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Source: Acta Ornithologica, 36(1) : 13-18

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

URL: https://doi.org/10.3161/068.036.0109

ACTA ORNITHOLOGICA
Vol. 36 (2001) No. 1

Laying interruption in the Tree Sparrow *Passer montanus*

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Pinowski J., Barkowska M., Hahm K.-H., Lebedeva N. 2001. Laying interruption in the Tree Sparrow *Passer montanus.* Acta Ornithol. 36: 13–18.

Abstract. The work was carried out in the villages of the Łomianki commune near Warsaw, Poland (52°20′N, 20°50′E) in 1994 and 1995. From among 315 clutches of Tree Sparrows studied, 20 exhibited one-day interruptions in the laying of first and second broods, while 2 were characterised by two-day interruptions. Amongst third broods, there was just a single one-day interruption noted in each year of the study. Interruptions did not occur immediately prior to the laying of the last egg in a clutch. Only in the case of the first brood in 1995 could a period of cold account for interruptions; in the remaining cases, the phenomenon must have been influenced by non-meteorological factors. The Tree Sparrow resembles the House Sparrow *Passer domesticus* in having far fewer interruptions to laying than other small hole-nesting birds, such as tits *Parus* spp. This is probably a reflection of the genus *Passer* having evolved in dry areas, where the accumulation of body reserves in the female prior to laying is an adaptation reducing the length of the breeding period to match the time associated with the rainy season, when food is abundant.

Key words: laying interruption, eggs, Tree Sparrow, *Passer montanus*

Received — May 2000, accepted — Nov. 2000

INTRODUCTION

Bird species are known to differ in the frequency with which the laying of clutches is interrupted, but the causes of this phenomenon are not always clear. Such interruptions characterise between 20 and 40% of broods among Great Tits *Parus major* (Winkel 1970, Schmidt & Hamann 1983), Blue Tits *Parus caeruleus* (Schmidt & Hamann 1983, Nilsson & Svensson 1993) and Pied Flycatchers *Ficedula hypoleuca* (Winkel & Winkel 1974, Schmidt & Hamann 1983), but fewer than 11% of those of the House Sparrow *Passer domesticus* and Tree Sparrow (Seel 1968, Schifferli 1976, Simwat 1977).

The laying interruption may be linked with the energy balance in the female (Winkel 1970, Winkel & Winkel 1974, Dhondt et al. 1983, von Haartmann 1990, Lundberg & Alatalo 1992, Nilsson & Svensson 1993, Yom-Tov & Wright 1993, and others) or with a shortage of certain nutrients, e.g. essential sulphur amino acids such as cysteine and methionine (Ramsay & Houston 1997, 1998, Houston 1999). Unlike other groups of birds, the small passerines lay a single egg each day. Some of them accumulate the majority of the nutrients needed for producing eggs in the course of actual laying, thus storing little in their bodies in the time before the first egg is laid (Drent & Daan 1980, Carey 1996, Perrins 1996 and others). House Sparrows accumulate around one-third of the nutrients needed to produce eggs prior to the laying of the first egg, according to data from Europe (Schifferli 1976, Pinowska 1979, Schifferli 1980), but not so clear in North America (Krementz & Ankney 1986, 1988). Having even larger clutches than sparrows, tits store smaller amounts of nutrients in their bodies, taking the food needed to form eggs while laying (Perrins 1996). In this case, males provide females with additional food (Royama 1966, Krebs 1970).

The aim of the present study has thus been to study the incidences and to explain the causes of interrupted laying in the Tree Sparrow.

STUDY AREA, MATERIALS AND METHODS

The investigation was carried out between 15 April and 20 August 1994 and repeated between 20 April and 20 July 1995 in the villages in Łomianki commune — all situated about 15 km NW of Warsaw, Poland (52°20′N, 20°50′E). In all, 200 nest boxes were erected. These were inspected daily between 09.00 and 14.00, with eggs being marked with a permanent marker on the day of laying and measured for length (L) and diameter (B) to an accuracy of 0.05 mm. In 1995 the eggs were actually weighed, to an accuracy of 0.01 g. In 1994, however, the egg weights had been calculated on the basis of the regression between the weight (W) and the product LB^2, which is approximately proportional to the egg volume and is given by the equation $W = 0.546LB^2$ ($r = 0.90$). Meteorological data were obtained from the Meteorological Station of the Kampinos National Park, 15 km to the west of the study area.

The mean weights of eggs were compared in 4- and 5-egg clutches laid concurrently with and without interruptions. Multifactor analysis of variance was applied in assessing the influence on any differences of such factors as year of study, brood, clutch size and sequential numbers of eggs in clutches. In interrupted clutches the influence of the year of study was investigated, as were the effects of brood and clutch size on mean weights of eggs before and after interruptions. As egg size is an individual feature of a particular female, a comparison carried out in parallel with the above concerned the mean weights of eggs in clutches with or without interruptions, as well as the deviations of egg weights from the mean for the clutch in the cases of eggs laid before and after the interruption. Differences in these means were again assessed using multifactor ANOVA to check for any influence of the year, brood number or clutch size.

RESULTS

Eight (5.4%) of the 148 Tree Sparrow clutches studied in 1994 were shown to have had interruptions in laying (9 instances in all), including one lasting two days. In turn, of the 167 clutches studied in 1995, 10 (6.0%) were found to have featured interruptions (11 instances in all). Again, one interruption was of two days' duration. Interruptions in laying were mainly encountered in first and second broods. Third broods were only found to exhibit single interruptions (one in each of the two years; Table 1). Interruptions were rarely reported on the penultimate day of egg-laying (Table 2), and no connection whatever could be made between their occurrence and meteorological conditions (Fig. 1), other than in 1995, when first-brood interruptions in laying were quite probably influenced by a drop in temperature (Fig. 1).

Table 1. Laying interruption in relation to laying sequence and number of eggs. In brackets: number of clutches with laying interruption preceding particular egg.

Brood	Clutches	Number of eggs (and interruptions) in laying sequence									
		1	2		3		4		5		6	7
1994												
I	87	87	87		86	(1)	84	(2)	80			40
II	40	40	40	(3)	39	(1)	39	(1)	37		20	0
III	21	21	21	(1)	21		20		16		2	0
1995												
I	91	91	91		86	(2)	84	(4)	69	(1)	30	0
II	49	49	49		49	(2)	49	(1)	42		21	1
III	27	27	27	(1)	27		26		22		6	0
Σ	315	315	315	(5)	308	(6)	302	(8)	266	(1)	119	7
interruptions (%)				1.6		2.0		2.6		0.4		

Table 2. Laying interruptions in various passerine birds according to laying sequence (S). n — number of eggs, i% — percent of interruptions preceding certain egg. Sources: [1]Schmidt & Hamann 1983, [2]Winkel & Winkel 1974, [3]this work

	Parus major[1]		*Parus caeruleus*[1]		*Ficedula hypoleuca*[1]		*Ficedula hypoleuca*[2]		*Passer montanus*[3]	
S	n	i%	n	i%	n	i%	n	i%	n	i%
2	468	2.7	387	2.1	52	7.6	149	2.0	315	1.6
3	468	1.5	387	2.5	52	5.7	149	4.0	308	2.0
4	468	1.7	387	1.3	52	1.9	149	4.0	302	2.6
5	468	1.2	387	0.5	52	1.9	149	4.0	266	0.4
6	458	1.5	387	2.1	37		144	2.7	119	
7	446	1.7	387	1.5	1		138	4.3	7	
8	397	1.0	377	0.2			110			
9	317	1.6	369	1.6			38			
10	200	1.0	302	0.8			20			
11	148	0.6	246	0.8						
12	85	3.5	169							
13	13		109	0.9						
14			44							
15			30							

No significant differences were noted between the mean weights of eggs in clutches without interruptions (2.20 ± 0.18 g, n = 380) and clutches with interruptions (2.20 ± 0.20 g, n = 75), even though they were laid at the same time (5-way ANOVA: F = 0.045, ns; factors checked: year, brood, clutch size, number of eggs in laying sequence). The mean weights of eggs in interrupted clutches did not differ significantly from those in uninterrupted clutches (2.19 ± 0.15 g, n = 17, vs. 2.19 ± 0.17, n = 67; 4-way ANOVA: F = 0.000, ns, factors checked: year, brood and clutch size).

Similarly, clutches in which interruptions did occur exhibited no differences in egg weights before or after such interruptions (respective means 2.22 ± 0.21 g, n = 39 vs. 2.18 ± 0.15 g, n = 35; 4-way ANOVA: F = 1.33, ns; checks for influence of year, brood and clutch-size). Furthermore,

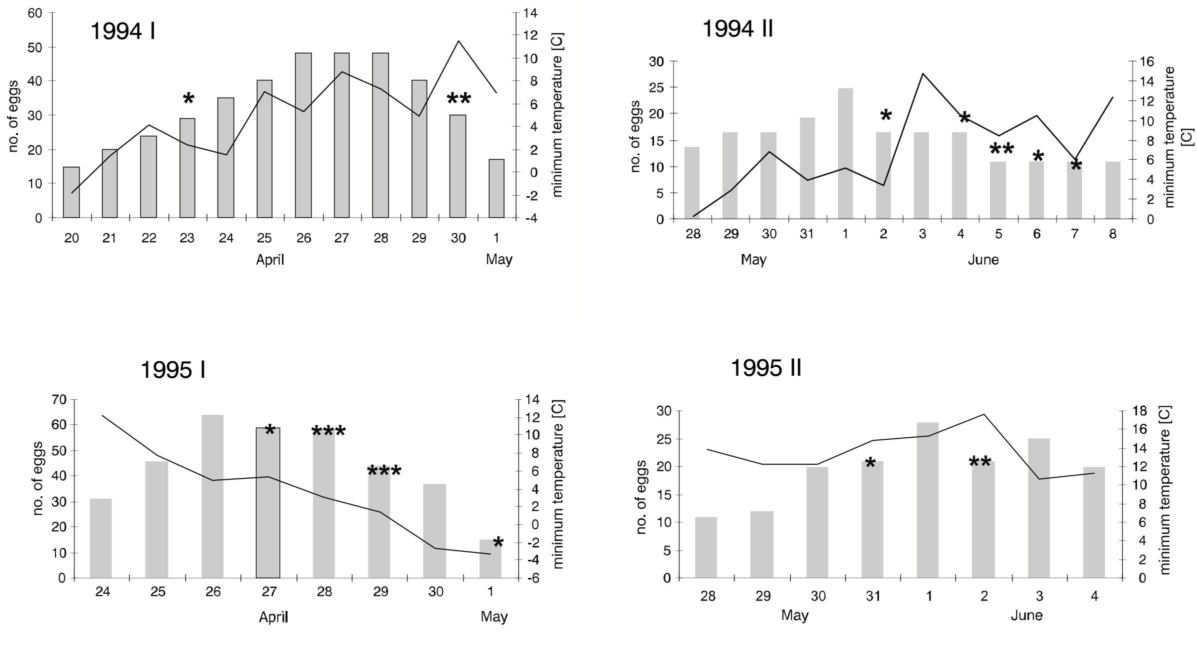

Fig. 1. Time periods of interrupted laying in both broods in 1994 and 1995. One interruption (star; both days of two-day interruption marked); numbers of eggs laid on the given day (bars); minimum temperature (line).

the deviations of egg weights from the mean egg weight in clutch did not differ significantly between eggs laid before an interruption (0.01 ± 0.10 g, n = 39) or after it (0.00 ± 0.09 g, n = 39) (4-way ANOVA: F = 0.123, ns; factors checked: year, brood and clutch size).

DISCUSSION

The egg-laying interruptions in *Passer* species noted in our study were as rare here as in the areas studied by other authors, with the exception of the Russet Sparrow *Passer rutilans* on Hokkaido in 1996 (Chae 1998). In contrast, other passerine species are subject to far more frequent interruptions in egg-laying (*Parus* vs. *Passer* except *P. rutilans*: $\chi^2 = 266.4$ df = 1, n = 1870, p < 0.0001; *Ficedula* vs. *Passer* except *P. rutilans*: $\chi^2 = 113.7$ df = 1, n = 1550, p < 0.0001; Table 3). A majority of authors have linked such interruptions with a temporary return of cool weather (Winkel 1970, Winkel & Winkel 1974, Schmidt & Hamann 1983, von Haartmann 1990, Lundberg & Alatalo 1993, Yom-Tov & Wright 1993, and many others). Such interruptions most often occur 2–4 days after the onset of cooler weather (Winkel & Winkel 1974, von Haartmann 1990, Lundberg & Alatalo 1993). Climatic factors like temperature, wind and humidity can exert a direct influence on the energy balance of females, or an indirect influence via a shortage of food. The extent to which a species depends on endogenous resources for egg-production is a reflection of many factors, most especially the quality of the diet available to the bird at this time (Drent & Daan 1980, Ankney & Alisauskas 1991, Houston 1999 and others). Different species may accumulate differing amounts of fat and proteins (especially essential amino-acids) prior to the laying of the first eggs (Drent & Daan 1980, Houston 1999, and others). The type of strategy exhibited by a species in this regard should be considered as influencing the frequency of occurrence of interruptions in laying if the energetic stress or lack of appropriate amounts of nutrients is the cause. It should be rarer in species accumulating significant reserves in their bodies than in those that do not lay down such reserves.

Table 3. Laying interruptions recorded in various species of passerine birds. n — number of clutches examined, i % — percentage of clutches with interruptions, * — first clutches only.

Species	n	i %	Sources
Parus major	224	23	Schmidt & Hamann 1983
	43	21	Winkel 1970
	28	29	Winkel 1970
Parus caeruleus	55	27	Nilsson & Svenson 1993
	100	37	Schmidt & Hamann 1983
Ficedula hypoleuca	55	16	Schmidt & Hamann 1983
	75	25	Winkel & Winkel 1974
Passer domesticus	15	6.7	Simwat 1977
	831	1.3	Seel 1968
Passer montanus	259	0.8	Seel 1968
	315	6.3	this work
*Passer rutilans**	49	4.1	Chae 1998 (1994–1995)
	35	46	Chae 1998 (1996)

Sparrows of the genus *Passer* originate from the semiarid zones of Africa, where the breeding period must be kept as closely matched as possible to the brief period of abundance of food around the rainy season (Summers-Smith 1988). A similar situation applies to Zebra Finches *Poephila guttata* (Houston et al. 1995, Houston 1999) in Australia, and to the Red-Billed Quelea *Quelea quelea* of Africa (Jones & Ward 1976). It therefore comes as no surprise that sparrows lay down large amounts of fat and protein prior to the laying of the first egg (Schifferli 1976, 1980, Pinowska 1979).

Experiments carried out by Nilsson & Svensson (1993) showed that the provisioning of extra food for female Blue Tits prior to egg-laying had a significant effect in reducing the frequency of interrupted clutches, and this irrespective of air temperature. In turn, in the House Martin *Delichon urbica*, Bryant (1975) was able to link interruptions in laying with a lack of food.

Our studies on sparrows indicated neither differences in the dimensions of eggs laid by a given bird before and after an interruption, nor differences between interrupted and uninterrupted broods laid simultaneously by different birds. In contrast, differences of these kinds were found in Blue Tits by Nilsson & Svensson (1993). As has been noted for other passerines, the interruptions in laying found in sparrows occurred most frequently after the first, second, third or fourth egg, and only very rarely before the day on which the last egg in a given clutch was laid (Tables 1 and 2). The absence of interruptions before the last egg was laid can be attributed to the fact that the peak energy and nutrient requirement for yolk formation in a given clutch was over. In addition, the follicles and post-ovulatory follicles are resorbed, thus the energy and nutrient requirements are reduced (King 1973, Pinowska 1979, Meijer et al. 1989, Magrath 1992). Song Thrushes *Turdus philomelos* (Silva 1949), and sparrows other than *Passer rutilans* in 1996 (Chae 1998) have been found to exhibit one-day, or very rarely two-day interruptions in laying (Seel 1968, Simwat 1977, Chae 1998 and our materials). In contrast, interruptions of two days and more are shown to be a very common occurrence in both tit species (Winkel 1970, Schmidt & Hamann 1983, Nilsson & Svensson 1993) and Pied Flycatchers (Winkel & Winkel 1974, Schmidt & Hamann 1983).

While the House Sparrow accumulates 30% of the necessary nutrients a few days before the laying of the first egg (Schifferli 1976, 1980, Pinowska 1979), the Blue Tit lays down hardly any nutrients at all prior to laying (Perrins 1996). However, as in Great Tits, the male of this species feeds the female assiduously during the period when eggs are being laid, thereby covering the additional costs borne by her as she produces eggs (Royama 1996, Krebs 1970). Taken together, these facts may well account for the greater infrequency of laying interruptions in sparrow species. In turn, the presence of interrupted second and third broods in our material would indicate causes wholly other than climatic. Thus, for example, the loss of a male and his replacement by another has been shown to account for interrupted laying in the House Sparrow (Veiga 1993).

The data presented here seem to indicate that the accumulation of energetic and nutrient reserves in sparrows prior to the laying of the first egg explains the considerably greater infrequency of laying interruptions as compared with other small passerines. In the Tree Sparrow at least, it may also account for the rarity of interruptions longer than one day, as well as for a lack of differences of the kind that were noted in Blue Tits by Nilsson & Svensson (1993), i.e. between the weights of eggs laid in interrupted and uninterrupted broods, as well as in given broods before and after an interruption. The authors associate these differences with differing evolutionarily-conditioned life strategies among the species considered.

Linguistic revision by Peter Senn

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STRESZCZENIE

[Przerwy w znoszeniu jaj u mazurka]

W przeciwieństwie do innych grup ptaków małe gatunki wróblowych znoszą codziennie po jednym jaju i gromadzą większość nutrientów (substancji odżywczych) potrzebnych do budowy jaj w trakcie ich znoszenia (Drent & Daan 1980, Carey 1996, Perrins 1996 i inni). Samice wróbla domowego gromadzą około $^1/_3$ nutrientów potrzebnych do budowy jaj w swym ciele przed zniesieniem pierwszego jaja (Schifferli 1976, 1980, Pinowska 1979) natomiast zjawisko to nie występuje u sikor (Perrins 1996). Celem prezentowanej pracy było zbadanie częstości występowania przerw w znoszeniu jaj u mazurka, porównanie pod tym względem z innymi gatunkami małych ptaków wróblowatych oraz próba wyjaśnienia różnic.

Badania prowadzono w okolicach Warszawy w gminie Łomianki (52°20′ N, 20°50′ E). W 1994 roku w 148 zbadanych zniesieniach mazurka w 8 zniesieniach stwierdzono 9 przerw, a w 1995 roku odpowiednio w 167 zniesieniach — 10 przerw (Tab. 1). W obu latach stwierdzono po jednej przerwie dwudniowej, inne były jednodniowe. Przerwy występowały w lęgach pierwszych i drugich, a w lęgach trzecich tylko po 1 przerwie jednodniowej w każdym roku. Nie stwierdzono przerw bezpośrednio poprzedzających zniesienie ostatniego jaja (Tab. 1 i 2). Ciężary jaj w zniesieniach, w których występowały przerwy nie różniły się od ciężarów jaj składanych w tym samym czasie w zniesieniach bez przerw. Również jaja znoszone przed przerwą nie różniły się ciężarami od jaj znoszonych po przerwie.

Większość autorów (Winkel & Winkel 1974, von Haartmann 1990, Lundberg & Alatalo 1992 i inni) za przyczynę przerw w znoszeniu jaj uważa pogorszenie się warunków pogodowych, zwłaszcza spadek temperatury powietrza. W naszych badaniach nie stwierdzono związku między temperaturą a przerwami w znoszeniu jaj. Jedynie w I lęgu w 1995 r. obniżenie się temperatury mogło być przyczyną przerw występujących w tym czasie, jednak związek ten nie był statystycznie istotny (Fig. 1).

U mazurka, podobnie jak u wróbla domowego i u wróbla cynamonowego *Passer rutilans*, przerwy w znoszeniu jaj występują o wiele rzadziej niż u sikor i muchołówki żałobnej (Tab. 3). Samice wróbla domowego gromadzą zapasy nutrientów przed zniesieniem pierwszego jaja, co może tłumaczyć rzadsze występowanie przerw w znoszeniu jaj u tego gatunku. Zapewne analogiczny mechanizm odpowiada za rzadsze, w stosunku do sikor (Perrins 1996), występowanie takich przerw u innych gatunków z rodzaju *Passer*, w tym i u mazurka (Tab. 2 i 3). Naszym zdaniem czynniki pogodowe są tylko jednym z wielu czynników warunkujących przerwy w znoszeniu jaj, np. czynniki socjalne mogą również grać pewną rolę w tym zjawisku.