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Nest construction during autumn display and winter roosting in the Tree Sparrows *Passer montanus*

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Abstract. A 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 and broods. Nestlings, juveniles, and adults captured in mist nets were ringed with different combinations of colour rings to identify their age during visual observations in the autumn sexual display period. Before the autumn display, breeding nests were dyed in order to identify nest material added during the autumn display period. In winter, nest boxes were inspected to catch the birds roosting in them at night. The study was conducted in optimal and marginal habitat types. In the optimal habitat during the autumn sexual display, adult birds were much more abundant than in the marginal habitat. During the breeding season, 41% of the nest boxes were occupied in the optimal habitat, compared with 8% in the marginal habitat. The respective figures during the autumn display were 95% and 45%. Autumn nests were built in 83% and 12% of the nest boxes, respectively, and in winter, 35% and 7% of nest boxes, respectively, were used by birds for night-time roosting at night. The autumn display continued from early September to the end of October. For roosting at night in winter (November–March), Tree Sparrows selected nests according to their insulating quality. Most often they roosted in nest boxes containing nests from the breeding season with autumn nests built over them, then, in descending order of frequency, in nest boxes with autumn nests built in empty boxes, in boxes with breeding nests, and in completely empty boxes. Among birds roosting at night and captured on the first survey in winter, 86% were represented by pairs that had built those nests during the autumn display. Young birds that did not build autumn nests typically roosted at night in tree crowns. This implies that the construction of autumn nests is primarily a consequence of the autumn sexual display, and secondarily may be an adaptation for winter survival. The winter survival rate was significantly higher in juvenile Tree Sparrows that were found in nest boxes on winter nights than in those that were not.

Key words: Tree Sparrow, *Passer montanus*, autumn sexual display, autumn nests, winter roost, nest boxes, survival rate

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INTRODUCTION

Many bird species sing, form pairs, or even build nests in autumn, but these activities are not always related to the autumn sexual behaviour (Wingfield et al. 1997, Soma & Wingfield 1999, Wingfield & Silverin 2002, for reviews). Populations of the same species, and even different age groups within the same population, can show different levels of sex hormones and behaviours (Marshall & Coombs 1957, Lincoln et al. 1980). The purpose of these behaviours can be different; for example, occupation of a territory to secure adequate food resources for winter (e.g. Enoksson 1990, Friedmann 1995). During the autumn display, Tree Sparrows not only form pairs and defend territories but also can build nests that differ in the degree of their advancement (Pinowski & Noskov 1981). According to some authors, autumn nests are built to provide shelter for roosting at night in winter (Creutz 1949, 1960, de Bethune 1961, Keil 1962, Weise & Fahnert 1992), whereas some others argue that autumn nests are only a consequence of the autumn sexual behaviour (Berck 1961–1962, Deckert 1962, Turček 1962), and this controversy has not been settled yet.

Autumn display is costly in terms of energy (singing — Searcy & Andersson 1986, Oberwerger & Goller 2001, Nowicki et al. 1998, 2000, and others; territorial defence — Dolnik 1995; nest building — Withers 1977, Dolnik 1991, 1995). If the autumn display is costly, it should provide some balancing benefits to be tolerated by natural selection. The response of fleeing of roosting Tree Sparrows from the tree hole upon the approach of an observer (Creutz 1960, Pinowski 1967a) indicates the absence of hypothermia in these birds and, consequently, a greater dependence on shelters protecting them from heat loss. The greatest loss of energy threatens during long winter nights, and one of the ways to reduce the loss of heat at night can be nest building, or selecting an insulating shelter, as suggested by several authors (e.g. Andreev 1980, Pravosudov & Grubb Jr. 1997, Carey & Dawson 1999). The purpose of this paper is to test the hypothesis that the nests built by Tree Sparrows as a result of the autumn sexual display and used by them for nocturnal roosting reduce the loss of energy during winter.

STUDY AREA, MATERIAL AND METHODS

The data were collected from 1960–1972, however some analyses are based on the material originating from shorter periods, indicated in the paper.

The study was carried out between the Kampinos National Park and the Vistula river, north-west of Warsaw, Poland (52°20′N, 20°50′E). This area includes ten villages surrounded mainly by arable land. During 1960–1962, 616 nest-boxes were erected in trees, in 10 groups forming 10 colonies of Tree Sparrows, each comprising 27–115 nest-boxes. A more detailed description of the study area is given elsewhere (Pinowski 1966, 1967b, 1968).

The nest boxes were cleaned each spring before the breeding season. All boxes were checked at least once a week from April to September (31140 inspections, 1417 broods) to record e.g. type of nest, number of broods, and to ring the nestlings (for details see Pinowski 1968).

Autumn sexual behaviour

At the end of August, from 1961–1965, prior to autumnal occupancy, the nest box contents were dyed to see whether the birds added new material during the autumnal sexual period. After the cessation of autumn display, in the first days of November, the boxes were checked again. They contained 321 nests at various stages of construction, built during the autumn sexual period.

All nestlings and individuals captured during night inspections of nest boxes or in mist nets located in crop fields and in breeding colonies were ringed with individually-numbered aluminium and colour rings. To allow identification in the field, four groups of birds were ringed with differently coloured rings: 1) adult birds, 2) juveniles from early broods ringed as nestlings (till 19 June), 3) juveniles from late broods (after 19 June) ringed as nestlings, and 4) juveniles from unknown sources ringed when captured in mist-nets. Tree Sparrows from each colony had a different colour of rings. A total number of 10692 Tree Sparrows were ringed over the study period (7026 nestlings, 666 individuals in nest boxes, and 3000 in mist nets).

The behaviour of Tree Sparrows during the autumn display was observed in two colonies located in a 30-year-old pine forest: Optimal comprising 33 nest boxes, located near buildings close to the forest edge; and Marginal comprising 30 nest boxes, located in a small clearing 1 km from the forest edge. Nest boxes were arranged in five rows located 5 m apart. The colony Optimal bordered to the north on the building of the Field Station of the Institute of Ecology, PAS, located on a 300x100 m glade. No natural tree holes were present in these colonies, where Tree Sparrows could nest, perform autumn display, and roost at night. Tree Sparrows prefer nesting near buildings, in small woods among crop fields, and at forest edges, and generally avoid forest interior (see Pinowski 1965, 1967b). There were 75 and 196 hours of observations in an Optimal colony, and 73 and 32 hours in a Marginal colony in 1961 and 1962. The Tree Sparrows displaying at least 5 times at a given nest box were viewed as its users. In the winters of 1961-1962, the number of Tree Sparrows arriving to both colonies for nocturnal roosting was counted between 24 October 1961 and 2 February 1962. These were years of high Tree Sparrow numbers (see Pinowski 1968).

Roosting in winter

Nocturnal inspections (6080 inspections) of all nest-boxes in all colonies were conducted monthly in order to record the number of Tree Sparrows roosting in the nest-boxes from November to March 1961–1966.

We estimated winter survival rates (winter defined as 1 November–28 February) of Tree

Sparrows ringed in the study area in 1961–1966. All birds included in the capture-mark-recapture (CMR) analysis were ringed in their first year as nestling or juveniles and they were recognized as juveniles till 28 February next year. We analysed 2143 capture histories over 7 years (1961–1967) with 596 birds marked as nestlings and 1547 birds initially ringed as juveniles in their first year of life. Recapture was conducted mainly in the non-winter periods (1 March–31 October). A bird captured at least once was treated as present during this period. The capture effort differed between the years, which resulted in a time-dependent recapture probability. We classified birds into those captured in the nest-boxes at night and those captured only in mist nets and never in nest-boxes between 1 November and 28 February. The total number of birds fulfilling these criteria and found to spend winter nights in nest-boxes was 82.

CMR models were fitted using the MARK software (White & Burnham 1999). Model selection followed Burnham & Anderson (2002). The results were tested according to Zar (1999) using the Statistica for Windows 2000 software (Wilcoxon test, Kruskal-Wallis test, homogenity χ^2, χ^2, t-test). The variation of mean values was characterised by the standard deviation.

RESULTS

Autumn display in the Optimal and Marginal colonies

The first Tree Sparrows arrived at the breeding colony late in August or in the first half of September. In the Optimal colony 41% of the nest boxes were used in the breeding season, compared with only 8% in the Marginal colony. During the autumn display 95% of nest boxes were used in the Optimal colony, compared with 45% in the Marginal colony. In the Optimal colony, Tree Sparrows built autumn nests in almost 83% of the boxes, but in the Marginal colony in 12%. In the Optimal colony, Tree Sparrows used almost 35% of the nest boxes for night roosting, compared with 7% in the Marginal colony (Table 1). From November, Tree Sparrows in the Optimal colony roosted in nest boxes and in tree crowns near boxes, whereas in the Marginal colony almost exclusively in tree crowns (Fig. 1). In both these colonies more Tree Sparrows roosted at night than used nest boxes during the autumn display (Table 1, Fig. 1).

In the Optimal colony, the proportion of adults to juveniles during visual observations was 0.77 (0.88 vs. 1.14 birds/h of observation) and was higher than in the Marginal colony 0.14 (0.30 vs. 2.12 birds/h of observation) (χ^2 = 54.81, df = 1, n = 803, p = 0.0000).

Roosting in the autumn-winter period

The flock of Tree Sparrows arriving to the Optimal colony for nocturnal roosting comprised two groups of birds: one roosted in shrubs where nest boxes were absent, the other roosted about 150 m apart near nest boxes (Fig. 1). On average, 37% of Tree Sparrows roosted in tree crowns near nest boxes (mean from the 10-day period prior to the inspection of nest boxes at night), and only 4% in nest boxes on 26 November 1961. On 20 December 1961, 40% roosted near nest boxes and 21% in nest boxes.

Tree Sparrows could choose a nest box for roosting at night as 60 to 80% of nest boxes with nests of different kinds were unused (Fig. 2). In winter, roosting Tree Sparrows preferred nest boxes with autumn nests built upon nests from the breeding season and then those with autumn nests built in empty boxes, followed by those with a breeding nest without an autumn nest, as compared to empty boxes (χ^2 = 156.69, df = 3, n = 4104, p = 0.001) (Fig. 2). The number of Tree Sparrows roosting in a given colony in winter was related to the percent of autumn nests in this colony (R^2 = 40.5%, n =16, p = 0.008). This analysis is based on data from all colonies and study years. The nest built during the autumn display

Table 1. Percentage of nest boxes occupied by the Tree Sparrows in optimal and marginal colonies (data from 1961 and 1962 combined). * — test with Yates correction.

Colonies	Optimal (N = 66)	Marginal (N = 60)	χ^2	df	p
Nest boxes occupied during breeding season	41	8	10.51*	1	0.0020
Nest boxes occupied during autumn sexual display	95	45	6.78	1	0.0092
Nest boxes with autumn nests	83	12	22.35*	1	0.0000
Nest boxes occupied for roosting	35	7	8.53*	1	0.0035

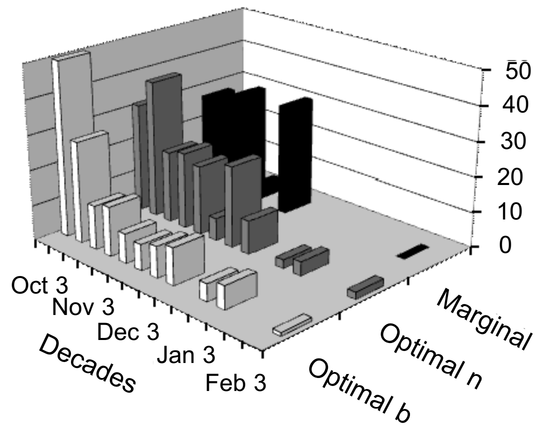

Fig. 1. Numbers of Tree Sparrows roosting at night in optimal and marginal colonies. Optimal n – Tree Sparrows roosting in colony Optimal in nest boxes or in tree crowns above nest boxes; Optimal b — Tree Sparrows roosting in shrubs 150 m from the colony Optimal; Marginal — Tree Sparrows roosting only in tree crowns in colony marginal (4 times in nest boxes).

by a pair of birds served as a roosting place for the same pair throughout the winter (86%, 36/42; homogenity $\chi^2 = 12.28$, df = 1, p = 0.0005). The remaining 14% were not recorded during the autumn display at any nest box. For this analysis we used data only for Tree Sparrows captured in nest-boxes at night on the first inspection in a given autumn-winter season, because after being captured they often moved to other nest boxes.

Among 666 individuals captured when roosting in nest boxes at night in all colonies, in 17 cases the sex of both roosting birds was known, these were male and female.

Preference for nest boxes after capture on nest during roosting

Only 8.3% (55/666) of the Tree Sparrows roosting in nest boxes were recaptured during the same winter, in 24 cases in the same box. No differences were found between years (Kruskal-Wallis test: $H_4 = 2.60$, n = 31, p = 0.46).

Tree Sparrows that changed the roosting site after capture moved to nest boxes with nests of the same kind as the nest in the box where they were captured, but this is statistically not significant (Table 2) (Wilcoxon sign test = 1.78, p = 0.077, n = 18). Only one bird moved from the autumn nest built over the breeding nest to an empty box.

Age of Tree Sparrows roosting in nest boxes

Tree Sparrows started roosting in nest boxes at the end of the autumn display in the second half of October. The proportion of adult to juvenile Tree Sparrows roosting in nest boxes was high in November, decreased in December, and was increasing until March (Fig. 3). Flocks of Tree Sparrows foraging in crop fields and captured in mist nets were dominated by juvenile birds (apart from January when the difference in the proportion of adult to juvenile birds was not significant (test for difference in proportions, p = 0.46, n = 51 and 48) (Fig. 3). The proportion

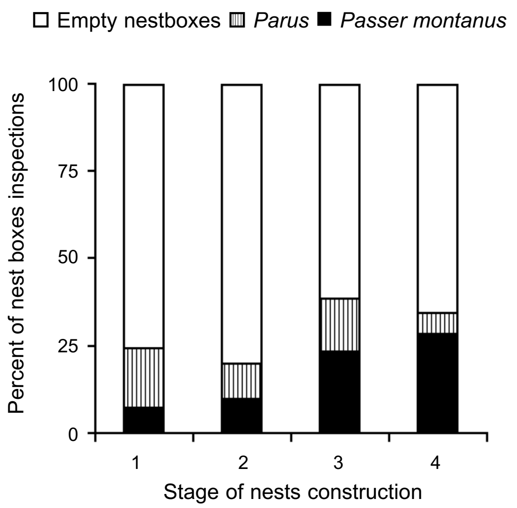

Fig. 2. Choice of nest boxes for roosting at night in relation to the nest type in them. Nest stage: 1 — empty nest-boxes, 2 — only old nest from breeding season, 3 — autumn nest built in an empty nest box, 4 — autumn nest built on the nest from the breeding season.

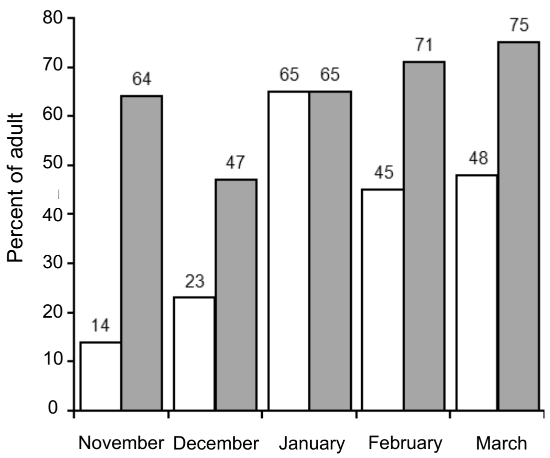

Fig. 3. Percentage of adult Tree Sparrows roosting at night in nest-boxes as compared with their percentage foraging in flocks in the fields. Grey — captured in nest-boxes on roosts, white — captured in flocks in fields.

of adult Tree Sparrows in crop-field flocks was much lower than their proportion at roost in nest-boxes captured in the same period (Wilcoxon matched pairs, $n = 5$, $Z = 1.79$, $p < 0.05$).

Tree Sparrows roosted in groups of 3–4 birds during coldest spans when mean temperatures at night varied between about 8–10°C below freezing (Kruskal-Wallis test: $H_2 = 18.80$, $n = 661$, $p = 0.001$)(Fig. 4).

Winter survival in relation to roosting in nest boxes or outside

When estimating winter survival rates, we used two different criteria as grouping variables: hatched early vs. late in the season or using vs. not using nest-boxes during winter. The sample size of nest-box users did not allow us to apply both criteria simultaneously, i.e. to make four groups. The latter type of grouping data better explained the variation in survival and resulted in lower AIC values. Goodness-of-fit tests were not significant, i.e. models fit the data. The best model assumed time-dependent (1) survival rate during the first winter of life, different between nest-box users vs. non-users; constant survival, equal in both groups in subsequent winters (2) and time-dependent recapture probability (Tables 3 and 4). The second best model, which was not significantly different from the best one (Tables 3 and 4), assumed group-dependent but time-independent (1) survival in adult birds.

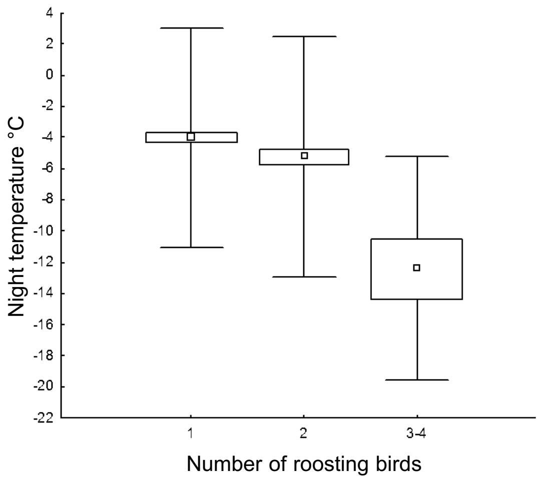

Fig. 4. Relationship between the number of Tree Sparrows roosting together in a nest box and the ambient temperature at night: mean temperature in the evening (19:00 p.m.), minimum temperature, and morning temperature (7:00 a.m.) on the night of checking.

Table 2. Choice of nest type after capture on nest during roosting at night. Nest type: 1 — empty, 2 —with nest from the breeding season, 3 —with autumn nest, 4 — with nest from the breeding season overtopped by autumn nest.

First nest type	Nest type used for roosting after capture at night			
	4	3	2	1
4	5	2	4	1
3	0	1	0	0
2	0	1	3	0
1	1	0	0	2

DISCUSSION

The time of moult of juvenile Tree Sparrows depends on the date of hatching. The sooner they hatch, the sooner they moult (Pinowski 1968), although the later they hatch, the shorter is the period when they are in juvenile plumage (Deckert 1968, Gaginskaya et al. 1981). Only birds which completed moult start autumn display. For this reason, juveniles, especially of the second and third broods, start autumn display later in the season (Pinowski 1965, Pinowski et al. 2006b). It is known that young birds occupy marginal habitats in autumn (e.g. Kluyver & Tinbergen 1953, Kalela 1954, 1958, Newton 1992, Lambin et al. 2001). Young Tree Sparrows forced to disperse to marginal habitats do not have time to build nests before the end of the autumn display, and with the advent of cold weather they do not roost in nest boxes but in tree crowns close to nest boxes. Roosting of juvenile Tree Sparrows outside nest boxes indicates that autumn nests are built as a consequence of the autumn display, rather than as a shelter for winter.

Autumn display in optimal versus marginal habitats

The course of the autumn display in optimal habitats differed from that in marginal habitats. In the optimal habitat (colony Optimal) the proportion of adult Tree Sparrows was higher than in the marginal habitat (colony Marginal). In the optimal habitat almost all nest boxes during autumn sexual display were occupied, and Tree Sparrows built autumn nests in almost all of them. In the marginal habitat nearly half the nest boxes were used, and only 3–4 autumn nests were built in them, showing that not all juvenile Tree Sparrows built autumn nests, although they performed autumn display in this colony. More birds arrived to both

Table 3. Two best models explaining winter survival rates in Tree Sparrows. Phi — the survival rate, p — the recapture rate. The first model has a survival rate (phi) which is age-dependent with two age classes (a2, first winter vs. all subsequent winters); the survival rate of the two groups (birds known and not known to spend winter nights in nest-boxes) was significantly different; in the first age class (juveniles) survival was time-dependent (g*t), whereas in the second age class (adults) it was time-independent = constant (c). The second model differed from the first one by assuming group-dependent but time-independent survival rate (g*c) in the second age class (adults); in the first age-class (juveniles) it was group- and time-dependent (g*t), as the first model. Recapture probability (p) was time-dependent in both models, p(t).

MODEL	AICc	Delta AICc	AICc weight	Model likelihood	No. of parameters	Deviance
Phi(a2-g*t/c) p(t)	2104.54	0.00	0.73	1.00	19	17.20
Phi(a2-g*t/g*c) p(t)	2106.56	2.02	0.27	0.36	20	17.20

colonies than roosted in nest boxes. This indicates that autumn nest building determines roosting of Tree Sparrows in nest boxes. Tree Sparrows that did not build autumn nests roosted outside. In autumn, Tree Sparrows started nest building after pair formation, and this depended on the age of birds. The first pairs were formed by adult birds and juveniles from early broods (Pinowski et al. 2009). Adult birds used mainly nest boxes for roosting as indicated by a higher percentage of adults roosting in nest boxes as compared with their percentage in flocks foraging in crop fields, that is, in the whole population. Thus, juveniles roosted more often outside nest boxes. In the marginal colony, juvenile Tree Sparrows participated in the autumn display, but few of them had time for nest building, giving few nest boxes for nocturnal roosting in winter.

Relationship between autumn display and building autumn nests

From the beginning of the autumn display, Tree Sparrows roosted at night in tree crowns or in shrubs near to the nest boxes they used. From late October or early November in the autumn-winter period, pairs of birds roosted in their autumn nests. Two Tree Sparrows roosting together were always male and female, as already noted by several authors (e.g. Creutz 1949, 1960, Ilyenko & Zagorodnaya 1961, García-Navas et al. 2008). Most of the Tree Sparrows roosting singly were females. As Creutz (1949) put it: "first these are mainly males, from February females predominate, and in March again the proportion and number of females increase".

Most often, the Tree Sparrows captured when roosting in nest boxes moved to other boxes with

Table 4. Parameterization of the best capture-mark-recapture (CMR) model.

Parameter	Estimate	SE	95% Confidence Interval Lower	95% Confidence Interval Upper
Surv. juv, no nest-box, 60/61	0.189	0.056	0.103	0.323
Surv. juv, no nest-box, 61/62	0.129	0.016	0.101	0.163
Surv. juv, no nest-box, 62/63	0.106	0.039	0.051	0.209
Surv. juv, no nest-box, 63/64	0.446	0.140	0209	0.710
Surv. juv, no nest-box, 64/65	0.138	0.059	0.057	0.297
Surv. juv, no nest-box, 65/66	0.257	0.191	0.046	0.711
Surv. ad, both groups, all years	0.118	0.027	0.074	0.183
Surv. juv, nest-box user, 60/61	0.616	0.166	0.289	0.863
Surv. juv, nest-box user, 61/62	0.217	0.023	0.175	0.266
Surv. juv, nest-box user, 62/63	0.168	0.060	0.080	0.321
Surv. juv, nest-box user, 63/64	1.000	0.268 E-07	0.999	1.000
Surv. juv, nest-box user, 64/65	0.390	0.163	0.143	0.710
Surv. juv, nest-box user, 65/66	0.244	0.182	0.045	0.691
Recapture 1961	0.279	0.077	0.155	0.451
Recapture 1962	1.000	0.425 E-06	0.999	1.000
Recapture 1963	0.375	0.120	0.181	0.620
Recapture 1964	0.130	0.030	0.081	0.201
Recapture 1965	0.322	0.115	0.145	0.571
Recapture 1966	0.780	0.464	0.017	0.999

a similar nest type, most of them, however, moved to roosting places that we did not check.

Tree Sparrows had an excess of nest boxes for nocturnal roosting. Typically, they selected boxes containing nests from the breeding season and the added autumn nests, then autumn nests built in empty boxes, followed by boxes with breeding nests but without autumn nests, and finally by empty boxes. Thus, they showed preference for nest boxes containing autumn nests. This gradient of preference coincides with the insulating quality of nests (Pinowski et al. 2006a). The loss of energy during roosting under experimental conditions was mainly determined by ambient temperature (R^2 = 0.9060, F = 1021.714, p = 0.0000) and, to a small extent, by nest type (R^2 = 0.0121, F = 15596, p = 0.0001, n = 108). The loss of Tree Sparrow body mass during winter roosting depends on the weight of nest used for roosting: the heavier the nest, the less the weight loss (A. Haman unpubl. data). Reduction of energy loss by only a few percent in winter can be crucial for survival until the next day (Houston & McNamara 1993). Ilyenko & Zagorodnaya (1961) also found that Tree Sparrows roosted in old nests from the breeding season or in autumn nests. Different results were reported from the warmer environment of Spain, where García-Navas et al. (2008) found that Tree Sparrows did not select nest boxes for roosting on winter nights based on the nest type they contained. However, as the nest boxes were checked every week, their results could be an artefact to a large extent because the captured birds were likely to move among nest boxes. In this paper we demonstrated that only 3.6% of the Tree Sparrows captured in nest boxes at night once a month did not change the roosting place. Tree Sparrows investigated in Spain were not individually marked when they constructed autumn nests in specified nest boxes, so it was not possible to associate the bird with particular nest box at night.

Competition with other bird species for nest boxes was of no importance as only 0.006% of nest boxes were used at night by birds dominant over Tree Sparrows, such as Great Spotted Woodpecker *Dendrocopos major*, Nuthatch *Sitta europaea*, or House Sparrow *Passer domesticus*, and 0.085% of the nest boxes were used by tits *Parus* sp. — the birds over which Tree Sparrows are dominant. It should be added that 60–80% of the nest boxes were not used for roosting at night by any bird (J. Pinowski unpubl. data, Fig. 2).

Greater numbers of Tree Sparrows start nocturnal roosting in nest boxes from November when temperatures are decreasing. Busse & Olech (1968) found that the proportion of nest boxes occupied by roosting Tree Sparrows was negatively correlated with the air temperature at noon. In our population at a minimum temperature of +0.6°C and an evening temperature of +3.7 only 4% of the birds which arrived for nocturnal roosting to the Optimal colony occupied nest boxes at night, but at a minimum temperature of -25.5°C and an evening temperature of -19.5°C as many as 21% roosted in nest boxes. One of the reasons that they avoided roosting in nest boxes at mild temperatures is the infestation of nest boxes with fleas and mites (Fend'a & Pinowski 1997, Cyprich et al. 2002, Mazgajski 2007). Also predation by *Martes* sp. can deter birds from roosting in nest boxes at night (see Ekner & Tryjanowski 2008).

Energetics

The birds roosting at night in empty boxes saved 18% of energy as compared with the birds roosting in trees. The birds roosting in nest boxes with autumn nests built over the breeding nests saved 36% of energy (Pinowski et al. 2006a). Consequently, the strategy of Tree Sparrows should be the choice of nest boxes with a higher insulating quality for roosting. Our data show that Tree Sparrows sexually active in autumn roosted in autumn nests, especially in the nests they built in autumn. Only on the most frosty nights, more than two Tree Sparrows of unknown sex and age aggregated in nest boxes. Only Creutz (1949) and Ilyenko & Zagorodnaya (1961) found that both sexes were represented in similar aggregations. Roosting in groups can save much energy (Davydov 1981, Chaplin 1982, Gavrilov 1991). The onset of roosting in nest boxes coincided with low temperatures at the end of October and November, reducing the energy costs of night survival.

The data collected confirm earlier observations that the autumn nest serves as a roosting place from late October until March or even later, depending on weather conditions (Pielowski & Pinowski 1962, Busse & Olech 1968, Pinowski 1965, 1966, Löhrl 1978, Pinowski & Noskov 1981, Summers-Smith 1995). Some authors argue that Tree Sparrows build autumn nests as a shelter for winter, but do not relate this behaviour to autumn sexual activity (Niethammer 1937, Creutz 1949, 1960, Keil 1961). Most authors, however, suggest that nest building is a consequence of the autumn sexual behaviour (Turček 1962, Pinowski 1965, 1966, 1967b, Pinowski & Noskov

1981, Summers-Smith 1995). Data presented in this paper provide new evidence for the linkage of winter roosting in nests with autumn display, as sparrows performing the autumn display at these nests and building autumn nests in them also use them for roosting in winter, while juvenile sparrows starting autumn display too late roost at night outside nest boxes in tree crowns or in shrubs near the boxes at which they displayed.

The importance of autumn nests for winter survival

Tree Sparrows roosting in nest-boxes survived winter in higher proportion than those roosting in trees. As shown by our survival estimates based on CMR data, spending winter nights in nest-boxes is indeed associated with a high likelihood of surviving the winter. Juvenile Tree Sparrows roosting at night in nest boxes have a greater chance of surviving the winter than juveniles which do not roost in nest boxes. The survival of birds two or more years old does not depend on their roosting in nest boxes in winter. Adult birds dominate over juveniles in the choice of nests during the autumn display, also the proportion of adults roosting at night in nest boxes is higher than in the whole population. According to Lempaszak (1988), more adults than juveniles roost in nest boxes in winter. It is possible that adult Tree Sparrows, as being more experienced, chose better shelters for roosting at night than do juveniles, and this accounts for the absence of differences in winter survival of this age group of birds no matter whether they roost in nest boxes or in other places, for example, in villages in heated buildings. Free living birds are influenced not only by changes in ambient temperature but also by other factors such as the type of nest in a nest box, or wind speed and direction (Pinowski et al. 2006a). Tree Sparrows choose nests for roosting with respect to their insulating quality.

If the probability of successfully surviving the winter increases with the quality of autumn nest construction, natural selection should promote those individuals with intense sexual behaviour at this season. Perhaps natural selection eliminates most birds from late broods that do not participate in autumn display, and roost at night in trees (Pinowska et al. 1995), this reducing their chance for survival. Mist-net captures of Great Tits *Parus major* directly after awakening showed that the plumage of birds that had not roosted in nest boxes often was very wet after rainy night, with all the negative consequence for survival (Drent 1987). About 14% of the young Tree Sparrows from the first brood survive until May next year, whereas only 5% from second and third broods (Pinowska et al. 1995). Lempaszak (1988) emphasized that among juveniles, those of the first broods most often roost in nest boxes during winter, and those of the second and third broods only occasionally. This confirms our observations on the relationship between the roosting of juveniles in nest boxes and building autumn nests. In the temperate zone, winter mortality in Tree Sparrows largely depends on the depth and duration of snow cover (Pinowski & Pinowska 1985), which can significantly reduce population size, even causing local extinction (Pinowski 1967b, 1968).

Other authors also emphasize the importance of shelters for winter survival, protecting against heat loss during winter nights (for review see Pravosudov & Grubb Jr. 1997). Kluyver (1957) documented that the dominance of males over females in the Great Tit when choosing a better roosting place increased the winter mortality in females, and of juveniles as compared with adults. Likewise, the dominance of Great Tits over Blue Tits *Cyanistes caeruleus* in competition for better roosting places increased the mortality of Blue Tits during winter (Dhondt et al. 1991). All the data presented above show that the autumn display in Tree Sparrows leads to the pair formation and construction of autumn nests. In one case, a Tree Sparrow even laid eggs in November (Hasse 1962).

The mechanisms of natural selection determining the autumn display can vary between species (Hegner & Wingfield 1986, Logan & Hyatt 1991, Weggler 2000, Forstmeier 2002, Wingfield & Soma 2002). Hegner & Wingfield (1986) suggested that autumnal display is adaptive because: 1) it allows individuals to initiate reproduction earlier in the subsequent spring, a factor that normally correlates with increased breeding success; 2) it provides an opportunity to establish pair bonds and nesting sites in the autumn, thus being able to take advantage of favourable 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 more protein and fat reserve 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) in House Sparrow and other multi-brooded species (e.g *Mimus polyglottos* Logan 1992), pairs that initiate breeding earlier fledge more young, because early nesting allows individuals to attempt more broods each season.

The same advantages can be observed in Tree Sparrows. However, this species experiences very high winter mortality of approximately 85% (Pinowski 1968), and behaviour promoting winter survival must be favoured by natural selection, including autumn display and associated nest building.

All these facts provide evidence that building autumn nests as an effect of autumn sexual display by Tree Sparrows can be important for winter survival.

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STRESZCZENIE

[Budowa gniazd podczas zalotów jesiennych i nocowanie zimą w skrzynkach lęgowych u mazurka]

Mazurki odbywają zaloty jesienne, tworzą pary i budują gniazda jesienne, w których następnie nocują w czasie zimy. Stopień zaawansowania budowy gniazda zależy od terminu utworzenia pary, a ten zależy od wieku ptaków. Bardziej zawansowaną konstrukcję gniazda budują ptaki stare i młode z pierwszego lęgu. W kolonii marginalnej, w której mazurki gnieździły się tylko sporadycznie, zaloty jesienne odbywały prawie wyłącznie ptaki młode zajmując połowę skrzynek, jednak gniazda jesienne zbudowane zostały tylko w kilku skrzynkach. Wskazuje to, że para w okresie zimowym ze zbudowanym w czasie zalotów jesiennych gniazdem związana jest dwojako; jako z miejscem snu i jako z gniazdem z okresu zalotów i dlatego mazurki w kolonii marginalnej, gdzie odbywały zaloty prawie wyłącznie ptaki młode, zbyt późno rozpoczynające

zaloty jesienne aby mogły zbudować gniazdo jesienne, nocowały w koronach drzew i krzewach, a prawie nigdy w skrzynkach. W kolonii optymalnej znaczna część ptaków przylatujących na nocleg także nie nocowała w skrzynkach, prawdopodobnie były to ptaki młode. Determinantem nocowania w skrzynce lęgowej jest utworzenie pary i zbudowanie gniazda jesiennego. Dobór naturalny faworyzuje ptaki stare i młode z wczesnych lęgów, które wcześnie przystępują do zalotów jesiennych i budują gniazda jesienne zapewniające lepsze schronienie w okresie zimy, w porównaniu z ptakami młodymi z późniejszych lęgów, które nie budują gniazd jesiennych i nie nocują w skrzynkach.