

Post-breeding aggressive territorial behaviour in Eurasian Tree Sparrows (*Passer montanus*): territory or mate defence?

Pohniedzne agresívne teritoriálne správanie u vrabca poľného (Passer montanus): hájenie teritória alebo partnera?

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Abstract. *The genetic interests of males and females usually differ. Whenever female fitness depends on an access to limited resources such as male parental care, competitive interactions among females are expected to evolve. There are numerous studies reporting female-female aggression during the breeding season, but this subject has not been examined for the post-breeding period. Here we examine female-female aggression in the Eurasian Tree Sparrow *Passer montanus* occurring during the autumn courtship period. We show that aggressive behaviour between nest owners and intruders is common and often fierce during the post-breeding courtship period. Importantly, females more frequently perform this behaviour than male nest owners and it is sex- but not age-specific (i.e. birds interfere with individuals of the same sex, but regardless of their age). This study, focusing on the post-breeding period, corroborates the idea that female territorial aggression can be involved in mate monopolization rather than simply serving as a territory defence strategy. Moreover, aggressive territorial behaviour of nest owners towards intruders can also serve as a signal of mate quality during the pair-formation period. We propose that examining female territorial behaviours during the post-breeding period can provide additional insights into the causes of diversity in avian mating systems.*

Key words: *antagonistic behaviour, sexual conflict, post-breeding period, mating systems*

Introduction

The genetic interests of males and females usually differ, which leads to sexual conflict regarding the level of parental care or the number of simultaneous social partners (Trivers 1972, Wittenberger & Tilson 1980, Clutton-Brock 1991, see Chapman et al. 2003).

Traditionally, the literature on mating systems is centred on the role of male behaviour. It was only since the 1970s when the subject started to be examined from the female's

perspective, revealing that females choose mates with superior genotypes, high paternal investment and skills enhancing fitness of their progeny (e.g. Wasser & Waterhouse 1983, Rosenqvist & Berglund 1992, Gowaty 1996, 1997, Shuster & Wade 2003). Whenever the female's fecundity or the ability to rear young depends on an access to limited resources such as male parental care, competitive interactions among females are expected to evolve (Hardy & Williams 1983). Indeed, it has been proposed that the diversity of mating systems can partly

be due to female intra-sexual competition e.g. by female aggression towards the potential mates of their male partners (Veiga 1990).

Wittenberger & Tilson (1980) suggested five conditions for monogamy to evolve in birds with the aggression of mated females towards other females representing one of the conditions. There are numerous studies reporting female-female aggression during the breeding season (Breihagen & Slagsvold 1988, Davies 1989, Møller 1986, Veiga 1990, 1992, Slagsvold et al. 1992, Slagsvold 1993, Slagsvold & Liljfeldt 1994, Gowaty 1996, Liker & Székely 1997, Rosvall 2011). Moreover, female aggression can indeed inhibit multiple females from settling at the male's territory (Struchbury & Robertson 1987, Gowaty & Wagner 1988, Hobson & Sealay 1989, Sandell & Smith 1996, 1997, Sandell 1998). Though the occurrence of female-female aggression during the post-breeding period would corroborate the role of aggression in preserving social monogamy, this subject has not been examined for the post-breeding pair-formation period.

Here we examine aggression behaviour by nest owners towards nest intruders in Eurasian Tree Sparrow *Passer montanus* (hereafter only Tree Sparrow). The behaviour is studied during the post-breeding period when pair formation takes place in sexually mature birds following the breeding season and post-breeding/post-juvenile moult. Based on ringing data and behavioural observations, we aim to establish the basic qualitative and quantitative characteristics of aggressive territorial behaviour by nest owners against intruders. We address if territorial aggression by pair members can represent a territory defence strategy or it can rather be viewed as a strategy by nest owners, particularly females, to monopolize their social mates.

Materials and methods

Study area and species

The study was carried out between the Kampinos National Park and the Vistula River, NW of Warsaw, Poland (52°20' N, 20°50' E). The fo-

cal nest-box colony, established in 1960 and comprising 33 nest boxes, was located along the forest edge (22 nest boxes) and interior (11 nest boxes) of a 30-year-old pine forest near a former field station of the Institute of Ecology, PAS. Nest boxes were arranged in five rows and were located 5–8 m apart. No natural tree holes were present in the focal colony. Nest boxes were used for nesting dominantly by Tree Sparrows (1961: 18, 1962: 15 and 1963: 4 pairs). In addition, 6, 5 and 3 pairs of Great Tits *Parus major* and 1, 4 and 1 pairs of European Pied Flycatcher *Ficedula hypoleuca* nested in the focal colony in 1961, 1962, and 1963, respectively. One pair of Eurasian Wryneck *Jynx torquilla* nested in the colony in 1961.

The Tree Sparrow is a small, sedentary, semi-colonial, cavity-nesting passerine (Sasvári & Hegyi 1994, 2000, Summers-Smith 1995), defending a territory within 2 m of its nest site (Sano 1974, 1988). At the end of the breeding season, adult and fully-grown juvenile Tree Sparrows leave the breeding colony to moult. During this period flocks are formed in feeding and roosting sites outside nesting colonies (Pinowski 1965, 1967). Timing of moult completion of juvenile and adult Tree Sparrows is gradual: 15, 30 and 99% of all Tree Sparrows finish their moult by mid-September, end-September, and mid-October, respectively (Pinowski et al. 2009). After the moult period and a gradual return to nesting colonies, from the beginning of September until the end of October, younger immature birds normally prospect nest sites while adult and older immature birds defend a nest site and perform autumn courtship (Pinowski et al. 2014).

In 1961, Tree Sparrow nest owners were observed at 31 nest-boxes during the autumn courtship period, but nest owners were identified unambiguously only at 18 nest-boxes. At least one nest owner per nest box was identified at 23 of 32 and 8 of 23 nest-boxes in 1962 and 1963, respectively.

Behavioural observations

Antagonistic behaviour of Tree Sparrows, which was the primary focus of this study, was collect-

ed each year during the autumn courtship period from the beginning of September to the beginning of November in 1961–1963. The species' autumn courtship activity normally commenced about an hour after sunrise and continues until noon, but the duration depends on weather. Courtship activity was shorter on rainy and cool days when birds spent more time away from the colony feeding in fields (Pinowski 1966, 1967, Pinowski et al. 2009). Birds were observed nearly every day from early morning until noon. In total, birds were observed during 128 days (38, 50 and 40 days in 1961, 1962 and 1963, respectively). Observations were conducted from two positions within the colony, using a 10 × 50 binocular. The observer rotated between the two positions in hourly intervals during the whole time of bird presence in the colony.

The ring combination (see Pinowski et al. 2014 for details on ringing) and behaviour of individual birds and time of observation were recorded for all birds sighted at or near a nest box. In total, birds were observed for 760 hours during the three years. In addition to the period of autumn courtship, sexual and antagonistic behaviour of Tree Sparrows was observed during the breeding period (involving first broods only) to detect eventual cases of polygyny.

During the autumn courtship period multiple Tree Sparrows can be observed at or near single nests. The same birds observed at the nest at least three times during three different days or during two days each day spending at the nest at least three hours were considered to be pair members and nest owners. Most important evidence for the association of specific birds with a given nest box during the autumn courtship period were observations of nest building behaviour, copulation attempts, pair perching on the nest box and night roosting in the nest box in winter, and the occupation of the nest box by the birds in the immediately preceding or following breeding seasons (Pinowski & Noskov 1981, Pinowski et al. 2006, 2008, 2009). In addition, nest owners were inferred based on their antagonistic responses to intruders. In contrast, intruding/prospecting birds not holding a nest site refer to 1) strange individuals present within

1 m of the nest box and identified by ring combination, 2) individuals on the roof of the nest box, looking at the entrance hole from the roof, perching at the entrance hole and inspecting nest content in the absence of identified owners, and 3) individuals chased by identified owners and engaged in fights with them, mostly with female owners. In this study, the term “chasing” is used when the owners gave warning calls *tre-tre* and actively drove the bird away from the nest box area (ca. 1m radius). The term “fighting” is used when the act of chasing was combined with physical attack represented by aerial fights eventually followed by combats on the ground.

Data analysis

The difference in the frequency of aggressive behaviour occurrence between males and females within pairs was tested using the Sign test because the data used represents matched samples. The difference in the proportion of aggressive males and females of different age was tested with the Binomial test. The deviation between the observed and expected frequencies of aggressive behaviour with respect to age was tested with the Chi-square test. The tests were calculated with Statistica 7 (StatSoft, Tulsa, OK, USA) and R software (R Core Team 2014).

Results

Focal colony mating system structure

The structure of a focal colony during the breeding and autumn courtship periods is quantitatively described in Table 1. No case of polygyny was detected during the breeding period in 1961–1963. In 1961, one of the pairs (1/18, 6%), for which pair member identity was determined, was polygynous during the post-breeding period. An immature male, an immature female, and a female of unknown age formed the pair. Each of the two females occupied a different nest box. In 1962, one polygynous pair (1/23, 4%) was recorded during the autumn courtship period. In this case, it was an adult male first paired with a female of unknown age and an adult female. Later on during autumn, two im-

Table 1. Breeding and post-breeding parameters of a Tree Sparrow colony studied between 1961 and 1963.
Tab. 1. Hniezdné a pohniezdne ukazovatele sledovanej kolónie vrabca poľného v r. 1961 až 1963.

Colony parameters / Charakteristiky kolónie	Year / Rok		
	1961	1962	1963
No. of all nest boxes / Počet všetkých búdok	33	33	33
No. of nest boxes used during the breeding season / Počet búdok obsadených počas hniezdnej sezóny	18	15	4
No. of nest boxes used during the autumn courtship period / Počet búdok obsadených počas obdobia jesenného toku	31	32	23
No. of nest boxes with autumn nests / Počet búdok s vybudovanými jesennými hniezdami	28	27	12

mature females replaced these females. In 1963, two monogamous pairs, in both cases comprised of adult birds, each occupied two nest boxes, but no case of polygyny (0/8, 0%) was detected during the autumn courtship period.

Description of post-breeding antagonistic behaviour

Post-breeding antagonistic behaviour between nest box owners and nest box visitors was observed from September 16 till October 21, from September 8 till October 13, and from October 2 till 11 in 1961, 1962, and 1963, respectively. The frequency of antagonistic interactions peaked at days when prospectors most intensively visited nest boxes. The following stimuli elicited an antagonistic response of nest owners in the post-breeding period: 1) nest visitors entering the nest box and 2) nest visitors perching at the entrance hole and the roof of the nest box. When a pair held two nest boxes during the autumn courtship period, female owners chased intruders away from the secondary nest box, then returning to the primary nest box. In the polygynous trios, each of the females occupied and defended their own nest box.

The antagonistic behaviour normally involved only chasing. In some cases, female owners entered their nest box immediately after chasing. If nest owners failed to chase intruders away, aggression escalated into an aerial foot-gripping fight with birds usually falling, locked together, to the ground where their combat continued. It was possible to approach such locked birds within the reach of the hand. The combatants flew up and down to the ground up to six times during their fight. With one exception, we only recorded physical aggression of

nest owners towards nest visitors. The single exception involved a case when a male visitor chased a male nest owner, but tolerated the nest owner's female partner.

The fights between nest owners and intruders tended to occur more often at nest boxes situated 20 m from the forest edge compared to nest boxes situated at the forest edge—of 12 nest boxes where we detected fights, 7 nest boxes were located in the forest interior. Furthermore, all (7/7) fights occurring during 1962 and 1963 at nest boxes situated 20 m from the forest edge occurred at those nest boxes, which had not been occupied in the previous breeding season and which were rarely prospected during the autumn courtship period.

Sex and age determinants of post-breeding antagonistic behaviour

Female nest box owners were more likely than male owners to be involved in chases with intruders. Namely, when single nest owners momentarily defended nest boxes, 2 male and 15 female nest box owners were observed to chase intruders (Sign binomial test, $Z = 2.91$, $p = 0.004$). Similarly, 7 male and 16 female nest box owners chased intruders alone when both partners were momentarily present at the nest box ($Z = 1.67$, $p = 0.095$). A joint response by male and female nest owners was observed on 37 occasions with 54% (20/37) of the joint chases occurring when multiple intruders visited the nest box.

With respect to fighting behaviour, female owners were generally more likely than male owners to be involved in physical interference with intruders. Five female and no male owners were observed to attack intruders in cases when

single nest owners were momentarily present at nest boxes ($Z = 1.79$, $p = 0.074$), and eight female and no male owners were observed to fight intruders in cases when both owners were present at nest boxes ($Z = 2.47$, $p = 0.013$). Only a single case of a joint fight of nest owners with an intruder was observed during three years – a male joined his female partner who initiated the attack with an intruder.

Chases by nest box owners of known age were performed mostly by adult birds, but this was significant only for male owners (male owners: 19 adult vs. 6 immature birds, binomial test, $p = 0.015$; female owners: 13 adult vs. 11 immature birds, binomial test, $p = 0.839$). Yet, after considering the proportion of adult to immature nest box owners of both sexes (81.3% and 53.3% of males and females, respectively, were adults), the frequency of chases performed by adult birds did not differ from expected frequencies (males: $\chi^2 = 0.45$, $p = 0.502$; females: $\chi^2 = 0.01$, $p = 0.935$). Five adult and three immature female nest owners and a single immature male nest owner were observed to fight intruders.

Chased or fought intruders predominantly comprised immature birds (2 adult vs. 24 immature birds, binomial test, $p < 0.001$), irrespective of the sex of the birds chasing them (female chasers: 1 adult vs. 16 immature birds, binomial test, $p < 0.001$; male chasers: 1 adult vs. 8 immature birds, binomial test, $p = 0.039$). The observed proportion of chased/attacked immature to adult intruders did not differ from the expected proportion (in 84.4% cases, intruders were immature birds; $\chi^2 = 1.24$, $p = 0.266$).

Discussion

This study reports that antagonistic behaviour between nest owners and intruders is common and often fierce during the post-breeding courtship period in Tree Sparrows, suggesting it can substantially affect the birds' time and energy budgets. Antagonistic behaviour was more frequently performed by females and took place within sexes. Though adult male nest owners initiated more chases than immature male nest

owners, after accounting for the proportion of adult to immature nest owners, the frequency of antagonistic encounters was not related to the owner's age for neither sex. Finally, antagonistic encounters, particularly in terms of fighting behaviour among females, occurred dominantly in a relatively poorer breeding habitat.

Intra-sexual antagonistic behaviour among territory owners and intruders is not exclusive to Tree Sparrows (c.f. Sano 1974, 1988). A similar pattern was described for Common Magpie *Pica pica* (Birkhead 1979), Eurasian Nuthatch *Sitta europea* (Mattyhsen 1986), Tree Swallow *Tachycineta bicolor* (Stutchbury & Robertson 1987), Common Blue Tit *Cyanistes caeruleus* (Kempaeners 1994), or Common Starling *Sturnus vulgaris* (Sandell 1998). Based on ringing data, we show for a sexually monomorphic species that the frequency of antagonistic behaviour is higher in female than male nest owners, but it is not related to age in neither sex. Thus, antagonistic territorial behaviour in Tree Sparrows during the post-breeding courtship period is sex- but not age-specific. Superficially, these results indicate that in Tree Sparrows individuals of each sex select and defend a specific nest site and leave mate selection up to intra-sexual competition. Moreover, our results suggest sexual conflict between nest owners whereby females attempt to monopolize the reproductive effort of their social partners.

Though a wealth of literature exists on female mate and nest selection in birds, for which males initially acquire nest sites, the subject is not clear. For example, Leffelaar & Robertson (1985) suggested that female Tree Swallows compete over males with nest-sites, rather than for a male or a nest-site alone. For European Pied Flycatcher, however, which has similar nest site requirements as Tree Sparrows, a series of studies indicated that females choose the quality of the nest site and its surroundings, rather than the quality of male nest owners (Alatalo et al. 1984, 1986, Slagsvold 1986). Yet, more recent studies have pointed out that females routinely use multiple cues when selecting a mate and his territory (Burley 1981, Dale & Slagsvold 1996, see Candolin 2003).

Tree Sparrows rarely survive four years and both sexes participate in parenting (Summers-Smith 1995). Even though males do not develop a brood patch and their incubation is less efficient (Pinowski et al 1973, Anderson 1978), both sexes take an approximately equal share in feeding young (Summers-Smith 1995, Samchuk et al. 1981). Consequently, in line with the latter studies, it is unlikely that female choice in Tree Sparrows operates passively and solely through territory acquisition because male parental contribution is an important determinant of female nesting success in this biparental and short-lived species.

One of our important findings is a high proportion of joint chases conducted by male and female nest owners against intruders. Moreover, male chases against intruders occurred several times more often when their mates were momentarily with them at nest boxes. Therefore, even though antagonistic behaviour in Tree Sparrows is sex-specific, both mates often conduct it simultaneously and its occurrence appears to depend on mate presence. Consequently, antagonistic behaviour in Tree Sparrows during the autumn period may not only serve to defend a territory from intruders, but can also be a component of courtship display with the intensity of this behaviour reflecting individual quality. This suggestion is similar to that on female infanticidal behaviour in House Sparrows *Passer domesticus*, stating that female aggressive behaviour can serve as a signal of quality and facilitate female acceptance in the male's territory (Veiga 2004).

Our results revealed that the frequency of antagonistic behaviour was disproportionately higher in female than male nest owners. Moreover, with a single exception, physical interference among nest owners and intruders occurred only among females. Finally, female-female physical interference dominantly occurred in a poorer nesting habitat of woodland interior where male parental assistance is likely of high importance. These results conclusively point to the existence of sexual conflict in Tree Sparrows with female aggressive behaviour possibly representing an adaptation to monop-

olize the reproductive effort of their mates and keep them socially monogamous (c.f. Veiga 1990). Such a female adaptation would not be superfluous because paternal investment in Tree Sparrows is substantial during the breeding season with males contributing to nest building, incubation and chick rearing (Pinowski 1966, 1967, Pinowski et al. 1973, Pinowski & Pinowska 2009). Moreover, though such information is not available for Tree Sparrow, polygynous male House Sparrows were found to invest in the nests of secondary females significantly less than in their primary nests (North 1980, Veiga 1990). Finally, similarly as reported for House Sparrow, we observed male Tree Sparrows to tolerate strange females prospecting their territory and occasionally create polygynous bonds during the autumn courtship period. Nevertheless, polygyny has only rarely been detected during the breeding season in Tree Sparrow (Creutz 1949, Berck 1961–1962, Deckert 1962, Sano 1974, 1988, Weise 1992) with some of the aforementioned studies attaining polygamy only by manipulating nest-site availability using nest-boxes. Therefore, while female aggressive behaviour can be viewed as a female monopolization attempt of male parental care, one would expect polygyny to occur more regularly and at higher rates in Tree Sparrow.

It is intriguing to contrast the results of this study with those reported by Veiga (1990, 1992, 2004) for a closely related House Sparrow. First, while female-female territorial interference is common in both species during the pair formation period, social polygamy during the breeding period appears to show higher rates in House Sparrows (see Anderson 2006). Second, in contrast to social polygamy rates, genetic polygamy rates seem comparable between the two species (Cordero et al. 2002, Seress et al. 2007), even though the range of extra-pair paternity levels in House Sparrow is known to vary considerably across populations and years (see Anderson 2006). We suggest that it would be worthwhile to investigate the within-population relationships between the intensity of female-female competition and the degree of social and genetic polygamy in the species

with variable mating systems such as House and Tree Sparrows. That is to say, in addition to male paternity assurance and female extra-pair copulation behaviours, female-female aggressive behaviour could be an important determinant not only of social but also genetic mating systems.

In conclusion, we provide correlational evidence that female territorial aggression can be involved in mate monopolization rather than simply serving as a territory defence strategy. It is not surprising that this female behaviour is conspicuous during the post-breeding courtship period because, due to elevated winter mortality, the number of sexually active birds is markedly higher in the autumn compared to spring courtship periods (Pinowski 1968). Consequently, we propose that examining female territorial behaviours during the post-breeding period can provide important insights into the causes of diversity in avian mating systems. Finally, our study lends tentative support to the idea that aggressive territorial behaviour of nest owners towards intruders during the pair-formation period can also serve as a signal of female quality, facilitating mate acceptance at the territory and strengthening the pair bond in biparental species such as Tree Sparrow. Further studies should experimentally assess if male quality or operational sex ratio affect the level of female intra-sexual aggression during the pair-formation period and how the latter relates to variation in mating systems.

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Súhrn

Genetické záujmy samcov a samíc sú zvyčajne odlišné. Kedykoľvek reprodukčný úspech samíc závisí od prístupu k limitujúcim zdrojom, akými sú napríklad samčia rodičovská starostlivosť,

dá sa očakávať evolúcia zložitých kompetitívnych vzťahov medzi samicami. Hoci existuje viacero štúdií o sexuálnej agresivite medzi samicami, pre mimohniezdne obdobie nebola táto problematika doposiaľ študovaná. V tejto práci sme sledovali teritoriálnu agresivitu medzi samicami vrabca poľného (*Passer montanus*) v pohniezdnom období počas jesenného toku. Zistili sme, že agresívne správanie medzi majiteľmi hniezdných búdok a cudzími vtákmi je aj v pohniezdnom období bežné a často veľmi intenzívne. Samice vykazovali všeobecne vyššiu frekvenciu agresívneho správania ako samci, pričom agresívne správanie bolo pohlavne ale nie vekovo špecifické (t.j. vtáky napádali jedincov rovnakého pohlavia ale nezávisle od veku). Táto práca podporuje hypotézu, že samičie teritoriálne agresívne správanie môže u niektorých vtáčích druhov predstavovať stratégiu na monopolizáciu partnerov a nemusí byť prostým prejavom hájenia teritória. Agresívne teritoriálne správanie u vrabca poľného tiež môže slúžiť ako signál individuálnej kvality, ktorý je určený partnerom počas obdobia vytvárania a utužovania párových zväzkov. Výsledky tejto práce naznačujú, že teritoriálne agresívne správanie v pohniezdnom období môže objasniť určitú variabilitu v rozmanitosti vtáčích rozmnožovacích systémov.

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