

The Effect of Trends in Ambient Temperature on Egg Volume in the Tree Sparrow *Passer montanus*

Authors: Barkowska, Miłostawa, Pinowski, Jan, and Pinowska, Barbara

Source: *Acta Ornithologica*, 38(1) : 5-13

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: <https://doi.org/10.3161/068.038.0105>

BioOne Complete (complete.bioone.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

The effect of trends in ambient temperature on egg volume in the Tree Sparrow *Passer montanus*

Miłosława BARKOWSKA¹, Jan PINOWSKI^{2*}, Barbara PINOWSKA²

¹Department of Ecology, Institute of Zoology, University of Warsaw, Banacha 2, 02-097 Warszawa, POLAND

²Centre of Ecological Research, Polish Academy of Sciences, Dziekanów Leśny, 05-092, Łomianki, POLAND

*Corresponding author

Barkowska M., Pinowski J., Pinowska B. 2003. The effect of trends in ambient temperature on egg volume in the Tree Sparrow *Passer montanus*. Acta Ornithol. 38: 5–13.

Abstract. The effect of ambient temperature before and during laying on egg volume in birds has been studied by many authors. The objective of this paper is to show that trends in daily temperatures changes can also influence egg volume. The study was carried out near Warsaw, Poland in 1994 and 1995. We ascertained the laying sequence, size and volume of 1070 eggs in 211 clutches of the Tree Sparrow. The effect of the trend in temperature on the mean egg volume in a clutch explained 0.4% of its variation (0.03% to 4.2%, depending on the brood-period), and the effect of actual temperature explained 0.9% (0.5% to 1.6% depending on the brood-period). The joint effect of temperature and its trend explained 3.1% (1.7% to 8.9% depending on the brood-period) of variation in the mean egg volume in a clutch. The authors discuss possible mechanisms of the effect of temperature and temperature trend on egg volume.

Key words: Tree Sparrow, *Passer montanus*, egg volume, ambient temperature

Received — April 2003, accepted — June 2003

INTRODUCTION

The effect of ambient temperature before and during laying on egg size in birds has been analysed by many authors (van Noordwijk 1984, Bolotnikov et al. 1985, Järvinen & Ylimaunu 1986, Pikulski 1986, Järvinen 1991, 1994, Näger & van Noordwijk 1992, Perrins 1996, Stevenson & Bryant 2000 and others). Egg laying is made possible due to the storing by females of additional energy and nutrients needed for egg formation, which depends on food availability and suitable weather conditions (King 1973, Ricklefs 1974, Kendeigh et al. 1977, Martin 1987, Houston et al. 1995ab, Carey 1996, Houston 1999 and others). It is not clear, however, if the effects of temperature are related to a disturbance in the energy balance of females during laying and in related processes (Walsberg 1983, Rahn et al. 1985, O'Connor 1978, Näger 1990, Järvinen 1991 and others), or if the only limit the

amount of nutrients needed for egg formation (Bolton et al. 1992, Houston et al. 1995a, b, c, 1999, Carey 1996, Williams 1996, Ramsey & Houston 1997, 1998, 1999 and others).

Temperatures below the lower critical level equal to 20°C for Tree Sparrow (Pinowski & Kendeigh 1977) increase energy demands for thermoregulation, thus they reduce the amount of energy that can be allocated for egg production (O'Connor 1978, Walsberg 1983, Rahn et al. 1985, Näger 1990, Järvinen 1991 and others). Most studies have been conducted in subarctic and temperate climatic zones during the onset of laying, when temperature should have the greatest impact on the energy balance in females (Ojanen et al. 1978, 1981, Ojanen 1983a, van Noordwijk 1984, Järvinen & Ylimaunu 1986, Järvinen & Pryn 1989, Järvinen 1991, 1994, Näger & van Noordwijk 1992 and others). In the Goldcrest *Regulus regulus*, for instance, as much as 11% of the variation in egg

size can be explained by the effect of temperature (Haftorn 1986).

Temperatures close to the upper critical temperature can also have a negative effect on egg size, as found by Kendeigh (1941) for free-living House Wrens *Troglodytes aedon* and by Lorenz & Almquist (1936), Huston et al. (1957), Mueller (1961), Clark & Amin (1965), and others for domestic hens.

Järvinen & Väisänen (1984), van Noordwijk (1984), Haftorn (1986), Järvinen & Ylimaunu (1986), Näger & van Noordwijk (1992), Näger & Zandt (1994), and others examined the effect of mean, minimum and, less often, maximum temperatures over periods of several days (3–11) before the laying date of a given egg. Ojanen et al. (1981), Ojanen (1983a), Järvinen & Pryl (1989), and Magrath (1992) analysed the effect of temperature on successive days before the dates of laying of consecutive eggs. The latter, also applied in the present paper, seems to be better because the energy expenditures of females in the period prior to laying increase to the onset of laying and, then decrease with the laying of successive eggs (Krementz & Ankney 1986).

None of these studies analysed the effect of trends in temperature change prior to laying, however. The objective of this paper is to show that trends of change in daily temperatures can exert a greater influence on egg volume in the Tree Sparrow *Passer montanus* than the mean, minimum, or maximum temperatures in the period prior to laying.

STUDY AREA, MATERIAL AND METHODS

The study was carried out in the villages of Dziekanów Leśny, Dziekanów Polski, and Kielpin, situated between the Vistula river and the Kampinos National Park, about 15 km NW of Warsaw (52°20'N, 20°50'E), where 200 nest-boxes were erected. As no differences were found in egg size among these villages (Pinowski et al. 2001a), all the data were pooled and analysed jointly. The data were collected from 15 April to 20 August in 1994 and from 20 April to 20 July in 1995. Air temperatures were taken from the weather station of the Kampinos National Park, located 15 km west of the study area. During the laying period, nest-boxes were inspected daily between 09.00 and 14.00 (EST). Eggs were marked with a permanent marker on the day of laying, so we knew the laying sequence. The egg length (L) and maximum

breadth (B) were measured to the nearest 0.1 mm, using vernier callipers. Using this formula:

$$V = 0.51 \times L \times B^2$$

we calculated the egg volume (Hoyt 1979).

In total, 1070 Tree Sparrow eggs of 211 clutches were analysed (for details see Pinowska et al. 2002).

ANOVA for correlation was used to analyse the effect of temperature on egg volume. All correlations between temperature and egg volume were calculated for each brood and year separately. Correlations were calculated for minimum, mean, and maximum temperatures on each day of the period from day 7 prior to the laying date of the first egg to the laying date of the third egg.

Mean, minimum or maximum temperatures were analysed for each day in the period preceding laying for clutches with small (1.66–1.90 cm³), medium (1.91–2.20 cm³), and large (2.21–2.77 cm³) mean egg volume.

To characterise changes in temperatures by using one number, we calculated trends of changes in temperature — a linear function describing changes in daily temperatures on successive days during the periods of 10, 9 or 8 days from days 7, 6, or 5 prior to the date of laying of the third egg, for the minimum, mean, and maximum daily temperatures separately. The trends were calculated to the date of laying of the third egg because after that day, the demands for nutrients in laying females decline (Krementz & Ankney 1986).

The joint effect of temperature and trend in temperature was analysed by using two-way regression and coefficient of determination of the two-way regression. The independent variables were the minimum, mean, and maximum temperatures of the days 7, 6, and 5 preceding the laying of a given egg, and the slope coefficient of the trend in these temperatures in the period from the same days to the laying date of the third egg. The dependent variable was the mean egg volume in a clutch. In all, nine variants of the relationships between egg volume and temperature or its trend were calculated in this way.

We expected that among many correlations calculated, some were overestimated and some were underestimated. Even if temperature had no effect on egg volume, about 5% of the correlations could significantly differ from zero. In this case, however, significant correlations would occur at random in each brood, and coefficients of determination would take random values independent of such factors as the brood, clutch size, sequence of laying, number of days prior to laying, and daily temperature.

The effect of temperature as a function of time on egg volume was estimated as a geometric mean of the coefficients of determination between mean egg volume in a clutch and the maximum, mean, and minimum temperatures for each day separately in the period from day 7 preceding the laying date of a first egg. Its value expressed in percentage gives the amount of variation in egg volume explained by temperature.

The distributions of the coefficients of determination calculated for the minimum, mean, and maximum temperatures were clearly skewed. For this reason they were compared by using the multifactor analysis of variance. The coefficients of determination were transformed by the formula: $\log(r^2 + 0.001)$, and the distributions of the coefficients of determination calculated by different methods (correlations with daily temperatures, correlations with trends of changes in daily temperature, and two-factor correlations) were compared using the Kruskal-Wallis one-way analysis of variance by ranks.

Characteristics of Tree Sparrow egg volume under study

The Tree Sparrow is resident in the study area and has a mean weight of 22.3 g, (Pinowski 1965, 1967). These birds can raise three broods a year. The volume of Tree Sparrow eggs varied from 1.42 to 3.15 cm³ (mean 2.10 ± 0.18 cm³). The mean egg volume in a clutch varied from 1.66 to 2.77 cm³ (2.10 ± 0.15 cm³ on the average). Typically, first eggs in the clutch were the lightest (and the smallest) and penultimate eggs were the heaviest (and the largest) (Pinowski et al. 2001a).

RESULTS

In all, 120 correlations were calculated between the mean egg volume in a clutch and the minimum, mean, and maximum daily temperatures on each day in the period from day 7 before the date of the first egg to the date of the third egg. (3 temperatures × 10 days × 4 brood-periods: the first broods in 1994 and 1995 and the second and third broods combined in 1994 and 1995). Eleven significant correlations (ten positive and one negative) were found for the first brood in 1994 (Fig. 1), and one negative between the minimum temperature in the period of five days prior to laying and the mean egg volume in a clutch for the second and third broods combined ($r = -0.320$, $F = 11.16$, $p < 0.01$).

In the first brood of 1994, the correlation between the mean and maximum daily temperatures and the mean egg volume in a clutch from day 2 before the laying date of the first egg to the laying date of the third egg was positive. On day 4 before laying of the first egg, the correlation between the minimum temperature and the mean egg volume in a clutch was negative, whereas on day 6 before the laying date of the first egg, the correlation between the maximum temperature and the mean egg volume in a clutch was positive (Fig. 1).

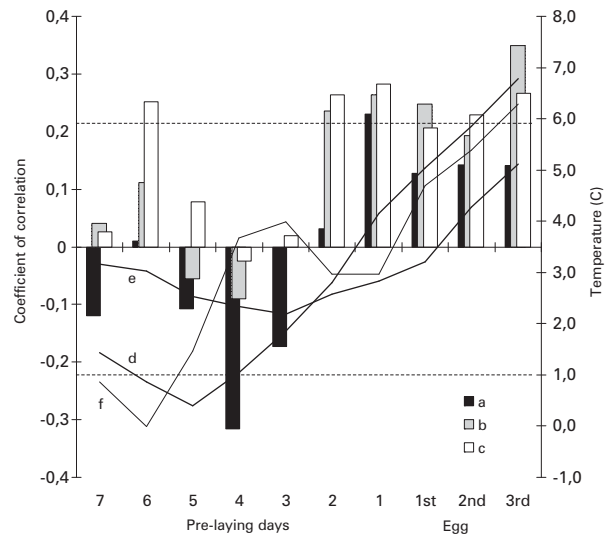


Fig. 1. Correlations of the mean egg volume in a clutch with the minimum (a), mean (b), and maximum (c) daily temperatures on each day of the period from day 7 prior to the date of the first egg to the date of the third egg (bars), and the mean minimum temperatures for clutches with large (d), medium (e), and small (f) mean egg volume during the same period (lines) in the first brood of 1994. Dotted line — significant level for correlations at $p < 0.05$.

In the second and third broods of 1995, significant negative correlations were found between the mean egg volume in a clutch and minimum, and mean maximum daily temperatures in the period preceding egg laying and the first days of egg laying (Fig. 2).

Clutches were categorised into those with small mean egg volume (1.66–1.90 cm³), medium mean egg volume (1.91–2.20 cm³), and large mean egg volume (2.21–2.77 cm³). For each of these categories, the mean minimum temperatures were calculated on each day for the periods from day 7 before the date of the first egg to the date of the third egg. For first brood clutches with the largest mean egg volume in 1994, a positive trend was observed in the minimum

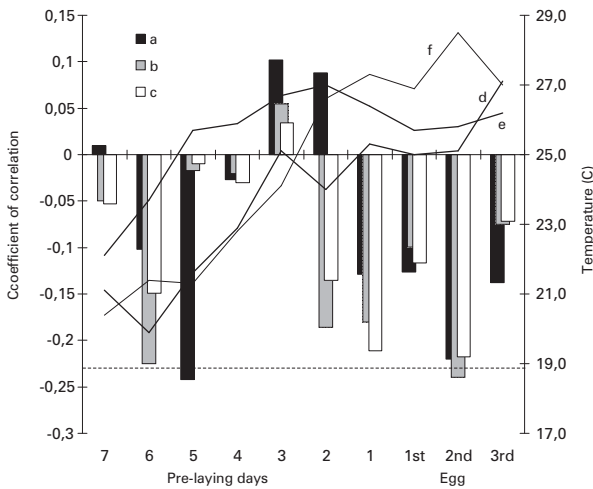


Fig. 2. Correlations of the mean egg volume in a clutch with the minimum (a), mean (b), and maximum (c) daily temperatures on each day of the period from day 7 prior to the date of the first egg to the date of the third egg (bars), and the mean maximum temperatures for clutches with large (d), medium (e), and small (f) mean egg volume during the same period (lines) in the second and third broods of 1995. Dotted line — significant level for correlations at $p < 0.05$.

temperature from day 5 before the date of the first egg to the date of the third egg. For clutches with the medium mean egg volume, the increasing trend in the minimum temperature was less pronounced, and for clutches with the lowest mean egg volume, changes in the minimum temperature were irregular (Fig. 1). For the second and third broods of 1995, the smallest eggs were laid at the highest maximum temperatures (over 27°C) on each day from the first egg to the third egg, and their laying was preceded by a period of rapidly increasing temperatures (from 22°C, Fig. 2). For clutches with an average mean egg volume, changes in temperature were less pronounced, and for clutches with the highest mean egg volume, temperature increased at the lower level on the average than for clutches with lowest mean egg volume (Fig. 2).

In total, 36 correlations were calculated between the slope coefficient of the trend in temperature and the mean egg volume in a clutch, of which only those for the first brood of 1994 were significantly different from zero. A significant positive effect of the trend in temperature on the mean egg volume was found during the period from day 5 before the laying date of the first egg to the laying date of a given egg for minimum temperatures ($r = 0.252$, $F = 4.61$, $p < 0.05$), and during the periods from day 5 ($r = 0.314$, $F = 7.44$

$p < 0.01$), day 6 ($r = 0.272$, $F = 5.42$, $p < 0.05$) and day 7 ($r = -0.248$, $F = 4.41$, $p < 0.05$) before the date of the first egg for mean temperatures.

Of 36 two-factor correlations (with temperature and trend jointly), 6 were significantly different from zero. Five of them concerned the first brood of 1994: the mean egg volume in a clutch was positively related to temperature and trend in temperature (Fig. 3).

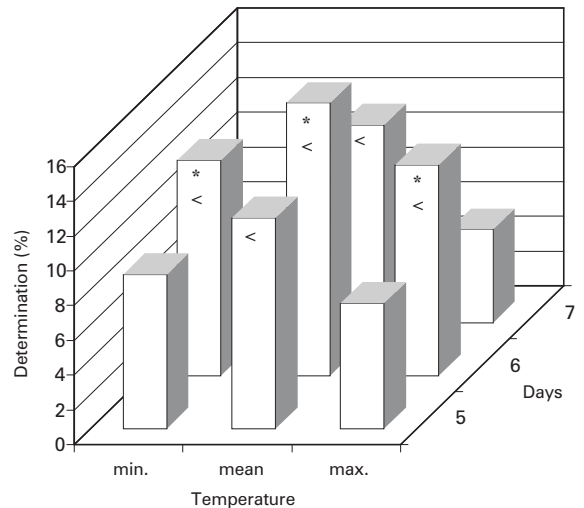


Fig. 3. Coefficients of determination for a two-factor regression of the mean egg volume in a clutch on temperature of days 5, 6, or 7 before laying of the first egg, and on the slope of trends in temperature during the periods from the same days to the date of the third egg for the first brood of 1994. * and < — coefficient of determination at $p < 0.05$, * — portion explained by temperature at $p < 0.05$, < — portion explained by trend at $p < 0.05$.

The analysis of the effect of temperature (minimum, mean and maximum) on the mean egg volume in a clutch explained 0.9% of its variation. This effect was dependent on the year and brood (three-way ANOVA: $F = 3.99$, $p < 0.01$). The highest mean (geo-mean) coefficient of determination was found for the first brood in 1994, when temperatures were lowest, and for the second and third broods in 1995, when temperatures were highest (Fig. 3, Table 1). The analysis of the trend in temperature on the mean egg volume explained 0.6% of the variation in the mean egg volume in a clutch. This relationship significantly depended on the brood (tree-way ANOVA: $F = 22.44$, $p < 0.001$). The highest mean (geo-mean) coefficient of determination was observed for the first brood in 1994, whereas in 1995, the effect of the trend in temperature for the first brood was very low (Table 1).

Table 1. Influence (%) of temperature and trend of temperature change (Tm + Tr). Geometric means of the coefficients of determination of the mean egg volume by the daily minimum, mean, and maximum temperatures on sequential days from day 7 before the date of the first egg to the date of the third egg, and by the trend in temperature during periods from days 7, 6, and 5 before the first egg to the date of the third egg.

Year	Brood	Tm %	Tr %	Tm + Tr %
1994	I	1.6	4.0	8.7
	II and III	0.5	0.5	1.6
1995	I	0.5	0.03	2.8
	II and III	0.9	0.2	3.4
	Total	0.9	0.6	3.4

The two-factor analysis with temperature and trend in temperature explained 3.4% of the variation in the mean egg volume in a clutch. This percentage was significantly dependent on the brood (three-way ANOVA: $F = 3.03$, $p < 0.05$, Table 1).

The analysis of the joint effect of temperature and its trend explained more variation in the mean egg volume in a clutch than did the sum of the effects of temperature and its trend calculated separately (Table 1).

DISCUSSION

The effect of daily minimum, mean, and maximum temperatures (which because of a strong interdependence among these temperatures was evaluated jointly as a geometric mean of the coefficients of determination R^2 calculated for each of these temperatures separately; see the Methods) accounted for 0.5 to 1.6% of the variation in the mean egg volume in a clutch, depending on the year and brood (Table 1). Similar results (1-4%) for other small passerine birds were obtained by Ojanen et al. (1981).

To our knowledge, however no previous study has estimated the effect of the trend of temperature change on egg volume. The largest eggs were laid when the minimum temperature increased from 0°C to 7°C (Fig. 1). The trend in temperature explained from 0.03 to 4.0% of the variation in egg volume, depending on the year and brood, whereas the temperature and trend jointly explained from 1.6% to 8.7% of variation (Table 1).

In the first brood of 1994, we found negative correlations between egg volume and minimum temperatures on day 4 prior to laying (Fig. 1, Pinowska et al. 2002). Magrath (1992) also found

negative correlations between egg volume and minimum air temperature before laying in the Blackbird *Turdus merula*. In the Tree Sparrow, volumes of the first, second and third eggs were negatively correlated with the minimum temperature on days 5 and 6 prior to laying of the egg (Pinowska et al 2002). Magrath did not analyse these statistically non-significant, but recurrent relationships, although these results seem to be inconsistent with the increased food requirements of females during the period of egg formation. This pattern can be explained, however by the significant effect of the trend of temperature change observed in the present study.

Possible mechanisms of the effects of temperature on egg volume

1. Energy balance in females

Many authors (Ricklefs 1974, Schifferli 1976, 1980, Murphy 1978, Pinowska 1979, Ojanen 1983b, Järvinen & Väisänen 1984, and others) have reported that the production of eggs by passerines is energetically expensive, although others (Krementz & Ankney 1986, Ward 1996) have found that egg production is not expensive. The cost of egg production in the Tree Sparrow is about 9% of the field metabolic rate. We based our calculations of the field metabolism of laying Tree Sparrows on the data presented by Williams (1987), who found that the field metabolic rate of incubating Savannah Sparrows *Passerculus sandwichensis* was $79.3 \text{ kJ} \times \text{day}^{-1}$. Dividing this value by the mean weight of incubating females (20.4 g), we obtained an estimate of $3.8 \text{ kJ} \times \text{g}^{-1} \times \text{day}^{-1}$. Ward (1996) reported that the field metabolic rate of laying Barn Swallows *Hirundo rustica* was 9% greater than that of incubating females. We multiplied the mean weight of laying Tree Sparrows (22.3 g) by the $3.8 \text{ kJ} \times \text{g}^{-1} \times \text{day}^{-1}$, and added 9% to obtain an estimate of the field metabolic rate of laying Tree Sparrow of $94.3 \text{ kJ} \times \text{day}^{-1}$.

We found a positive effect of temperature on the mean egg volume of the clutch in first broods in 1994 for mean and/or maximum temperatures on day 6 before laying and from day 2 before laying to the laying of the third egg (before 25°C maximal temperature). We also found a negative effect of temperature during warm periods of laying during second and third broods in 1995.

Many authors argue that the effect of temperature on egg size is most pronounced for the period from 3 to 5 days before the date of the first egg (van Noordwijk 1984, Järvinen 1991), which is understandable because 95% of the yolk is formed

during that period (Ricklefs 1974, Schifferli 1976, Ojanen 1983a). However, many passerines (Nilsson & Svensson 1993, Ward 1995, and others), including Tree Sparrows (Pinowski et al. 2001b), can interrupt laying during spells of adverse weather. In Tree Sparrows interruption of laying is most frequent when the energy demands for egg production are the highest, that is, after the first, second, third, or fourth egg, and only rarely before the day on which the last egg in a clutch is laid (Pinowski et al. 2001b). In the present study, as in van Noordwijk (1984) and Näger & Zandt (1994), only mean daily temperatures below 10°C affected egg size. Experiments conducted by Näger & van Noordwijk (1992) show that temperature can affect egg size, but natural variation in temperature usually explains only a small proportion of the observed variation in egg size (Ojanen et al. 1981, Haftorn 1986).

The present study suggests that trends in temperature change affect egg size to a greater extent than does the temperature on a given day. Tree Sparrows lay clutches with the largest mean egg size when the minimum temperature increases from 0°C on day 5 prior to the laying date of the first egg to about 7°C on the laying date of the first egg (Fig. 1). Low temperatures have been shown to give rise to hyperphagia in birds (Kendeigh et al. 1956, Kendeigh 1969, Dykstra & Karasov 1992).

2. The effect of temperature on egg size through the availability of animal food

The effect of weather conditions, including ambient temperature, on food availability for female Tree Sparrows during oogenesis is unknown. We know, however, that weather influences the composition of animal food fed to nestlings. On rainy days, the availability of insects is reduced and the proportion of plant food increases, as does the proportion of *Diptera* among insects. On sunny days, the proportion of Coleoptera and Lepidoptera increases. On windy days, Tree Sparrows forage on the ground and the proportion of adult Coleoptera, Acrididae, and Araneae increases, whereas *Diptera* and Lepidoptera are less frequent (Grün 1964). It is not known whether such changes in diet composition affect the availability of requires nutrients (see however Ramsay & Houston 2003).

For egg production, females need the sulphur containing amino acids methionine and cysteine in their diet, as they cannot synthesise these amino acids (Houston et al. 1995abc, Williams & Cooch 1996, Houston 1999). It is well known that during oogenesis, many granivorous birds feed on animal food composed mainly of invertebrates, which contain more protein (Ankney & Scott 1980). This

is also the case for the House Sparrow (Pinowska 1975), and thus probably also for the Tree Sparrow, as the diet of these two species are similar during the breeding period (Anderson 1984).

3. Temperature-dependent changes in the intestines of females

Hyperphagia caused by low ambient temperatures is associated with an increase in intestinal length, which increases the efficiency of food absorption (Dykstra & Karasov 1992). In small passerines, food intake in females during the period of rapid egg formation, that is, 3–4 days prior to the date of the first egg (Walsberg 1983), increases as a consequence of increased requirements for energy and nutrients at that time. These effects of hyperphagia may, however, be partially counteracted by the change in diet, as increased in the proportion of animal food have a negative effect on the length of intestines (Karasov 1996). Nonetheless, Ankney & Scott (1988) found a 10% increase in the intestinal length in laying Brown-headed Cowbirds *Molothrus ater*. In the American Robin *Turdus migratorius* and Starling *Sturnus vulgaris*, the adaptation of intestinal length to hyperphagia requires 3 days (Levey & Karasov 1989), while other physiological adaptations, such as retention time of food, changed even faster (Dykstra & Karasov 1992). This could account for the delay between the cause (temperature and its changes) and effect (egg size) in the Tree Sparrow.

Hyperphagia related to the acquiring and storing, it resources for egg laying that immediately follows hyperphagia caused by low temperatures may allow the female to avoid a period of transition and additional loss of energy for reconstruction of the intestines needed for the period of the maximum oogenesis. This may result in saving of energy and to a more efficient utilization of food, and may explain both the paradoxical, positive effect of low temperatures 5 days before laying on egg volume and the positive effect of a trend of increasing temperature on egg volume.

These hypotheses, explaining both the effects of temperature and the trend in temperature change, are not contradictory and the mechanisms they involve can act simultaneously. But the hypothesis stating that variation in Tree Sparrow egg size is related to the availability of the animal food supply mediated through weather conditions cannot explain the effect of trend in temperatures on egg volume. We suggest that our results are best explained by the hypothesis that temperature affects egg size through the energy balance/budget of the female, although the mechanisms postulated by

the two remaining hypotheses can also contribute to the relationship between ambient temperature and variation of egg size in the Tree Sparrow.

The role of temperature versus other factors affecting egg volume

Many authors agree that 60–80% of the variation in egg size can be attributed to the maternal effects (Ojanen et al. 1979, van Noordwijk et al. 1981, Potti 1993, 1999), but it is not possible to separate the direct additive genetic variance from the maternal environmental variance (Roff 1997). In the Goldcrest, the mean temperature during the periods of 3, 4, 5, 7, or 9 days before laying accounted for 7–10% of the variation in egg weight, and during the period of 11 days for 11% (Haftorn 1986). In Starlings, this was 10–15%, in the Great Tit *Parus major* about 1% for all eggs, but 10–20% for the last-laid egg (Ojanen et al. 1981). In the Pied Flycatcher *Ficedula hypoleuca* the highest correlation explained only a small proportion of the variation in the total (about 1%), and not much more for the first and last eggs about 4% (Ojanen et al. 1981). In the present study, the effect of temperature on egg volume explained 1.6% of the variation, and the effect of the trend in temperature change, 4.2%. The joint effect of temperature and its trend explained up to 8.7% of the variation in egg volume (Table 1).

The positive effect of low temperatures on the volume of Tree Sparrow eggs of the first brood in 1994, when mean and even maximum temperatures often dropped below 10°C, clearly indicates the importance of temperature to the energy budget of females, but it does not exclude an indirect effect through the available food supply in sufficient amounts and of adequate nutritive value. The negative effect of high temperature during the laying of the second and third clutches in 1995 is indicative of the importance of temperature to the energy budget of females through limiting their capability for laying larger eggs. Under climate conditions of Poland, the activity of insects consumed by Tree Sparrows cannot be limited by high temperature.

According to our unpublished data, egg volume influences the weight of nestlings of the Tree Sparrow only for day 4 after hatching. This is also true for other small passerines (Williams 1994, Ward 1996, Styrsky et al. 1999, Styrsky 2000).

ACKNOWLEDGMENTS

We wish to thank J. Bańbura, M. Cichoń, E. Rajska-Jurgiel and A. Wasilewski for reviews of an

earlier draft, and to T. R. Anderson for linguistic suggestion. We are grateful K.-H. Hahm and N. Lebedeva for assistance in field works.

REFERENCES

- Anderson T. R. 1984. A quantitative analysis of overlap in nestling diets of village populations of sparrows (*Passer* spp.) in Poland. *Ekol. Pol.* 32: 693–707.
- Ankney C. D., Scott D. M. 1980. Changes in nutrient reserves of breeding Brown-headed Cowbirds. *Auk* 97: 684–696.
- Ankney C. D., Scott D. M. 1988. Size of digestive organs in breeding Brown-headed Cowbirds *Molothrus ater*, relative to diet. *Can. J. Zool.* 66: 1254–1257.
- Bolotnikov A. M., Shurakov A. I., Kamensky J. N., Dobrinsky L. N. 1985. [Ecology of early ontogenesis of birds]. *Akad. Nauk USSR, Ural Sci. Centr., Sverdlovsk.*
- Bolton M., Houston D. C., Monaghan P. 1992. Nutritional constraints on egg formation in the Lesser Black-backed Gull: an experimental study. *J. Anim. Ecol.* 61: 521–532.
- Carey C. 1996. Female reproductive energetics. In: Carey C. (ed.). *Avian energetics and nutritional ecology*. Chapman and Hall, New York, pp. 324–374.
- Clark C. E., Amin M. 1965. The adaptability of chickens to various temperatures. *Poultry Sci.* 44: 1003–1009.
- Dykstra C. R., Karasov W. H. 1992. Changes in gut structure and function in House Wrens (*Troglodytes aedon*) in response to increasing energy demands. *Physiol. Zool.* 65: 422–442.
- Grün G. 1964. Untersuchungen zur Ökologie und wirtschaftlichen Bedeutung des Feldsperlings, *Passer montanus* (L.), unter besonderer Berücksichtigung seiner Ernährungsweise. Ph.D. thesis, Univ. Greifswald, Greifswald.
- Haftorn S. 1986. Clutch size, intraclutch size variation, and breeding strategy in the Goldcrest *Regulus regulus*. *J. Ornithol.* 127: 291–301.
- Houston D. C. 1999. Nutritional constraints on breeding birds. In: Adams N. J., Slotow R. H. (eds). *22 Int. Ornithol. Congr., Durban: Johannesburg, Bird Life South Africa*, pp. 52–66.
- Houston D. C., Donnan D., Jones P. J., Hamilton I., Osborne D. 1995a. Changes in the muscle condition of female Zebra Finches *Poephila guttata* during egg laying and the role of protein storage in bird skeletal muscle. *Ibis* 137: 322–328.
- Houston D. C., Donnan D., Jones P. J. 1995b. The source of the nutrients required for egg production in Zebra Finches *Poephila guttata*. *J. Zool. London* 235: 469–482.
- Houston D. C., Donnan D., Jones P. J. 1995c. Use of labelled methionine to investigate a protein storage function of avian muscle to contribute to egg production. *J. Comp. Physiol. B* 165: 161–164.
- Hoyt D. F. 1979. Practical methods of estimate volume and fresh weight of birds eggs. *Auk* 96: 73–77.
- Huston T. M., Joiner W. P., Carmon J. L. 1957. Breed differences in egg production of domestic fowl held at high environmental temperatures. *Poultry Science* 36: 1247–1254.
- Järvinen A. 1991. Proximate factors affecting egg mass in subarctic hole-nesting passerines. *Ornis Fenn.* 68: 99–104.
- Järvinen A. 1994. Global warming and egg size of birds. *Ecography* 17: 108–110.
- Järvinen A., Pryl M. 1989. Egg dimensions of the Great Tit *Parus major* in southern Finland. *Ornis Fenn.* 66: 69–74.
- Järvinen A., Väisänen R. A. 1984. Reproduction of Pied Flycatchers (*Ficedula hypoleuca*) in good and bad breeding seasons in a northern marginal area. *Auk* 101: 439–450.

- Järvinen A., Ylimaunu Y. 1986. Intraclutch egg-size variation in birds: physiological responses of individuals to fluctuations of environmental conditions. *Auk* 103: 235–237.
- Karasov W. H. 1996. Digestive plasticity in avian energetics and feeding ecology. In: Carey C. (ed.). *Avian energetics and nutritional ecology*. Chapman and Hall, New York, pp. 61–84.
- Kendeigh S. C. 1941. Length of day and energy requirements for gonad development and egg-laying. *Ecology* 22: 237–248.
- Kendeigh S. C. 1969. Energy responses of birds to their thermal environments. *Wilson Bull.* 81: 441–449.
- Kendeigh S. C., Dolnik V. R., Gavrilov V. M. 1977. Avian bioenergetics. In: Pinowski J., Kendeigh S. C. *Granivorous birds in ecosystems*. Cambridge Univ. Press, Cambridge, pp. 127–204.
- Kendeigh S. C., Kramer T. C., Hamerstrom F. 1956. Variations in egg characteristics of the House Wren. *Auk* 73: 42–65.
- King J. R. 1973. Energetics of reproduction in birds. In: Farner S. (ed.). *Breeding biology of birds*. National Academy of Sciences, Washington, D. C., pp. 78–107.
- Krementz D. G., Ankney C. D. 1886. Bioenergetics of egg production by female House Sparrows. *Auk* 103: 299–305.
- Levey D. J., Karasov W. H. 1989. Digestive responses of temperate birds, switched to fruit or insect diet. *Auk* 106: 675–686.
- Lorenz F. W., Almquist H. J. 1936. Seasonal variations in egg quality. *Poultry Sci.* 15: 14–18.
- Magrath R. D. 1992. Seasonal changes in egg-mass within and among clutches of birds: general explanations and a field study of the Blackbird *Turdus merula*. *Ibis* 134: 171–179.
- Martin T. E. 1987. Food as a limit on breeding birds: a life-history perspective. *Ann. Rev. Ecol. Syst.* 18: 453–487.
- Mueller W. J. 1961. The effect of constant and fluctuating environmental temperatures on the biological performance of laying pullets. *Poultry Sci.* 40:1562–1571.
- Murphy E. C. 1978. Seasonal variation in reproductive output of House Sparrow: the determination of clutch size. *Ecology* 59: 1189–1199.
- Murphy E. C., Haukioja E. 1986. Clutch size in nidicolous birds. *Current Ornithol.* 4: 141–180.
- Näger R. 1990. On the effects of small scale variation in temperature and food availability on laying date and egg size in Great Tits (*Parus major*). In: Blondel J., Gosler A., Lebreton J.-D., McCleery R. (eds). *Population biology of passerine birds*. NATO ASI Ser. vol G. 24, Springer-Verlag, Berlin-Heidelberg, pp. 187–197.
- Näger R. G., van Noordwijk A. J. 1992. Energetic limitation in the egg-laying period of Great Tits. *Proc. R. Soc. London B*, 249: 259–263.
- Näger R. G., Zandt H. S. 1994. Variation in egg size in Great Tits. *Ardea* 82: 315–328.
- Nilsson J. A. 1991. Clutch size determination in the Marsh Tit (*Parus palustris*). *Ecology* 72: 1757–1762
- Nilsson J. A., Svensson E. 1993. Causes and consequences of egg mass variation between and within Blue Tit clutches. *J. Zool. London* 230: 469–481.
- O'Connor T. 1978. Nest-box insulation and the timing of laying in the Wytham woods population of Great Tit *Parus major*. *Ibis* 120: 534–537.
- Ojanen M. 1983a. Effects of laying sequence and ambient temperature on the composition of eggs of the Great Tit *Parus major* and the Pied Flycatcher *Ficedula hypoleuca*. *Ann. Zool. Fenn.* 20: 65–71
- Ojanen M. 1983b. Egg development and the related nutrient reserve do depletion in the Pied Flycatcher, *Ficedula hypoleuca*. *Ann. Zool. Fenn.* 20:
- Ojanen M., Orell M., Väisänen R. A. 1978. Egg and clutch sizes in four passerine species in northern Finland. *Ornis Fenn.* 55: 60–68
- Ojanen M., Orell M., Väisänen R. A. 1979. Role of the heredity in egg size variation in the Great Tit *Parus major* and the Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scand.* 10: 22–28.
- Ojanen M., Orell M., Väisänen R. A. 1981. Egg size variation within passerine clutches effects of ambient temperature and laying sequence. *Ornis Fenn.* 58: 93–108.
- Perrins C. M. 1996. Eggs, egg formation and timing of breeding. *Ibis* 138: 2–15.
- Pikulski A. 1986. [Breeding biology and ecology of Savi's Warbler (*Locustella luscinioides*) at Milicz fish-ponds (preliminary report)]. *Ptaki Śląska* 4: 2–39.
- Pinowska B. 1975. Food of female House Sparrows (*Passer domesticus* L.) in relation to stages of the nestling cycle. *Pol. Ecol. Stud.* 1: 211–225.
- Pinowska B. 1979. The effect of energy and building resources of females on the production of House Sparrows (*Passer domesticus* [L.]) populations. *Ekol. Pol.* 27: 363–396.
- Pinowska B., Barkowska M., Pinowski J., Hahm K.-H., Lebedeva N. 2002. Influence of temperature on Tree Sparrow *Passer montanus* egg mass according to laying sequence. *Intern. Stud. Sparrows* 29: 33–47.
- Pinowski J. 1965. Dispersal of young Tree Sparrows (*Passer m. montanus* [L.]). *Bull. Acad. Pol. Sci. II Ser. Sci. Biol.* 13: 509–514.
- Pinowski J. 1967. Die Auswahl des Brutbiotops beim Feldsperling (*Passer m. montanus* [L.]). *Ekol. Pol. Ser. A.* 15: 1–30.
- Pinowski J., Kendeigh S. C. (eds). 1977. *Granivorous birds in ecosystems*, Cambridge Univ. Press, Cambridge.
- Pinowski J., Barkowska M., Hahm K.-H., Lebedeva N. 2001a. Variation in Tree Sparrow *Passer montanus* eggs. *Intern. Stud. Sparrows* 27–28: 5–34.
- Pinowski J., Barkowska M., Hahm K.-H., Lebedeva N. 2001b. Laying interruption in the Tree Sparrow *Passer montanus*. *Acta Ornithol.* 36: 13–18.
- Potti J. 1993. Environmental, ontogenetic and genetic variation in egg size of Pied Flycatchers. *Can. J. Zool.*, 71: 1534–1542.
- Potti J. 1999. Maternal effects and the pervasive impact of nestling history on egg size in a passerine bird. *Evolution* 53: 279–285.
- Rahn E., Sotherland P. R., Paganelli C. V. 1985 Interrelationships between egg mass and adult body mass and metabolism among passerine birds. *J. Ornithol.* 126: 263–271.
- Ramsay S. L., Houston D. C. 1997. Nutritional constraints on egg production in the Blue Tit: a supplementary feeding study. *J. Anim. Ecol.* 66: 649–657.
- Ramsay S. L., Houston D. C. 1998. The effect of dietary amino acid composition on egg production in Blue Tits. *Proc. R. Soc. London B*, 265: 1401–1415.
- Ramsay S. L., Houston D. C. 2003. Amino acid composition of some woodland arthropods and its implications for breeding tits and other passerines. *Ibis* 145: 227–232.
- Ricklefs R. E. 1974. Energetics of reproduction in birds. In: Paynter R. A. *Avian energetics*. Nuttall Ornithological Club, Cambridge, Massachusetts, pp. 152–292.
- Roff D. A. 1997. *Evolutionary quantitative genetics*. Chapman and Hall, New York
- Schifferli L. 1976. Factors affecting weight and conditions in the House Sparrow particularly when breeding. PhD thesis, University of Oxford.
- Schifferli L. 1980. Changes in the fat reserves in female House Sparrows *Passer domesticus* during egg laying. *Proc. Int. Ornithol. Congr.* 17: 1129–1135.
- Stevenson I. R., Bryant D. M. 2000. Climate change and constraints on breeding. *Nature* 406: 366–367.
- Styrsky J. D., Eckerle P., Thompson C. F. 1999. Fitness-related consequences of egg-mass in nestling house wren. *Proc. R. Soc. Lond. B* 266: 1253–1258.

- Styrsky J. D. 2000. Food-supplementation does not override the effect of egg mass on fitness-related traits of nestling House Wren. *J. Anim. Ecol.* 69: 690–702.
- van Noordwijk A. J. 1981. Genetic variation in egg dimensions in natural populations of the Great Tit. *Genetica* 55: 221–232.
- van Noordwijk A. J. 1984. Quantitative genetics in natural populations of birds illustrated with examples from the Great Tit, *Parus major*. In: Wahrmann K., Loeschcke V. L. (eds). *Population biology and evolution*. Springer-Verlag, Berlin-Heidelberg, pp. 67–79.
- Walsberg G. E. 1983. Avian ecological energetics. In: Farmer J. R., King J. R., Parkes K. C. (eds). *Avian Biology*, vol. VII, pp. 161–220.
- Ward S. 1995. Causes and consequences of egg size variation in swallows (*Hirundo rustica*). *Avocetta* 19: 189–201.
- Ward S. 1996. Energy expenditure of female Barn Swallows *Hirundo rustica* during egg formation. *Physiol. Zool.* 69: 930–951.
- Williams J. B. 1987. Field metabolism and food consumption of Savannah Sparrows during the breeding season. *Auk* 104: 277–289.
- Williams T. D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biol. Review* 68: 35–59.
- Williams T. D. 1996. Variation in reproductive effort in female Zebra Finches (*Taeniopygia guttata*) in relation to nutrient-specific dietary supplements during egg laying. *Physiol. Zool.* 69: 1255–1275.
- Williams T. D., Cooch E. G. 1996. Egg size, temperature, and laying sequence: why do Snow Geese lay big eggs when it's cold? *Functional Ecol.* 10: 112–118.

STRESZCZENIE.

[Wpływ trendu temperatury na objętość jaj mazurka]

Dotychczas prowadzono wiele badań nad wpływem temperatury na wielkość jaj. Analizowano wpływ uśrednionych wartości średniej temperatury dobowej, minimalnej, rzadziej maksymalnej w czasie od 3 do 11 dni (lub dłuższym) poprzedzających zniesienie jaja. Tylko kilku autorów badało wpływ temperatury w kolejnych dniach przed zniesieniem jaja. Tę metodę badań zastosowali autorzy niniejszego opracowania. Dotychczas nikt nie badał wpływu trendu temperatury na wielkość jaj co jest głównym celem pracy.

Zmiany temperatury scharakteryzowano regresją liniową między temperaturą minimalną (następnie średnią i maksymalną) a kolejnymi dniami: od 7 dnia (następnie od 6 i od 5 dnia) poprzedzającymi zniesienie pierwszego jaja do dnia, w którym samica zniosła trzecie jajo, zwaną dalej trendem temperatury minimalnej (odpowiednio średniej i maksymalnej). Wpływ trendu analizowa-

wano biorąc pod uwagę współczynnik nachylenia odpowiedniej prostej regresji do osi czasu. Łączny wpływ temperatury i trendu temperatury analizowano stosując dwuczynnikową regresję i współczynnik determinacji między średnią objętością jaja w zniesieniu a temperaturą oraz współczynnikiem nachylenia trendu zmian temperatury.

Stwierdzono, że na objętość jaj wpływały temperatury niskie w czasie pierwszego lęgu 1994 r. oraz wysokie w czasie drugiego i trzeciego lęgu 1995 r. (Fig. 1 i 2). Podczas pierwszego lęgu 1994 roku wystąpiły niskie temperatury i ich wpływ na średnią objętość jaj w zniesieniu tłumaczył 1.6% zmienności objętości jaj. Trend temperatury był odpowiedzialny za 4.0% zmienności objętości jaj, natomiast łączny wpływ trendu i temperatury aż za 8.7% zmienności jaj (Tab. 1). W drugim i trzecim lęgu 1995 roku temperatury maksymalne zbliżone były do górnej temperatury krytycznej mazurka. Temperatura odpowiedzialna była za 0,9% zmienności jaj, trend temperatury za 0.2% zmienności jaj a łączny wpływ temperatury i trendu temperatury wyjaśniał 3.4% zmienności objętości jaj (Tab. 1).

Zniesienia o największych jajach w czasie pierwszego lęgu 1994 poprzedził okres wzrostu temperatury od 0° do 7°C. Dla zniesień o jajach średnich i małych wzrost temperatury w tym okresie był mniejszy i nieregularny (Fig. 1). Temperatury występujące między drugim dniem przed zniesieniem pierwszego jaja a dniem, w którym składane było drugie jajo były dodatnio skorelowane ze średnią objętością jaja, natomiast temperatury minimalne 4 dnia przed rozpoczęciem zniesień były ujemnie skorelowane ze średnią objętością jaja w zniesieniu (Fig. 1). W drugim i trzecim lęgu 1995 wpływ temperatury na średnią objętość jaja w zniesieniu był ujemny (Fig. 2).

W dyskusji autorzy wyrażają pogląd, że trend temperatury wpływa na bilans energetyczny samicy. W okresie niskiej temperatury hiperfagia powoduje zwiększenie się przewodności pokarmowej a także wzrost jego zdolności trawiennych i chłonnych. Zdolności te może samica wykorzystać w okresie hiperfagii przed rozpoczęciem składania jaj i zaoszczędzoną energię konieczną do przebudowy układu pokarmowego zużyć na budowę większych jaj. Mechanizm ten tłumaczyłby dodatni wpływ na objętość jaj niskich temperatur występujących kilka dni przed rozpoczęciem zniesień (patrz Margrath 1992, Pinowska et al. 2002).