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The effect of egg size on growth and survival of the Tree Sparrow *Passer montanus* nestlings

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**Abstract.** The paper analyses the effect of egg dimensions (volume, breadth, and length) on the growth and development of Tree Sparrow nestlings on successive days of life. Egg size did not influence nestling mortality. It was found that for most days of nestling life, the mean volume and breadth of eggs were positively correlated with the mean mass of nestlings in the nest. Similarly, the deviation of the volume and breadth of a particular egg from the mean egg volume and breadth in the clutch was positively correlated with the deviation of nestling mass from the mean nestling mass in the nest. Nestling growth and development in terms of asymptotic mass (g), maximum growth rate (g/day), tarsus length, and longest remex length were also positively correlated with egg size. The effect of egg size was particularly pronounced in the period of termination of intensive growth rate, development of thermoregulation, and feather development. It is possible that larger eggs contain more microelements, hormones, antioxidants, and vitamins.

**Key words:** Tree Sparrow, *Passer montanus*, egg size, nestling growth, survival

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**INTRODUCTION**

Life history theory views the number and size of the offspring produced in a single reproductive event as having been adjusted by evolution to optimize individual fitness, including evolved reactions to environmental conditions (Stearns 1994). Egg size in birds shows a great deal of variation within avian populations but varies little within individuals (Christians 2002). Among many assumptions made by Bernardo (1996a) or quoted by him, there is one stating that offspring fitness increases as a function of per offspring investment, and that the amount of resources allocated to the propagule come at the cost to the parental decreased fecundity and hence fitness. Propagule size is the relevant variable affecting offspring fitness. According to Bernardo (1996b) “maternal effects then are a part of offspring’s phenotype that does not result from the action of its own genes and the interactions of those genes with its environment”. Maternal (paternal) effect is a direct effect of a parent’s phenotype on the phenotype of its offspring.

Poultry breeders know for a long time that larger eggs produce larger chickens that grow and survive better (e.g. Halbersleben & Mussehl 1922, Wiley 1950). In wild birds, the study of this problem was initiated in the 1970s (Parsons 1970, Schifferli 1973), but already in 1994, Williams
(1994) could sum up the results of 40 papers. Among them, only 11 deal with altricial birds, including nine passerines. After the review by Williams (1994), several papers were published on the relation of egg size to growth and survival of passerine nestlings (e.g. Smith et al. 1995, Smith & Bruun 1998, Reed 1999, Styrsky et al. 1999). Styrsky et al. (1999) found that the mass of nestling House Wren *Troglodytes aedon* was related to the mean egg mass in the clutch by day 6 in the first brood, and by day 10 in the second brood. Smith & Bruun (1998) found a similar relationship in Starlings *Sturnus vulgaris* by day 7, and Reed et al. (1999) even for a shorter period in Red-winged Blackbirds *Agelaius phoeniceus*.

Larger eggs may be advantageous for two reasons: 1) they may give rise to nestlings which are structurally larger or which hatch at a more advanced stage of development, 2) they may produce nestlings which hatch with larger nutrient reserves (O'Connor 1979). The relative importance of these two different effects of large eggs to offspring fitness may vary between species (Ricklefs et al. 1978).

In contrast to other groups of birds, maternal or paternal quality during the nestling period can have a greater effect on growth and survival of altricial birds than does egg size (Reid & Boersma 1990, Bolton 1991, Williams 1994). For this reason, maternal effect should be eliminated when analyzing the effect of egg size on nestling growth and survival. The strength of the relationship between egg parameters indicative of female condition and nestling performance has been evaluated only in part.

The objective of this paper is to test the hypothesis that egg size *per se* influences the growth, development, and survival of nestling Tree Sparrow. We will evaluate relationships between egg size and the mass of nestlings on successive days of life, as well as other parameters of nestling development. These problems have not been examined in this taxonomic and ecological group, and many authors emphasize that the effect of egg size on nestling fitness can differ among species (Ricklefs et al. 1978, Reed et al. 1999).

### STUDY AREA, MATERIAL AND METHODS

The study was carried out in the villages situated between the Vistula river and Kampinos National Park, about 15 km NW of Warsaw, Poland (52°20'N, 20°50'E), where 200 nest-boxes were erected. The data were collected from 15 April to 20 August in 1994 and from 20 April to 20 July in 1995. In total, 261 clutches (1332 eggs) were analyzed, including 125 in 1994 and 136 in 1995 (Table 1). They were dominated by 5-egg clutches (49%), and 6-egg clutches (38.7%). Other clutch sizes (3-, 4-, and 7-egg) were rare, so they were not analyzed. In the analyzed clutches, 1167 nestling Tree Sparrows were examined, including 560 in 1994 and 607 in 1995 (Table 1).

Eggs were marked with a permanent marker on the day of laying, so that we knew the laying sequence. The egg length (L) and maximum breadth (B) were measured to the nearest 0.1 mm, using vernier calipers. Using this formula:

$$V = 0.00051 \times L \times B^2$$

we calculated the egg volume in cm³ (Hoyt 1979).

To know from which egg a nestling hatched, nest-boxes were visited during hatching three times a day — in the morning (6.30–10.00), at

<table>
<thead>
<tr>
<th>Year</th>
<th>Brood</th>
<th>N of clutches</th>
<th>N of nestlings</th>
<th>N of nestlings hatched from known eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>all</td>
</tr>
<tr>
<td>1994</td>
<td>1</td>
<td>64</td>
<td>300</td>
<td>83</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>38</td>
<td>169</td>
<td>71</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>23</td>
<td>91</td>
<td>31</td>
</tr>
<tr>
<td>1995</td>
<td>1</td>
<td>58</td>
<td>264</td>
<td>55</td>
</tr>
<tr>
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<td>44</td>
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<td>112</td>
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<tr>
<td></td>
<td>3</td>
<td>34</td>
<td>141</td>
<td>68</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>261</td>
<td>1167</td>
<td>420</td>
</tr>
</tbody>
</table>
noon (11.00–14.00) and in the afternoon (16.00–20.00), depending on the stage of hatching. On the day of the expected hatching, the eggs were examined to detect a bulge on shell surface that indicated the position of the bill with egg-tooth. If it was present, a 2 × 2-mm opening was pierced in the shell and the bill of the hatching nestling was marked with a color. This method is described in detail by Lebedeva (1996). In this way we knew from which egg a nestling hatched (Table 1). Then, the legs of nestlings were individually marked with waterproof ink. Since the day of hatching, each nestling was weighed at the same time every day with Pesola spring balance (10 and 50 g capacity) to the nearest 0.1 g in 1994, and with an electronic balance to the nearest 0.01 g in 1995. After day 7, the nestlings were ringed with aluminium rings. In 1994, the length of the rachis and web of the longest remiges (5–7) were measured to the nearest 1 mm on days 12, 13, 14 of nesting life. In 1995, tarsus length of nestling of the second and third broods, aged 12–14 days, was measured to the nearest 1 mm. Tarsus length in the Tree Sparrow increases until day 10 (Fetisov & Gaginskaya 1981). Notes were taken of the date of detecting a dead nestling in the nest or disappearance of a nestling, also the date of destruction of the brood and the reason of destruction. Also

<table>
<thead>
<tr>
<th>Variable</th>
<th>Age (day)</th>
<th>n</th>
<th>Mean ± SD</th>
<th>k</th>
<th>R</th>
<th>F</th>
<th>df1</th>
<th>df2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg volume [cm³]</td>
<td>1076</td>
<td>2.05 ± 0.2</td>
<td>255</td>
<td>0.60</td>
<td>8.93</td>
<td>254</td>
<td>1101</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
<tr>
<td>Egg breadth [mm]</td>
<td>1076</td>
<td>14.4 ± 0.5</td>
<td>255</td>
<td>0.53</td>
<td>7.10</td>
<td>254</td>
<td>1101</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
<tr>
<td>Egg length [mm]</td>
<td>1076</td>
<td>19.4 ± 0.9</td>
<td>255</td>
<td>0.69</td>
<td>13.00</td>
<td>254</td>
<td>1101</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
</tbody>
</table>

| Nestling mass [g]   | 630       | 2.2 ± 0.5  | 186 | 0.51 | 4.54  | 185 | 444  | < 0.001 |
|                     | 757       | 3.5 ± 0.7  | 198 | 0.55 | 5.85  | 197 | 559  | < 0.001 |
|                     | 779       | 5.3 ± 1.1  | 203 | 0.53 | 5.44  | 202 | 576  | < 0.001 |
|                     | 771       | 7.6 ± 1.4  | 203 | 0.55 | 5.78  | 202 | 568  | < 0.001 |
|                     | 741       | 9.9 ± 1.8  | 196 | 0.58 | 6.24  | 195 | 545  | < 0.001 |
|                     | 750       | 12.4 ± 2.1 | 200 | 0.59 | 6.49  | 199 | 550  | < 0.001 |
|                     | 773       | 14.6 ± 2.4 | 203 | 0.58 | 6.46  | 202 | 570  | < 0.001 |
|                     | 729       | 16.3 ± 2.4 | 196 | 0.54 | 5.38  | 195 | 533  | < 0.001 |
|                     | 686       | 17.5 ± 2.7 | 189 | 0.56 | 5.64  | 188 | 497  | < 0.001 |
|                     | 700       | 18.3 ± 2.7 | 192 | 0.58 | 6.17  | 191 | 508  | < 0.001 |
|                     | 698       | 18.7 ± 2.8 | 193 | 0.59 | 6.29  | 192 | 505  | < 0.001 |
|                     | 690       | 18.9 ± 2.7 | 190 | 0.63 | 7.18  | 189 | 500  | < 0.001 |
|                     | 553       | 18.6 ± 2.8 | 168 | 0.66 | 7.45  | 167 | 385  | < 0.001 |
|                     | 354       | 18.2 ± 2.7 | 121 | 0.70 | 7.78  | 120 | 233  | < 0.001 |

| Asymptotic growth [g] | 794 | 18.2 ± 2.6 | 207 | 0.57 | 6.19  | 206 | 587  | < 0.001 |
| Max growth rate [g/day] | 794 | 2.6 ± 0.4  | 207 | 0.61 | 7.22  | 206 | 587  | < 0.001 |
| Time of growth [day]   | 794 | 10.2 ± 1.0 | 207 | 0.60 | 6.82  | 206 | 587  | < 0.001 |
| Difference between nestling mass and its asymptotic growth | 651 | 0.8 ± 1.8  | 180 | 0.58 | 6.07  | 179 | 471  | < 0.001 |
| Remex length [mm]      | 521 | 0.7 ± 2.3  | 160 | 0.71 | 9.06  | 159 | 361  | < 0.001 |
| Web length [mm]        | 346 | 0.6 ± 2.7  | 117 | 0.77 | 11.00 | 116 | 229  | < 0.001 |
| Tarsus length [mm]     | 12  | 31.5 ± 3.3 | 44  | 0.35 | 2.26  | 43  | 59   | < 0.01 |
|                       | 13  | 33.9 ± 3.0 | 79  | 0.42 | 3.26  | 78  | 166  | < 0.001 |
|                       | 14  | 36.1 ± 2.5 | 93  | 0.35 | 2.56  | 92  | 179  | < 0.001 |
|                       | 12  | 22.2 ± 3.7 | 44  | 0.24 | 1.76  | 43  | 59   | < 0.03 |
|                       | 13  | 26.4 ± 4.1 | 79  | 0.51 | 4.28  | 78  | 166  | < 0.001 |
|                       | 14  | 30.4 ± 4.0 | 93  | 0.47 | 3.62  | 92  | 179  | < 0.001 |

Table 2. Mean values and repeatability index (R) for all variables analyzed. n — number of eggs or nestlings analysed. Eggs that hatched and nestlings that fledged and were weighted at a given age were analysed. Parameters of the Richards curve were calculated for nestlings that fledged and were weighted at least 7 times until age of 11 days inclusive. k — number of clutches or broods. Repeatability of egg variables was calculated for clutches in which at least one nestling hatched; repeatability of nestling mass and parameters of Richards’ curve were calculated for nests from which at least one nestling fledged, the mass of dead nestlings being excluded.
the parasites found on nestlings or in the nest were described (Draber-Mońko 1997, Pinowski et al. 1997, Krumpal et al. 2000–2001). A more detailed description of the study area and methods is in Pinowski et al. (2000–2001), Pinowska et al. (2002a, 2002b) and Barkowska et al. (2003).

The following independent variables were considered: 1) total volume of all eggs in the clutch, 2) volume of individual eggs, 3) egg breadth, 4) egg length. The dependent variables comprised: 1) body mass of nestlings on successive 14 days of life, 2) asymptote of nestling growth calculated from Richards’ growth curve (Richards 1959), 3) maximum growth rate of a nestling calculated from Richards’ growth curve, 4) time of nestling growth calculated as the age at which nestlings reached 95% of the asymptote, 5) difference between the masses of nestlings aged 12, 13, and 14 days and the asymptotic mass, 6) length of remiges on days 12, 13, and 14, 7) length of the web on days 12, 13, and 14, 8) length of the tarsus on days 12, 13, and 14, 9) death of a nestling in the nest, or its disappearance, or fledging, 10) percentage of nestlings fledged in relation to clutch size and to the number of eggs hatched.

For statistical analyses we used program SPSS 10.1 PL for Windows and our own programs in Pascal 7.0. All results are presented as mean ± SD.

Differences in mean values of all variables between years or broods were evaluated by the analysis of variance (ANOVA) for six different broods. No cross-comparisons were made.

The variances were estimated by using the formulas presented in Lessells & Boag (1987) and Sokal & Rohlf (1995).

Because of a high repeatability of the values of all egg and nestling variables (Table 2), the following comparisons were made:

1. Mean egg size variables in the clutch with mean values of variables describing the mass growth and development of nestlings hatched from these eggs. This analysis is based on 261 nests in which eggs hatched and at least one nestling fledged.

2. Deviations of egg size from the mean value in the clutch with deviations of variables describing mass growth and development of nestlings hatched from these eggs from their mean values in the nest. This analysis was performed for 278 nestlings that hatched from a specified egg and fledged.

Analysis at point 1 include genetic and maternal effect as measured by the mean egg size in the clutch, and parental effect as measured by the mean growth and development of nestlings in the nest. At point 2, maternal and paternal effects are largely eliminated, and the comparison concerns the effect of egg size within the clutch (which markedly depends on the sequence of egg laying, Pinowski et al. 2000–2001) on genetic traits that determine better growth and development of nestlings in this nest.

Because of significant differences in egg size and in variables describing nestling growth and development between successive years and broods (see Results Table 3), we basically used the multifactor analysis of covariance (ANCOVA) and its part — the aggregate correlation (the average within class correlation; Blalock 1960, Lowry 1999–2000) for years and broods, as calculated from the formula:

\[ r_c = \frac{\sum_{year=1994}^{1995} \sum_{brood=1}^{3} \sum_{i=1}^{n_{year, brood}} (x_{year, brood, i} - \bar{x}_{year, brood})(y_{year, brood, i} - \bar{y}_{year, brood})}{\sqrt{\sum_{year=1994}^{1995} \sum_{brood=1}^{3} \sum_{i=1}^{n_{year, brood}} (x_{year, brood, i} - \bar{x}_{year, brood})^2 \sqrt{\sum_{year=1994}^{1995} \sum_{brood=1}^{3} \sum_{i=1}^{n_{year, brood}} (y_{year, brood, i} - \bar{y}_{year, brood})^2}}.\]

where:

- \( n_{year, brood} \) is the number of nestlings (nests) in a given year and brood,
- \( x_{year, brood, i} \) is an independent variable characterizing the size of an egg laid in a given year and brood, from which the i-th nestling hatched,
- \( \bar{x}_{year, brood} \) is the mean value of an independent variable for a given year and brood,
- \( y_{year, brood, i} \) is the value of dependent variable describing growth or development of the i-th nestling hatched in a given year and brood,
- \( \bar{y}_{year, brood} \) is the mean value of dependent variable in a given year and brood.

Using the analysis of covariance (ANCOVA, Blalock 1960, Lowry 1999–2000), we tested if the aggregate correlations are significantly different from zero.
Growth of nestling was compared with the Richards’ curve (Richards 1959) according to the formula:

\[ W(t) = \frac{A}{(1 + Re^{-Kt})^m} \]

where: \( W(t) \) — body mass [g] at \( t+1 \) days after hatching, \( A \) — asymptotic mass, \( R \) — integration constant, \( K \) — growth rate constant, \( m \) — reciprocal of shape parameter.

Parameters of Richards’ curve were estimated for each nestling separately, using nestling mass by day 11 inclusive. It can be assumed that by this day the assumptions of the Richards’ formula (Richards 1959) are valid. Only nestlings weighed at least 7 times during this time were analyzed.

It was assumed that if on day \( i \) the expected body mass of a nestling is \( W(i) \), then the variance of the possible body masses of this nestling on this day is proportional to \( W(i) \). This means that the square of the difference between the measured nestling mass, \( w_i \), and the expected mass from the Richards’ curve, \( W(i) \), is proportional to the expected mass \( W(i) \):

\[ (w_i - W(i))^2 = \epsilon_i^2 W(i) \]

where \( \epsilon_i \) represents some additive error.

Assuming that \( \sum_{i=0}^{11} \epsilon_i^2 \) calculated for each nestling should have a minimum value, the parameters of Richards’ curve were calculated as the solution to a system of non-linear equations obtained by equating to zero partial derivatives of the function:

\[ f(A, R, K, m) = \sum_{i=1}^{11} (w_i - W(i))^2 / W(i) \]

where \( W(i) = \frac{A}{(1 + Re^{-Kt})^m} \)

Calculations were performed by using author’s own program in PASCAL 7.0.

The following variables characterising nestling growth were considered (Ricklefs 1967): asymptotic mass \( A \); absolute growth rate (equals to slope of tangent to Richards’ curve at inflection point \( v_{max} = \frac{AK}{1 + \frac{1}{m} v_{max}} \) ) and time of growth (age at which nestling mass reached or exceeded 95% of the asymptotic mass), expressed by the formula:

\[ \frac{\ln R - \ln(0.95^{-1/m} - 1)}{K} \]

**RESULTS**

**The effect of egg size on nestling survival**

Of the total of 1167 nestlings, 868 (74.4%) survived until fledging, whereas 299 (25.6%) died or disappeared. The percentage of dead or disappeared nestlings differed between years and broods (Table 4, \( \chi^2 = 56.46, df = 5, p < 0.001 \)).

Mean egg size and deviations of egg size from the mean egg size in the clutch showed no difference between fledged and dead nestlings (volume: fledged 2.05 ± 0.17 cm³, dead 2.04 ± 0.17 cm³, \( F_{1,395} = 0.27, p > 0.06 \); breadth: fledged 14.36 ± 0.43 mm, dead 14.38 ± 0.47 mm, \( F_{1,377} = 0.20, p > 0.09 \); length: fledged 19.43 ± 0.92 mm, dead 19.28 ± 0.74 mm, \( F_{1,395} = 1.07, p > 0.3 \); deviation from: the mean volume: fledged: -0.000 ± 0.105 cm³, dead 0.005 ± 0.113 cm³, \( F_{1,377} = 0.190, p > 0.6 \); mean breadth: fledged 0.000 ± 0.286 mm, dead 0.017 ± 0.309 mm, \( F_{1,377} = 0.57, p > 0.8 \); mean length: fledged -0.013 ± 0.459 mm, dead 0.015 ± 0.469 mm, \( F_{1,377} = 0.763, p > 0.3 \)). Among clutches with at least one nestling hatched, 15.2% did not fledge nestlings at all, 66.2% fledged less nestlings than eggs laid, and 18.6% fledged all the nestlings hatched from all eggs laid.
Influence of egg size on nestling growth

Further analyses were performed only for nestlings that fledged. Mean values of dependent variables were calculated without nestlings that died. Deviations of dependent variables from mean values of variables in the nest were also calculated only for nestlings that fledged.

Nestling mass (weight)

The mean mass of nestlings that survived until fledging increased from 2.15 ± 0.46 g on day 1 to 18.86 ± 2.73 g on day 12, and it declined on days 13 and 14. Significant differences were found in nestling mass on each day of life for years and broods (Table 3).

Significantly positive aggregate correlations between the mean egg volume in the clutch and the mean nestling mass were found by day 12 inclusive, except for days 3, 4, and 5 (Fig. 1A). Aggregate correlations between the deviation of an egg volume from the mean egg volume in the clutch and the deviation of a nestling mass from the mean mass of nestlings in the nest were significantly different from zero on days 1, 2, 3, 4, 11, and 14 (Fig. 1B).

Significantly positive aggregate correlations between the mean egg breadth in the clutch and the mean mass of nestlings hatched from this clutch were found on days 1, 2, 6, 7, 11, and 12 (Fig. 2A). All aggregate correlations between the deviation of an egg breadth from the mean egg breadth in the clutch and the deviation of an nestling mass from the mean nestling mass in the nest were significantly positive, except for those on days 5, 6, 10, and 13 (Fig. 2B).

Table 3. Mean values (± SD) of the variables in successive years and broods, and significance of differences.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Age</th>
<th>1994</th>
<th>1995</th>
<th>ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Egg volume [cm³]</td>
<td></td>
<td>2.0</td>
<td>2.1</td>
<td>2.1</td>
</tr>
<tr>
<td>Egg breadth [mm]</td>
<td></td>
<td>14.3</td>
<td>14.5</td>
<td>14.5</td>
</tr>
<tr>
<td>Egg length [mm]</td>
<td></td>
<td>19.4</td>
<td>19.5</td>
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</tr>
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<td>2.2</td>
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</tr>
<tr>
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<td>3.5</td>
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<td>5.3</td>
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<td>18.0</td>
</tr>
<tr>
<td>Absolute growth rate [g/day]</td>
<td></td>
<td>2.59</td>
<td>2.7</td>
<td>2.6</td>
</tr>
<tr>
<td>Time of growth [day]</td>
<td></td>
<td>10.1</td>
<td>10.6</td>
<td>10.2</td>
</tr>
<tr>
<td>Difference between nestling mass and its asymptotic growth</td>
<td></td>
<td>0.3</td>
<td>1.1</td>
<td>0.6</td>
</tr>
<tr>
<td>Remex length [mm]</td>
<td></td>
<td>31.7</td>
<td>31.7</td>
<td>30.7</td>
</tr>
<tr>
<td>Remex length [mm]</td>
<td></td>
<td>33.6</td>
<td>34.4</td>
<td>33.8</td>
</tr>
<tr>
<td>Web length [mm]</td>
<td></td>
<td>22.1</td>
<td>22.3</td>
<td>22.4</td>
</tr>
<tr>
<td>Web length [mm]</td>
<td></td>
<td>25.6</td>
<td>27.6</td>
<td>27.2</td>
</tr>
<tr>
<td>Tarsus length [mm]</td>
<td></td>
<td>18.0</td>
<td>17.6</td>
<td>15.2</td>
</tr>
</tbody>
</table>
No aggregate correlations significantly different from zero were found between the mean egg length in the clutch and the mean nestling mass in the nest (Fig. 3A). But aggregate correlations between the deviation of an egg length from the mean egg length in the clutch and the deviation of a nestling mass from the mean nestling mass in the nest were significantly positive for nestlings aged 1, 2, and 3 days (Fig. 3B).

Table 4. Number and proportion (%) of nestlings that died in the successive years and broods.

<table>
<thead>
<tr>
<th>Year</th>
<th>Broods</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994</td>
<td>n</td>
<td>56</td>
<td>18</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>%</td>
<td>18.7</td>
<td>10.7</td>
<td>33.0</td>
</tr>
<tr>
<td>1995</td>
<td>n</td>
<td>93</td>
<td>73</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>%</td>
<td>35.2</td>
<td>36.1</td>
<td>20.6</td>
</tr>
</tbody>
</table>

Nestling growth curve

Parameters of the Richards’ growth curve as well as the maximum growth rate and growth time were characterised by significant repeatability indices in the nest (Table 2). All these variables were significantly dependent on the year and brood (Table 3).

Asymptote

Significantly positive aggregate correlations were found between the mean egg volume and the mean asymptotic growth of nestlings in the nest. Also significantly positive aggregate correlations were found between the deviation of an egg volume from the mean egg volume in the clutch, or the deviation of an egg breadth from the mean egg breadth in the clutch, and the deviation of the asymptotic growth of a nestling from the mean asymptote in the nest (Table 5).

Mean maximum growth rate

The mean maximum growth rate of nestlings in the nest was positively correlated with all the
three measurements: volume, breadth, and length of the eggs. The deviations of the maximum growth rate of a nestling from the mean growth rate of nestlings in the nest were positively correlated with the deviations of an egg breadth from the mean value in the clutch (Table 5).

Mean growth time

Mean growth time of nestlings in the nest, and the deviation of the growth time of a nestling from the mean for the nest were not significantly dependent on the egg size (Table 5).

The difference between nestling mass and its asymptote

The difference between nestling mass and its asymptotic growth was significantly dependent on the year and brood (Table 3).

No aggregate correlations significantly different from zero were found between egg size, mean egg size, and the deviation of an egg size from the mean egg size in the clutch, on the one hand, and respective variables characterizing the difference between the masses of nestlings and their asymptotic growth.

Remix and webs

No significant differences were found in the length of remiges for nestlings aged 12, 13, and 14 days between successive broods in 1994 (Table 3).

For nestlings aged 12 days, significantly positive aggregate correlations were found between the deviation of an egg size from the mean egg size in the clutch and the deviation of remex length of the nestlings that hatched from these eggs from the mean remex length in the nest. This relationship concerned egg volume ($r_c = 0.414$, $n = 42$, ANCOVA: $F_{1,38} = 7.86$, $p < 0.01$), egg breadth ($r_c = 0.333$, $n = 42$, ANCOVA: $F_{1,38} = 4.75$, $p < 0.04$), and egg length ($r_c = 0.424$, $n = 42$, ANCOVA: $F_{1,38} = 8.351$, $p < 0.01$). In nestlings aged 13 and 14 days no aggregate correlations significantly different from zero were found between the variables of the egg size and remex length.

The mean web length in nestlings aged 13 days showed significant differences between successive
broods in 1994 (Table 3). No difference was found for nestlings aged 12 and 14 days (Table 3).

The deviation of a web length from the mean web length in the nest for nestlings aged 12 days was positively correlated with the deviation of an egg volume from the mean egg volume in the clutch ($r_c = 0.305$, $n = 42$, ANCOVA: $F_{1,38} = 5.28$, $p < 0.03$). The mean web length in nestlings aged 12 days was negatively correlated with the mean egg breadth in the clutch ($r_c = -0.317$, $n = 41$, ANCOVA: $F_{1,37} = 4.14$, $p < 0.05$). But in nestlings aged 14 days the aggregate correlation between the mean web length and mean egg length was not significant ($r_c = 0.226$, $n = 43$, ANCOVA: $F_{1,38} = 0.30$, $p > 0.05$).

**Table 5.** Aggregate correlations for years and broods between the egg volume, breadth or length in the nest and the variables characterizing nestling growth: growth asymptote, maximum growth rate, and time of growth. $A$ — asymptotic mass [g], $v$ — maximum growth rate [g/day], $t$ — time of growth [day], $n$ — number of nestlings, $k$ — number of nests, ANCOVA, $*$ — $p < 0.05$; $**$ — $p < 0.01$, $***$ — $p < 0.001$.

<table>
<thead>
<tr>
<th>Egg variables</th>
<th>Mean $A$</th>
<th>Deviation of $A$ from mean</th>
<th>Mean $v$</th>
<th>Deviation of $v$ from mean</th>
<th>Mean $t$</th>
<th>Deviation of $t$ from mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean egg volume in clutch</td>
<td>$k = 222$</td>
<td>0.161*</td>
<td>0.195**</td>
<td>-0.041</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deviation of egg volume from mean</td>
<td>$n = 265$</td>
<td>0.138*</td>
<td>0.071</td>
<td>0.015</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean egg breadth in clutch</td>
<td>$k = 222$</td>
<td>0.176**</td>
<td>0.158*</td>
<td>-0.045</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deviation of egg breadth from mean</td>
<td>$n = 265$</td>
<td>0.213**</td>
<td>0.127*</td>
<td>0.049</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean egg length in clutch</td>
<td>$k = 222$</td>
<td>0.063</td>
<td>0.142*</td>
<td>-0.022</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deviation of egg length from mean</td>
<td>$n = 265$</td>
<td>-0.055</td>
<td>-0.059</td>
<td>-0.046</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
length in the nest, and the mean egg breadth in
the clutch was significantly positive \(r_c = 0.215,\)
\(n = 87,\) ANCOVA: \(F_{1,83} = 4.02, \ p < 0.05.\) No other
significant aggregate correlations were found
between egg sizes and web lengths.

**Relationship between tarsus length and egg size**

Tarsus was significantly longer in nestlings of
the second brood than in nestlings of the third
brood (Table 3).

Aggregate correlations between the mean egg
volume in the clutch and the mean tarsus length
in the nest, \(r_c = 0.31, \ n = 62,\) ANCOVA: \(F_{1,59} = 6.27,\)
\(p < 0.02\) and between the mean egg length in
the clutch and the mean tarsus length in the
nest \(r_c = 0.324, \ n = 62,\) ANCOVA: \(F_{1,59} = 6.90,\)
\(p < 0.02\) were significantly positive. No signifi-
cant aggregate correlations were found between
tarsus length and other variables of egg size.

No significant correlation was found between any
dependent variable analyzed and the clutch size.

**DISCUSSION**

The objective of our paper was to test if the
egg size per se can influence the growth, develop-
ment, and survival of Tree Sparrow nestlings. The
relationships between chick growth or survival
and egg size seems to be more clear in precocial
compared to altricial species. That is why this
issue was mainly investigated for precocial and
semiprecocial species (Williams 1994). Smith &
the results are consistent with the idea that larger
eggs may only confer an advantage in low-quality
environment.

**The effect of genetic factors**

When correlating the mean egg size in a
clutch and the mean nesting mass in the nest
we eliminated genetic, maternal, and parental
effects associated with differences in egg size in
the clutch, contributing to a small part of their
total variation (van Nordwijk et al. 1981). Many
authors have found that the variation of mean egg
size parameters is higher for clutches of different
females than for clutches of the same female or
among eggs from the same clutch (e.g. Bałbura
2002). Although repeatability does not have to
set the upper limit to heritability, and it can even
be smaller than heritability (Dohm 2002), van
Nordwijk et al. (1981) have found that in the
Great Tit the similarity of female repeatability to
heritability estimates based on daughter-mother
regression leads to the conclusion that 60–80% of
the variation in egg dimensions is genetic (see also

The repeatability of egg size of this study did
not differ from that of other species (Bałbura 1996).
The repeatability of nestling mass on successive
days varied from 0.50 to 0.69. The repeatability
of the growth asymptote, maximum growth rate,
time of growth and difference between the mass of
nestlings aged 13 and 14 days and the asymptote
varied from 0.71 to 0.76 (Table 2). Ricklefs & Peters
(1981) discovered only detectable hereditability
of parameters in the Richards’ curve. Gebhardt-
Henrich & van Noordwijk (1994) estimated the
heritability component in the asymptote but not
in the shape and slope parameters, that is, like
in our results expresses as repeatability (Table 2).

**The effect of egg size per se**

The present study showed two periods of the
effect of egg size per se on nestling growth: during
the first four days after hatching and after the
development of thermoregulation, termination
of intensive growth, and moult, that is at the end
of the nestling period (Figs 1B, 2B, 3B). During
the four days of the first period, differences
between the size of an egg and its mean value in
the clutch were positively correlated with differ-
ences between the mass of an nestling and the
mean nesting mass in the nest, though this was
a weak relationship that explained only a few
percent of the variation in egg volume, breadth,
and length (Figs 1B, 2B, 3B). Many authors found
a relationship between the mass of a nestling in
the day of hatching and the size of the egg from
which it hatched (review in Ward 1995). Nestling
growth in the first day of life depends on the
content of nutrients in the egg and on the amount
of food supplied by parents. According to Deckert
(1962), Tree Sparrow nestlings are fed as soon as
15 minutes after hatching. In the day of hatching,
nestling mass of Tree Sparrows accounted for 73%
of the egg mass (Pinowski, unpublished data),
like in other species of altricial birds (e.g. Nolan
& Thompson 1978, Ar et al. 1987, Margis 1991). We
do not know the rate of yolk sac resorption in Tree
Sparrows, but in Starlings, in which the yolk sac
accounts for 9.58% (in Tree Sparrow 6.03%) of the
body mass on the average (max. 10.7%), it is 63%
after the first day of life, 87.5% after the second
day, 92.5% after the third day, and 97.5% after the
day (calculated from Schmekel 1960). Thus,
positive correlations in the first days of life can result from the size of the yolk sac.

In the second period, a statistically significant correlation between the deviation of the volume of an egg from the mean egg volume in the clutch and the deviation of the mass of a nestling from the mean nestling mass in the nest occurred only for nestlings aged 11 and 14 days, and this was a weak relationship (Fig. 1B). For egg breadth, this relationship was significant over the nestling period, except for days 5, 6, 10 and 13 (Fig. 2B). For egg length no such relationship was found in older nestlings.

We can only speculate about the reasons for the correlation between egg size parameters and older nestling mass. Eggs are the source of many substances necessary for the development of specified organs or physiological functions, such as essential or semiessential aminoacids — taurine for bile production or cysteine for feather development (Bolotnikov et al. 1978, Houston 1999, Ramsay & Houston 1998, 2003), microelements, vitamins, carotenoids (Blount et al. 2002, Hörak et al. 2002, Royle et al. 2003), hormones (Schwabl 1993, Schwab et al. 1997, Lipar et al. 1999), or acquired immunogenic factors transferred by the female through eggs (Nordling et al. 1988, Apanius 1998, Grindstaff et al. 2003). Possibly the content of these substances depends on egg size. It cannot be excluded that the effect of egg size onnestling development is better pronounced in nestlings subjected to stress (Smith & Bruun 1998, Christians 2002).

In the Tree Sparrow population that we studied, the mass and breadth of eggs increased from the first to penultimate egg laid, and the first egg laid was the smallest one. The mass of the last egg laid in the clutch did not differ from the mean egg mass in this clutch. The length of eggs did not depend on the sequence of laying (Pinowski et al. 2000–2001). The effect of the sequence of laying on the growth of nestling analysed in this paper, that is, fledged ones, was significant only on day 2 after hatching and only for 5-egg clutches (Pinowska et al. unpublished). When analysing the relationship between the deviation of egg dimensions from the mean in the clutch and the deviation of nestling mass from the mean in the nest, we observed for how long the nestlings hatched from the largest eggs remain the largest in the brood. It has been shown that this relation occurred only in the first days after hatching until the yolk stored in the yolk sack was exhausted, and it practically disappeared afterwards (Figs 1B, 3B). This implies that the mass of nestlings hatched from the smallest eggs (laid as the first ones) rapidly equals the mass of siblings hatched from larger eggs.

The sequence of hatching corresponds to the sequence of siblings hatched from larger eggs.

In Tree Sparrows, egg breadth varies in a different way than does egg length. Egg breadth increases with the sequence of laying of the first four eggs.
and than it decreases and does not depend on the clutch size, whereas egg length does not depend on the sequence of laying but it does depend on the clutch size (Pinowski et al. 2000–2001). This indicates that egg breadth depends on anatomic traits of the female, for example, on the breadth of oviduct (van Noordwijk et al. 1981). Warham (1990) found a relationship between egg shape index (B/L) and pelvis width and depth in Petrels. We do not know how the egg breadth can influence the egg composition in the Tree Sparrow. Anderson & Deeming cited by Deeming (2002) showed that in the Houbara Chlamydotis undulata wet yolk was significantly correlated with breadth. Chylarecki (2000) provides evidence that in elongated eggs, breadth may be correlated mainly with the content of yolk and length with the content of albumen. We do not know the relationship between egg composition and egg volume in Tree Sparrows. In passerines the content of albumen increases with egg volume (Hill 1995). In Starlings the albumen mass increases with egg volume but the yolk mass decreases (Ricklefs 1977, 1984). The percentage of yolk remained constant as an egg mass increased for Great Tit but decreased for Pied Flycatcher (Ojanen 1983).

In this study, we have found a positive relationship between the mean egg volume or egg length and length of tarsus of nestlings in the nest. Finkler et al. (1998) have experimentally demonstrated that the length of tarsus depends on the content of albumen rather than yolk in the egg.

Effect of egg size on nestling survival

In the Tree Sparrow, the hatchability of small eggs is lower than that of large eggs (Pinowska et al. 2002a). But we did not find correlation between egg size and nestling survival, like many other authors (e.g. Jarvinen & Ylimaunu 1984, Magrath 1992, Smith et al. 1995 and Styrsky et al. 1999). Schifferli (1973) found such a correlation only for the second brood, Ojanen (1983) only in some years, and Smith & Bruun (1998) in a poorer habitat. All these papers concern passerines. Among other altricial birds, a positive relationship between egg size and nestling survival was found in Wood Pigeons Columba palumbus (Murton et al. 1974) and in Swifts Apus apus (O’Connor 1979). Among precocial and semiprecocial species, the relationship between egg size and chick survival has been more frequently recorded (Williams 1994).

Phenotypic selection occurs when the phenotypic value of a trait correlates with fitness. Among traits of passerine nestlings conferring selective advantage there are mass asymptote, tarsus length, growth rate, and fledging mass. These traits are correlated with survival, recruitment rate, and acquisition of territory (Gebhardt-Henrich & Richner 1998). We have found a correlation between the deviation of the volume of an egg from the mean value in the clutch and the deviation of a specified developmental trait of a nestling from the mean value of this trait in the nest: $R^2$ from 0.4 to 5.7%, depending on the day — for nestling mass, 1.9% for the asymptote, 4.5% for the maximum growth rate, 2.8% for the tarsus length, 11–18%, depending on the day — for remex length, and 8–12% for web length. Many authors (review in Gebhardt-Henrich & Richner 1998) provide evidence that these traits are correlated with fitness (survival, fecundity, acquisition of a better territory).

CONCLUSIONS

Egg size influences nestling size not only in the first days after hatching but also during the period of thermoregulation development and feather growth, it increases the chance of reaching greater body mass (the asymptote), structural size (tarsus length), and plumage development before fledging (length of remiges and webs), and all these may increase fitness.

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Translated by Barbara Diehl

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STRESZCZENIE

[Wpływ wielkości jaja (objętości, szerokości i długości) na wzrost i rozwój piskląt mazurka]


Do analiz statystycznych, jako zmienne niezależne przyjęto średnie wartości cechy metrycznych jaj w zniesieniu oraz odchylenia wymiarów jaja od....
średniego wymiaru jaja w zniesieniu. Zmiennymi zależnymi były średnie wartości cech wylatujących piskląt pochodzących z danego zniesienia oraz odczynienia czech pisklęcia od średniej cechy piskląt pochodzących z danego zniesienia.

Różnice wartości zmiennych oceniono za pomocą analizy wariancji (ANOVA).

Wzajemna zależność między zmiennymi zależnymi i niezależnymi analizowano za pomocą analizy kowariancji (ANCOVA) ze względu na istotne różnice prawie wszystkich analizowanych zmiennych między kolejnymi latami i lęgami (Tab.3). Jako podstawę analizy statystycznej przyjęto „aggregate correlation”, dla której istotność różnicy od zera sprawdzano przy pomocy ANCOVA.

Stwierdziliśmy istotne, chociaż słabe dodatnie korelacje między średnią objętością jaj i szerokością jaj w zniesieniu, a średnią masą piskląt w gnieździe dla większości dni rozwoju gniazdowego (Fig. 1A, 2A). Średnia długość jaj nie korelowała ze średnią masą piskląt (Fig. 3A).

Odczynienie objętości jaja od średniej objętości jaj w zniesieniu korelowało dodatnio z odczynieniem masy pisklęcia od średniej masy piskląt w gnieździe w czasie czterech dni po wykluciu i po zakończeniu intensywnego wzrostu pod koniec pobytu piskląt w gnieździe (Fig. 1B). Odczynienie szerokości jaja od średniej szerokości jaja w zniesieniu a odczynienie masy pisklęcia od średniej masy piskląt w gnieździe korelowało dodatnio niemal w każdym dniu życia piskląt, ale korelacje te wyjaśniały tylko kilka procent zmienności (Fig. 2B). Dla długości jaj związane taki (poza pierwszym dniem życia piskląt) nie istniał (Fig. 3B).

Średnie maksymalne tempo wzrostu dodatnio korelowało z każdą z analizowanych cech (Tab. 5). Średni czas wzrostu piskląt w gnieździe oraz odczynienie czasu wzrostu pisklęcia w gnieździe od średniego czasu pobytu piskląt w gnieździe nie zależały istotnie od zmiennych związanych z wymiarami jaj, ale miały tendencję ujemną. Długość lotki w 12 dni życia piskląt jako miara stopnia rozwoju dodatnio korelowała z każdą z analizowanych cech jaj. Odczynienie długości chorygowki pisklęcia od średniej długość chorągiewki piskląt w gnieździe korelowało z odczynnieniem objętości jaja od średniej objętości jaj w gnieździe. Odczynienie długości lotki pisklęcia od średniej długości lotki piskląt w gnieździe korelowało dodatnio z odczynieniem masy jaja od średniej masy jaj w gnieździe i wpływ tej cechy tłumaczył kilkanaście procent zmienności (Tab. 3).

Wielkość strukturalna piskląt w lęgu drugim była większa niż w lęgu trzecim. Korelacja przecienna była dodatnia dla średnich objętości jaj i długości jaj a tarsus (Tab. 3).

Wielkość jaj, poza okresem czerpania z zapasów zawartych w woreczku żółtkowym (do 4 dni), wpływa na wzrost i rozwój piskląt głównie w dniach rozwoju termoregulacji, intensywnego wzrostu i rozwoju upierzenia.