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AUTUMN SEXUAL DISPLAY IN TREE SPARROWS [*PASSER MONTANUS* (L.)] AS A COMPONENT OF THE WINTER SURVIVAL STRATEGY

ABSTRACT: The evolution of organisms leads to the elimination of behaviors that are costly in terms of energy. One of such behaviors in the Tree Sparrow *Passer montanus* is the autumn display during which these birds construct nests. The purpose of this paper is to find out if this behavior is a part of the strategy for winter survival.The study of Tree Sparrows was conducted near Warsaw, Central Poland. During the breeding season, nest boxes were checked to record the presence of Tree Sparrow nests. Before the autumn display, breeding nests were dyed in order to identify nest material added in the period of autumn display. Nestlings in nest boxes, juveniles, and adults captured in mist-nets were banded with different combinations of color bands to identify their age during visual observations in the period of autumn sexual display. Juveniles and adults caught in mist-nets were classified as molted or not molted birds. In winter, nest boxes were checked to catch the birds roosting in them at night. Autumnal sexual display in Tree Sparrows is similar to the spring display. Both adults and juveniles leave the breeding colony in August and return after molt. They form pairs, copulate and build nests in fall. The autumn display is continued from the first ten days of September to early November. The number of Tree Sparrows participating in the autumn display increases with the percentage of the birds that completed molt in the population. In the first half of September, 16% of the population completed molt, while 99% in mid-October. On the average, adult birds formed pairs on 11 September (SD: 7.7 days), and juveniles on 17 September (SD: 8.0 days). Nest construction was started, on the average, 14.2±8.7 days after pairing. The advance in nest building was dependent on the time of pair formation. Intensive nest building took place in the last 10-days period of September and in October. Early in November, nest building ceased with the onset of cool weather. The last birds to pair did not construct complete autumn nests and in winter they roosted in shrubs or in tree crowns . The building of autumn nest as a consequence of the autumn display, serving as a roosting place in winter, can be a consequence of natural selection promoting this behaviour.

KEY WORDS: autumn sexual display, pair formation, autumn nest building, strategy of winter survival, Tree Sparrow, *Passer montanus*

1. INTRODUCTION

According to the rules of survival strategy, energetically demanding behavior should be eliminated by natural selection (Stearns 1992, Weiner 1999, Ricklefs 2000). Although the autumn display in Tree Sparrows *Passer montanus* (L.) requires much energy

(Eberhardt 1994, Dolnik 1995, Ueta 1999, Oberweger and Goller 2001, Gil and Gahr 2002, Ward and Slater 2005), it has been preserved, implying that it is important for survival of this species. For small sedentary passerines, winter is a difficult period to survive, as decreasing temperatures and longer nights increase energy costs (Andreev 1980, Blem 1990, Pravosudov and Grubb 1997). In winter, Tree Sparrows feed on seeds of some weed species, the availability of which is declining along the depth of snow cover (Kovács 1966, Pinowski and Wójcik 1968, 1969, Pinowski and Pinowska 1985). Energy costs in winter can be reduced by roosting at night in a place lowering energy loss (Andreev 1980, Pinowski *et al*. 2006a). In the case of Tree Sparrows this can be a nest built as a consequence of the autumn display.

Autumn social displays have been described in many bird species living in the temperate zone (Morley 1943, Kalela 1958). This includes singing males, occupation and defense of territories, and pair formation (Lawn 1994, Weggler 2000, Forstmeier 2002, Wingfield and Soma 2002). The gathering of nest material has also been observed for several bird species (Morley 1943, Lincoln *et al*. 1980).

In Europe, few species, for example the Rook *Corvus frugilegus* L. (Coombs 1978), the Starling *Sturnus vulgaris* L. (Feare 1984) are known to lay eggs and as the Raven *Corvus corax* L. rear nestlings in fall (Mearns and Mearns 1989). In heated buildings, House Sparrows *Passer domesticus* (L.) (Feare 1984) can also nest in winter (Snow 1955, Matyuhin and Ivanitskii 1984, Kozak 1988). Whereas in North America, fall breeding was recorded in 69 of the 441 terrestrial species surveyed (Koenig and Stahl 2007). The authors of this list included pigeons and doves breeding from early spring until late fall, and the species breeding at any time of the year, dependent of the available food supply, such as *Loxia* spp. Many of these species were nesting in fall only in populations occupying southern states of the USA.

As a result of the mechanisms of natural selection, these autumnal displays can vary for different species (Logan and Hyatt 1991, Soma and Wingfield 1999, Weggler 2000, Forstmeier 2002). Autumnal displays in Tree Sparrows are almost as intensive as in spring. That is, like in spring, males select nest sites in fall (in our case nest boxes), attract females at them, females select males, and they form pairs, build nests, and copulate (Pielowski and Pinowski 1962, Pinowski 1966, 1967, García-Navas *et al.* 2008), but egg laying in fall was noted only on one occasion (Hasse 1962).

The purpose of the present study is to determine the relationship between the date of pair formation and the advancement of nest building during autumnal displays in the Tree Sparrow, and to find out whether the advancement in the building of autumn nests can be a part of the strategy for winter survival.

2. STUDY AREA

We studied Tree Sparrows during the years 1959–1973 (some analyses are based on the materials originating from shorter periods indicated in the paper) in villages and forest edges located 15 km northwest of Warsaw (52°20'N; 20°50'E), between the Kampinoski National Park and the Vistula River. The study was conducted in a suburban farmland with very small crop fields and extensive farming. Typical crops consisted of potatoes and rye interspersed with weeds. In gardens, vegetables were the dominant crop, often also with weeds . In the years of intensive observations of the autumn display, that is from 1 September to 10 November 1961, the mean daily temperature was 11.1±3.8°C, the minimum temperature was –1.9°C, and the maximum was +29.4°C. In 1962, the respective temperatures were 9.0±3.9°C, -6.6°C and + 27.6°C. Thick snow cover occurred in the winters 1962/1963, and l964/1965. The study area is described in detail in the following papers: breeding colonies in Pinowski 1966, 1967, 1968, weed communities in Kotowska 1988, Wójcik and Kmošek 1988, production of seeds in weeds in Pinowski and Wójcik 1968, 1969, and the effect of buildings on rural environment in Mackin-Rogalska *et al*. 1988.

3. MATERIALS AND METHODS

In each of these sites, that we called breeding colonies, from 27 to 144 nest boxes were erected on tree trunks, the damaged boxes being replaced with new ones. Nest boxes were cleaned in spring before the breeding season. All of them were checked at least once a week during the breeding season, from April to end of August prior to the autumn occupancy, and nest contents were dyed to see whether the birds added new material during the autumnal displays. After cessation of autumnal displays, in the first days of November, the boxes were checked again. They contained 321 nests in various stages of construction, built during the autumnal display period. Stages of construction included: 1 – empty box, 2 – old nest without addition of autumn nest, 3 – addition of the base or lining, or the base and lining over the old nest or in empty box, 4 – all layers (the base, lining and roof) built on the old nest.

During the breeding season the nestlings, at least eleven days old, were individually marked with an aluminum band, and plastic bands of various colors, so that the following groups could be distinguished: 1) adults, 2) juveniles banded as nestlings before 19 June (1st brood), 3) juveniles banded as nestlings after 19 June (2nd and 3rd broods), 4) juveniles caught in mist-nets, and 5) juveniles or adults without bands. In the autumn periods of 1961 and 1962 (September to November), sexual behavior of birds marked with color bands was observed in detail in one of the breeding colonies, called "Station", which was situated in a loose pine forest surrounding the buildings of the Field Station of the Institute of Ecology Polish Academy of Sciences. The Field Station is located 0.8 km from the forest edge. The autumn sexual behavior (chirping, display, copulation, fights, nest building, etc.) was watched through binoculars (10 × 50) at 35 nest-boxes in the colony. We assumed that the day when the male accepted the female was the date of pair formation, and that joint nest building and attempts at copulation confirmed pair formation. .

In 1961, 74 h 33 min, and in 1962, 196 h of observations were carried out in the colony "Station". Between 25 August and 30 November of 1960–1965, 1144 Tree Sparrows were captured in mist-nets from flocks foraging in arable fields in the afternoon to examine the stage of molt and, consequently, their readiness to begin the autumn display. Both the birds that completed molt and the birds in the course of molting foraged together in crop fields in the afternoon (Pinowski 1966, 1967, 1968). Mean numbers of Tree Sparrows per h noted in 10-day periods during the autumn display were used.

The standardized time for each bird was calculated with reference to the mean number of days from the date of pair formation for respective age groups. Kruskal-Wallis ANOVA was used to assess the age of Tree Sparrows in relation to the date of pair formation, and differences in the stage of nest construction in relation to the date of pair formation during autumnal displays.

4. RESULTS

Adults and juveniles left the breeding colony when the young of the last brood (3rd) fledged in August, and they came back after molt in the first ten-day period of September. The percentage of birds that completed molt increased rapidly so that in mid-October almost all Tree Sparrows were in new plumage

Table 1. Proportion of Tree Sparrows with completed molt during the autumn display (years 1960–1965). $\chi^2 = 712.62$, df = 6, $P \leq 0.001$

Period	n	% after molt
16–31 Aug	369	6
1–15 Sep	385	16
16–30 Sep	156	32
1–15 Oct	212	99
16–30 Oct	127	99
1–15 Nov	40	100
16–30 Nov	11	100

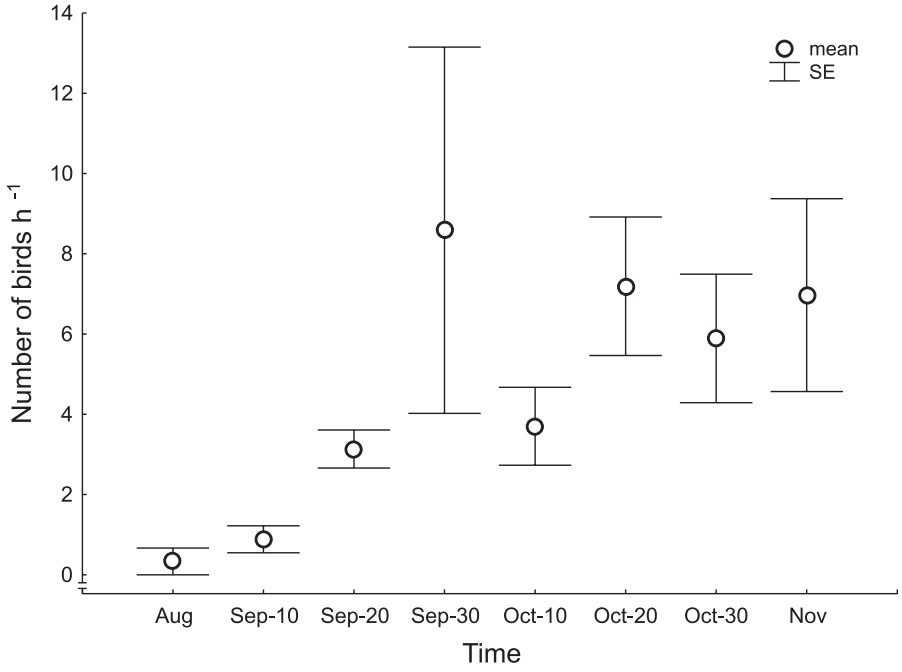

Fig. 1. Mean numbers of Tree Sparrows per hour noted in 10-days periods during the autumn display.

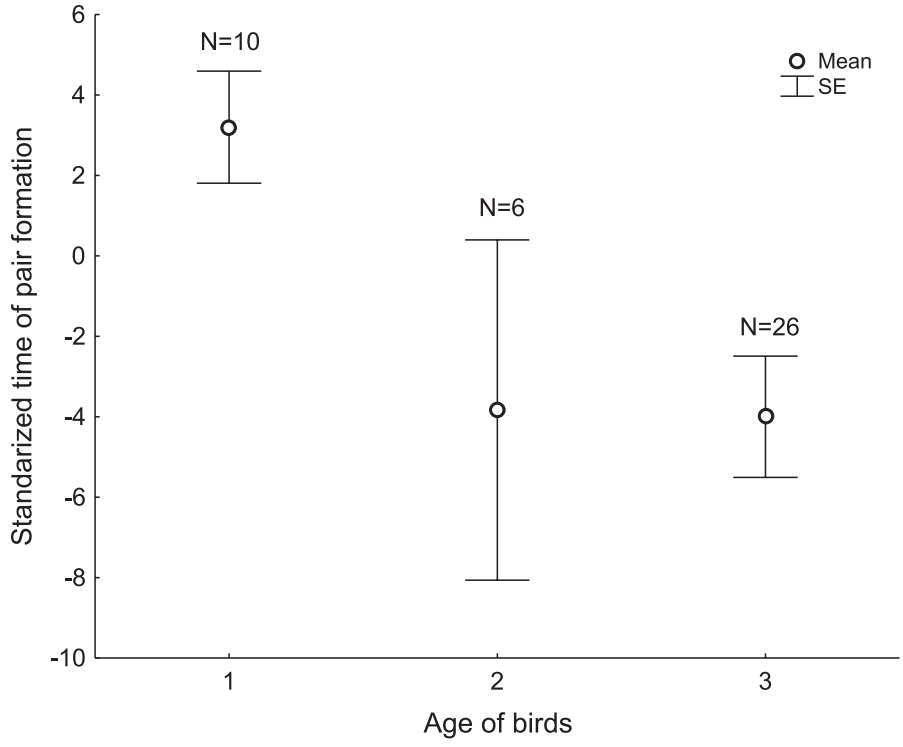

Fig. 2. The date of pair formation in the autumn display in relation to the age of Tree Sparrows. Age: 1 – both mates are juveniles, 2 – both mates are juveniles, but at least one bird of the 1st brood in pair, 3 – one or two adults paired (Kruskal-Wallis ANOVA; H2 = 5.92, N = 42, P = 0.052). The standardized time for each bird was calculated with reference to the mean number of days from the date of pair formation for respective age groups. Negative values below the mean refer to the pair formation earlier than the mean for a given age group, and positive values above the mean refer to the pair formation later than the mean number of days.

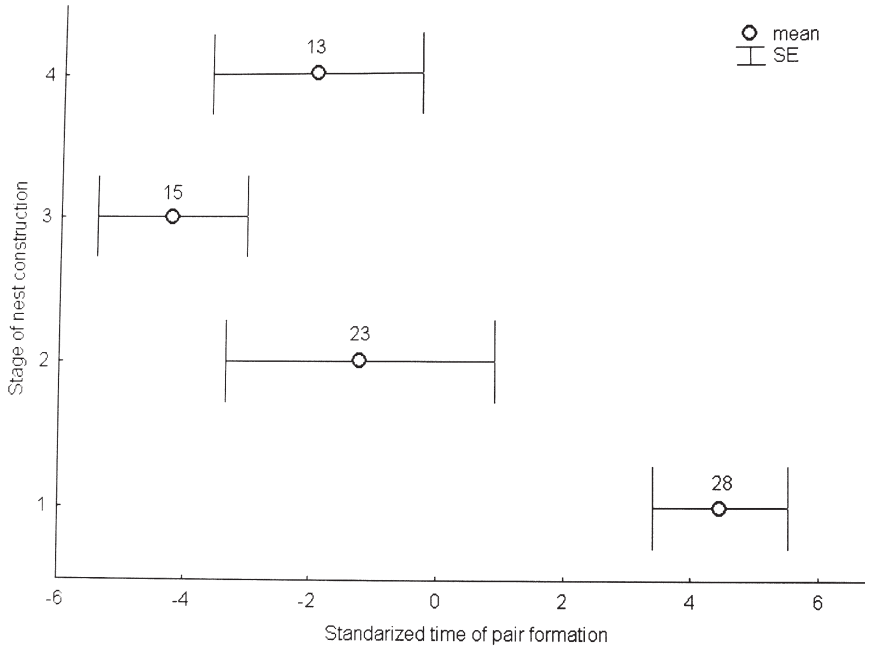

Fig. 3. The stage of nest construction in relation to the date of pair formation during autumnal displays. Nest stage: 1 – empty box, 2 – old nest without addition of autumn nest, 3 – addition of the base or lining, or the base and lining over the old nest from the breeding season, 4 – all layers (the base, lining and mound roof) built on the old nest from the breeding season. Positive and negative values as in Fig. 2. Kruskal-Wallis ANOVA: H3 =13.93, N = 79, *P* = 0.003.

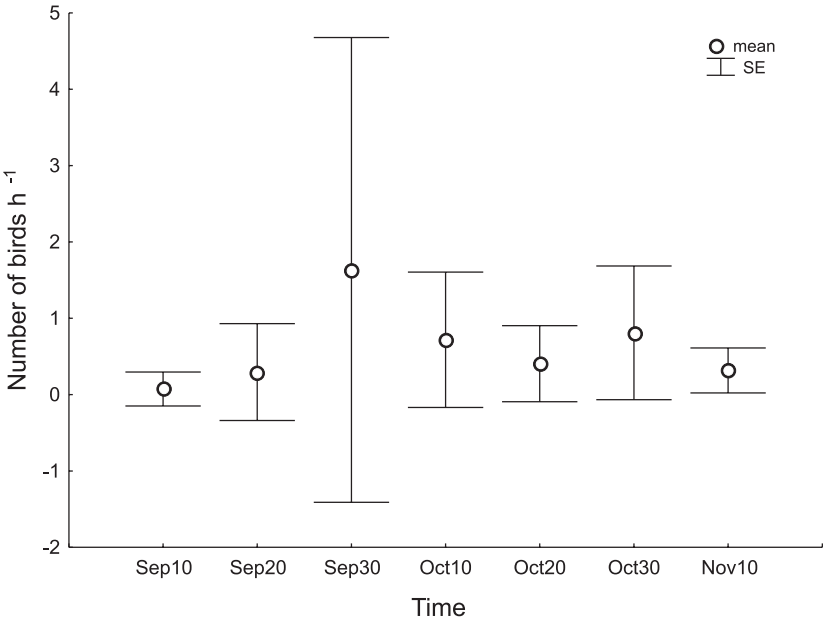

Fig. 4. Number of Tree Sparrows gathering nest material in 10-days periods during autumnal display (mean number of birds per hour of observation).

Table 2. Types of Tree Sparrow nests built in empty boxes during the autumn display

Nest type	n	%
Base	13	46
Lining	3	11
Base and lining	12	43
Complete nest: base, lining and roof	0	0

(Table 1). The increasing proportion of molted birds was associated with increasing numbers of birds participating in autumnal displays, including those birds already holding a nest box and those searching for a nest box (Fig. 1). On the average, adult males formed pairs on 11 September (SD: 7.7 days, n = 24) and juveniles on 17 September (SD: 8.0 days, n = 16) ($\chi^2 = 2.276$, df = 38, $P = 0.028$) (Fig. 2). The advance in nest building was dependent on the time of pair formation. The latest paired birds did not construct autumn nests (Fig. 3), especially that nests were built, on the average, 14.2±8.7 days (n = 31) after pair formation.

Adult birds started nest building in the first 10-d period of September, followed by juveniles. The intensive nest building took place in the last 10-d period of September and in October (Fig. 4). Early in November, nest building ceased with the onset of cool weather. The autumn nests constructed in nest boxes that were empty during the breeding season typically were lacking a roof (Table 2).

5. DISCUSSION

To our knowledge, this is the first study investigating the relationship between time of pair formation and advancement of nest building during autumnal displays. Our data show that Tree Sparrows returned to the breeding colony late in August or early in September, depending on the weather. The number of birds displaying and then forming pairs increased with the growing proportion of individuals that completed molt. Nest-building did not begin until pairs formed and then the number of birds building nests increased. Autumnal displays in Tree Sparrows continued through September and October. After 10 November, Tree Sparrows gathered nest material only occasionally in our study area. Tree Sparrows that constructed autumn nests in empty boxes did not complete their nests, and typically they did not build a roof.

Our study shows that the time at which the pair forms depends on age and determines how advanced the nest construction will be in autumn. Adults arrived first, and juveniles, especially from later broods that completed molt arrived later, and consequently, occupied less attractive boxes (e.g. empty). The males take possession of nest-boxes and females make their choice from displaying males (Pinowski 1965, Pinowski and Noskov 1981, Pinowski *et al.* 2006b). Pairs of Tree Sparrows use the autumn nest in winter for roosting at night (Pinowski 1965, 1967, Pinowski *et al.* 2008). Our preliminary data show that juvenile Tree Sparrows from later broods have lower chances of winter survival than adults and juveniles from the first broods (Pinowska *et al.* 1995). This may be due to poorer insulation of incomplete nests built during the autumnal displays (Pinowski *et al.* 2006b). The sooner they mate, the more time they have to build a nest in the period of autumnal displays and before the onset of cold weather early in November. That is also why the advance of nest construction depends on the time of pair formation. Early pair formation in the period of autumnal displays, that is a precondition for building an autumn nest, should be promoted by natural selection as it can enhance winter survival (Pinowski *et al.* 2008).

Many studies have investigated singing and defense of territories during autumnal displays and pair formation (Yamagishi 1991, Weggler 2000, Forstmeier 2003). Few studies have investigated the intensity of singing and aggression during autumnal displays (Hegner and Wingfield 1986, Gnielka 2001, Recholf 2003). Many authors note that nests were built in the autumn, but identify them as overnight and winter nests (Buttemer *et al.* 1987, Mazgajski 2002,

Michalek and Miettinen 2003, Anderson 2006). Some authors argue that Tree Sparrows build autumn nests as a shelter for winter, and they were not related specifically to autumnal displays (Creutz 1949, 1960, Keil 1961), but the majority of authors suggest that nest building is a consequence of autumnal displays (Berck 1961–1962, Deckert 1962, Turček 1962, Pinowski 1965, Summers-Smith 1995).

There are no studies investigating Tree Sparrow's hormonal changes during autumn display. House Sparrows nesting outside buildings show less autumn display (Hegner and Wingfield 1986) than Tree Sparrows. House Sparrow's testosterone levels in October and November were low (Hegner and Wingfield 1986). Other bird species that defend their territories and mate in autumn have also very low level of testosterone (Soma and Wingfield 1999, Wingfield and Soma 2002), however bird species that show autumn territorial aggression, pair bonding and build nests in sexual contexts in autumn (as do Tree Sparrows) have autumnal peaks of testosterone content (Wingfield *et al*. 1997).

The mechanisms of natural selection determining the autumn display can vary for different species (Logan and Hyatt 1991, Soma and Wingfield 1999, Weggler 2000, Forstmeier 2002). Hegner and Wingfield (1986) suggested that autumnal displays are adaptive because: 1/ they allow individuals to initiate reproduction earlier in the subsequent spring, a factor that normally correlates with increased breeding success; 2/ through the opportunity to establish pair bonds and nesting sites in the autumn, thus being able to take advantage of favorable conditions as soon as possible in the following spring; 3/ females that form pair bonds in the autumn also may be able to survive the winter months with greater amounts of protein and fat reserves because they are able to feed with less interruption from unpaired males. Females with greater nutrient reserves at the end of winter are able to lay larger and earlier clutches of eggs. 4/ for House Sparrow and other multi-breeders [e.g. *Mimus polyglottos* (L.) Logan, 1992] – pairs that initiate breeding earlier fledge more young as early nesting allows individuals to attempt more broods each season. Similar mechanism can be observed in Tree Sparrows. However, this species experiences winter mortality of approximately 85% (Pinowski 1968) and behavior promoting winter survival must be favored by natural selection.

According to Summers-Smith (1995) the Tree Sparrow evolved at the end of the Pleistocene in the valley of the Yellow River, north-eastern China, and is adapted to the use of rice, like the House Sparrow to the use of wheat. This is a bird of continental climate with severe winters but low precipitation, thus, a thin snow cover. It is more resistant to frost than the House Sparrow. In the Yakutsk (Russia) during extremely acute winters of the 1920s, the House Sparrow went extinct but the Tree sparrow survived (Nakhodkin 1988). In Poland it is not abundant in mountains with a thick layer of snow and it nests up to the height of 700 m above sea level (Mackowicz *et al*.1970, Dyrcz *et al*.1991,Walasz and Mielczarek 1992), occasionally observed up to 880 m above sea level (Cichocki after Walasz 2000). Its distribution in montane areas of other countries is similar (Bezzel 1987, Zang 1993).

In winter, Tree Sparrows live on seeds of several weed species such as *Echinochloa crus gali* (L.) P.B., *Setaria* viridis (L.) P.B., *S. glauca* (L.) P.B., *Digitaria ischaemum* (Schreb.) Muchlenb., and *Polygonum aviculare* L. (Somfai 1954, Kovács 1966, Simeonov 1963, Pinowski and Wójcik 1968, 1969, Krištin 1984). These weeds have soft stems that can be covered already with a thin layer of snow. Such weeds as *Chenopodium album* L. and *Amaranthus retroflexus* L. protrude from a snow layer 15–20 cm deep (own observations, Tomiałojć after Dyrcz *et al*. 1991, Witkowski 1964), but Tree Sparrows do not eat their seed readily (Pinowski *et al*. 1973). Under the conditions in the study area subjected to extensive management, the density of Tree Sparrows was determined by snowy winters such as that in 1962/1963, when the population of these birds broke down, and they abandoned breeding sites in marginal habitats located far from human habitations and forest edges (Pinowski 1967).

A critical period for Tree Sparrows is winter, and in particular, survival of long winter nights (Pinowski and Myrcha 1970). Win-

ter survival for young birds depends on the date of fledging. The younger the birds, that is, from later brood, have a lower chance to survive over winter (Pinowska *et al*. 1995). The younger the bird, the less time it has in the period of autumn display for pair formation and building an autumn nest (this paper). Young birds do not build autumn nests or cease building at an early stage, and they do not roost at night in nest boxes but in tree crowns or shrubs (Pinowski *et al*. 2008).

For nocturnal roosting, Tree Sparrows select nest boxes with respect to their insulating value, that is, in the following order: autumn nests built over nests from the breeding season, autumn nests built in empty boxes, nests from the breeding season, and empty boxes (Pinowski *et al*. 2008). Birds roosting in nest boxes with autumn nests over breeding nests can save even 36% of the energy, whereas less than half of that in empty boxes (Pinowski *et al*. 2006a). The survival of winter nights can depend even on minimal energy saving (Houston and McNamara 1993). This is why natural selection is likely to promote such a costly behavior as autumn display.

Many authors observed that snow cover precluding the access to food, along with low temperatures accounted for declines in Tree Sparrow populations (e.g. Pinowski and Pinowska 1985, Zang 1993). In some European countries, the decline in the Tree Sparrow population in farmland since the 1980s can be attributed to the intensification of agriculture (plowing stubble fields, application of herbicides) and its limiting effect on food supply in winter (e.g. Summers-Smith 1989, 1995, Zang 1993, Winkel 1994, Siriwardena *et al*. 2006, Wretenberg *et al*. 2007). Only Both *et al*.(2002) argue that the decline in the number of Tree Sparrows in the Netherlands is due to a reduced breeding success, rather than to increased winter mortality. The majority of authors consider winter mortality as the most important factor determining population size of the Tree Sparrow. The building of autumn nest as a consequence of the autumn display is a part of the strategy for winter survival.

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