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Significance of the breeding season for autumnal nest-site selection by Tree Sparrows *Passer montanus*

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Abstract. The Tree Sparrow is one of the species exhibiting classical autumn sexual behaviour. Autumn nest selection by this species was studied in Central Poland, especially with respect to the history of nest-boxes in the previous breeding season. During the autumn display, Tree Sparrows constructed nests significantly more often in boxes that had been occupied in spring by conspecifics, but only rarely in empty boxes, in boxes where House Sparrow *Passer domesticus*, tits *Parus* sp., Pied Flycatcher *Ficedula hypoleuca*, Redstart *Phoenicurus phoenicurus* had nested, or in boxes used by hymenopterans. During the autumn display, Tree Sparrows showed a preference for boxes where nestlings had hatched. Nests with nestlings in the breeding season are a cue used in selecting nest site in the autumn sexual behaviour.

Key words: Tree Sparrow, *Passer montanus*, autumnal nest, nest history, nest selection, public information

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Autumn sexual behaviour has been described for many birds that live in the temperate zone (e.g. Morley 1943, Kalela 1958). In general, autumn sexual behaviour is similar to the behaviour in spring, but with a lower intensity (Homann & Gwinner 1963). Some species even copulate and construct nests in autumn (Morley 1943) but only a dozen or so breed, so far mainly demonstrated in California (e.g. Orians 1960, Selander & Nicholson 1962, Payne 1969). Autumnal changes in the hormonal system of birds are similar to those at the onset of the normal breeding season in spring. Following the moult, birds become sensitive to photoperiod at a time when day length is still sufficiently long to elicit gonadal development. The resulting pro-

duction of gonadal steroids leads to the autumn sexual behaviour (Threadgold 1960, Lofts & Murton 1968, Spurr & Milne 1976, Lincoln et al. 1980). Moreover, increases in gonads and plasma androgens were noted in some species in autumn (review in Wingfield et al. 2001). Both ecological activity and physiological changes are relatively costly in terms of energy (e.g. Withers 1977, Dolnik 1991, Hansell 2000), so there must be fitness benefits in autumn sexual behaviour.

The Tree Sparrow *Passer montanus* is among the species with classical autumn sexual behaviour. In autumn, Tree Sparrows can occupy territories (nest-boxes), copulate, and build nests (e.g. Berck 1961–1962, Pinowski 1965), there is even an instance where one egg was laid (Hasse 1962). It

has been shown that autumn sexual behaviour, during which the birds occupy territories and form pairs, accelerates their breeding in spring (e.g. Nice 1964, Lofts & Murton 1968, Spurr & Milne 1976, Murton & Westwood 1977), and thus influences their realised reproductive success (Pinowski 1968). The duration of autumn sexual behaviour in the Tree Sparrow depends on weather conditions, and in Poland generally stops after the first frosts at the end of October (e.g. Pielowski & Pinowski 1962). In early autumn, the Tree Sparrow population is much larger than in the breeding season, and the birds are likely to be less selective in the choice of nest-boxes (Pinowski 1967). We are not aware of any papers analysing the importance of the breeding season for autumn nest-site selection. Most papers on the influence of public information on habitat selection mainly concern migratory birds, that very rarely perform autumn display. However, it is known that nests of conspecifics, nest success, feeding nestlings, and the like, are all cues for prospecting birds (e.g. Boulinier & Danchin 1997, Reed et al. 1999, Doligez et al. 2002, Pärt & Doligez 2003, Doligez et al. 2004a, 2004b, Safran 2004). Tree Sparrows, as resident birds with an intensive autumn display, are an interesting subject to study the role of autumn display in gathering public information for nest-site selection.

The aim of this study was to examine the importance of the history of nest-boxes in the previous breeding season in autumn nest-site selection.

The study was carried out in an area located between the Kampinos National Park and the Vistula river, north-west of Warsaw, Poland (52°20'N, 20°50'E), between 1961 and 1964. This area includes seven villages surrounded mainly by arable land. During 1960–1962, 357 nest-boxes were erected in trees, in 7 colonies comprising from 33 to 72 boxes. A more detailed description of the study area and the Tree Sparrow population is given elsewhere (Pinowski 1966, 1967, 1968). During the autumn display, these colonies consisted mainly of adult Tree Sparrows and juveniles from early broods, whereas juvenile birds, from later broods mainly occupied forest margin colonies, not considered here (Pinowski 1967).

The nest boxes were cleaned each spring before the breeding season. All nest boxes were checked at least once a week (total 31, 140 inspections) during the breeding season, from April to September in all years when the investigation was

carried out. The aim was to determine which nest-boxes were occupied by Tree Sparrows, the number of eggs in the nest, number of eggs hatched and number of nestlings fledged. In total, 1417 broods were followed (for details see Pinowski 1968).

Over the study period, at the end of August each year prior to autumn occupancy a total of 1174 nest-box checks were made. Nests were categorised and their contents dyed to determine if new material was added during autumn displays. Nest boxes were categorised as: 1 — nests of *Passer montanus*, 2 — nests of *Passer domesticus*, 3 — nests with moss: *Parus* spp. 4 — nests with leaves: *Ficedula hypoleuca*, or *Ph. phoenicurus*, 5 — nest-boxes occupied by hymenopterans, *Vespa* spp., or *Bombus* spp., 6 — empty nest-boxes.

Since previous studies have shown the importance of nesting success (particularly the presence of nestlings) in prospecting behaviour (e.g. Doligez et al. 1999, Reed et al. 1999, Danchin et al. 2001), we classified Tree Sparrows nests from the immediately previous breeding season according to the most advanced stage of development, regardless of brood timing. Thus, any nesting attempt with unhatched eggs or dead nestlings was disregarded if a subsequent attempt in the same box was successful in the same season.

After the cessation of autumn display, in early November, the boxes were checked again. During the years 1961–1964 they contained 304 nests in various stages of construction, built during the autumn display.

Tree Sparrows were individually marked with an aluminium and the group marked with colour plastic rings, so that the group of adults and juveniles could be distinguished. In the autumns of 1961 and 1962 (September to November), and in spring 1962 and 1963, sexual behaviour of birds (chirping, display, copulation, fights, nest building, and so on) marked with colour rings was observed in detail in one of the breeding colonies (for details see Pinowski 1965).

During the autumn display period, Tree Sparrows constructed significantly more nests in boxes that had been occupied by conspecifics in the immediately preceding breeding season than they did in boxes unoccupied or those occupied by other species in the breeding season ($\chi^2 = 145.80$, $df = 5$, $p < 0.001$) (Table 1).

Tree Sparrows built more autumn nests in nest-sites in which nestlings hatched, regardless of whether they fledged, than they did in boxes

Table 1. Contents of nest boxes used by Tree Sparrow for constructing autumn nest. N — number of nest boxes.

Nest box contents	Nest built or supplemented in autumn (%)
Nest of <i>Passer montanus</i> (N = 582)	58.2
Nest of <i>Passer domesticus</i> (N = 72)	25.0
Nest with moss: <i>Parus</i> spp. (N = 157)	16.6
Nest with leaves: <i>Ficedula hypoleuca</i> , <i>Ph. phoenicurus</i> (N = 88)	17.1
Nest of wasps, hornets, bumblebees (N = 60)	16.7
Empty nest-boxes (N = 215)	19.5
Total (N = 1174)	35.3

where the nests were deserted during construction, egg laying and incubation ($\chi^2 = 47.64$, $df = 3$, $p < 0.0001$) (Table 2). The percentage of the autumn nests constructed on successful nests of the first, second and third broods was similar (51.6%, 53.9% and 60.8% respectively, $\chi^2 = 4.08$, $df = 2$, $p = 0.13$). No difference was found in the percentage of autumn nests built on successful nests between boxes with one, two, or three broods (57.2%, 56.7% and 48.1% respectively, $\chi^2 = 1.55$, $df = 2$, $p = 0.49$).

Observations of colour-ringed birds showed that in the period of spring courtship only 16% ($n = 42$) of Tree Sparrows selected the same nest-boxes as in the period of autumn display.

The autumnal sexual activity of Tree Sparrows can lead to pair formation, occupation of nest sites, and nest building. The autumn nest serves as a roosting place from late October until March or even later, depending on weather conditions (e.g. Deckert 1962, Pinowski 1966, Summers-Smith 1995). This study shows that in autumn, Tree Sparrows selected boxes that were occupied by conspecifics in the breeding season and tended to avoid empty boxes and boxes with nests of other species (Table 1). Thus the nest of a Tree Sparrow itself and the associated parental activity were important cues for prospecting birds, as it was found in other species (e.g. Pärt & Doligez 2003, Safran 2004).

To our knowledge, the importance of the breeding season for gathering public information for autumn nest-site selection, and the importance of the autumn display period for nest-site selection in this period have not been examined before. The relative significance of this period may differ between adult birds that have the whole breeding

season for prospecting and juvenile birds (for which this period is shorter or longer, depending on the brood of their origin). For this reason it is necessary to distinguish between adult birds connected with their nests from the breeding season and juveniles not connected with any or only connected with a nest as a result of recent prospecting behaviour.

Adults arrived in autumn first, followed by juveniles from first brood, and then by juveniles from later broods (2nd, 3rd) (Pinowski 1965, Pinowski & Noskov 1981). The autumnal nests of adult birds tend to be more complete than those of juveniles during the autumn which build e.g. only base. Complete nest of the Tree Sparrow consists of three layers: base, lining and dome (Wasylik & Pinowski 1970, Országhova & Puchala 1997).

The advance in nest building was dependent on the time of pair formation. The juveniles from later broods paired later have not enough time to construct the autumnal nest (Pinowski, unpubl. data). A proportion of birds from the later broods do not take part in the autumn display since they end moult as late as the second half of October (Pinowski & Noskov 1981). The intensification of the gathering public information with advance of the autumn display suggests that this period is of basic importance for selection of nest site by juveniles.

The number of broods in a box during the breeding season did not affect the probability of a nest being built during the autumn. This shows that the number of broods in a given box is not indicative of the quality of a nest site for autumn display. The percentage of autumn nests did not depend on the brood for which the breeding nest was constructed, though a slightly higher (though not statistically significant) percentage of autumn nests were built on nests of the third brood,

Table 2. Autumn nests of Tree Sparrows in nests of conspecific with different histories in the breeding season. N — number of nest-boxes from breeding season.

Nest history	Nest-boxes with autumn nest (%)
At least one nestling fledged (N = 489)	58.8
Eggs hatched, but no nestlings fledged (N = 34)	55.8
Eggs were laid but did not hatch (N = 37)	18.9
Eggs were not laid (N = 22)	18.2
Total (N = 582)	52.2

implying that nests of the third brood may be of higher importance to prospecting birds. Tree Sparrows clearly select nests that hatched nestlings, no matter whether they are successful or not, and avoid nests deserted during their construction, egg laying, or incubation, (mostly due to human interference — see Pinowski et al. 1973). This is in agreement with other studies that indicate that for adults the experience from the breeding season is a basic cue for selection of a suitable nest site in autumn (Doligez et al. 1999).

Only 16% of Tree Sparrows during the period of spring courtship selected the same nest-boxes as in the period of autumnal display, because of: 1st: winter mortality is very high (ca. 85%) (Pinowski 1968); 2nd: probably breeding dispersal is intensive, because in spring many free nest-sites in the optimal habitats are available (Pinowski 1967).

From the point of view of the concept of public information on the selection of future breeding areas, especially for juvenile birds (Doligez et al. 1999, 2002, 2004a, 2004b, Pärt & Doligez 2003), the results presented here suggest that the most important cue for Tree Sparrows nest site choice is the presence of previous nests, as is the case of the Barn Swallow *Hirundo rustica* (Safran 2004). In the period of autumnal display, the density of birds and the activity of nest-box owners can be a cue for the selection of display site (Pinowski 1965, 1967, Pinowski & Noskov 1981).

This opens new perspectives for future studies focused on the questions whether the public information, pair formation, and nests constructed in the period of the autumn sexual behaviour enhance the survival of Tree Sparrows in winter, and whether the birds showing autumn display are favoured by natural selection.

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STRESZCZENIE

[Znaczenie okresu lęgowego dla wybiórczości miejsca na gniazdo w okresie zalotów jesiennych u mazurków]

Jesienią mazurki zajmują swoje terytorium, tworzą pary, kopulują i budują gniazdo. Badano wybór przez mazurki skrzynki lęgowej na gniazdo w czasie zalotów jesiennych w zależności od jej historii w okresie lęgowym. Stwierdzono, że w czasie zalotów jesiennych mazurki budują gniazda częściej w skrzynkach, które były zajęte przez ten sam gatunek w okresie lęgowym. O wiele rzadziej zajmują one puste skrzynki lub te, w których gnieździły się wróble, sikory, mucholówki żałobne, pleszki albo osy, szerszenie, trzmiele (Tab. 1). Najczęściej budowały gniazda w skrzynkach, z których w okresie lęgowym wyleciało choć jedno pisklę mazurka, lub straty w lęgach zaszły na etapie piskląt. O wiele rzadziej korzystały ze skrzynek z gniazdami, które uległy zniszczeniu na etapie jaja lub było zbudowane gniazdo, ale nie złożono w nim jaj (Tab. 2). Mazurki w okresie zalotów jesiennych budują gniazda niezależnie od liczby lęgów swego gatunku odbytych w danej skrzynce, oraz od lęgu z którego gniazdo mazurka pochodzi. Zaznacza się tendencja budowania częściej na gniazdach z lęgu ostatniego, to jest trzeciego (nieistotna statystycznie).

Praca ta otwiera nowe perspektywy badań nad mechanizmami działania doboru naturalnego utrzymującego zaloty jesienne u mazurków.