohren, mentor of M. Grossman and Professor Emeritus of Genetics, Purdue University Department of Animal Sciences, who dedicated part of his professional career to studying the genetics of hatchability in chickens.

REFERENCES


Landauer, W., 1951. The Hatchability of Chicken Eggs as Influenced by Environment and Heredity. Bulletin 262, revised. Storrs Agricultural Experiment Station, University of Connecticut, Storrs, CT.


