# DOMINANCE HIERARCHY AND STATUS SIGNALLING IN CAPTIVE TREE SPARROW (PASSER MONTANUS) FLOCKS

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Although the tree sparrow (*Passer montanus*) is a widespread species, its social behaviour in winter flocks is poorly known. In this study, we investigated whether (1) flock members form dominance hierarchies in their winter flocks, and (2) whether the size of the black throat patch (the 'badge') of birds is correlated with their dominance ranks, i.e. may have a status signal function. We found that tree sparrows formed linear dominance hierarchies in two of the three captive flocks we studied. The dominance rank of birds was positively correlated with their aggressiveness during feeding, i.e. high ranking birds initiated a higher proportion of their aggressive interactions than subordinates. Our results do not support unambiguously the status signalling function of the badge. On the one hand, badge size was the only significant predictor of dominance rank in one flock. In this flock, fighting frequency increased with increasing similarity of badge sizes and fights were especially common when both opponents had large badges. On the other hand, dominance rank was unrelated to badge sizes in the other two flocks. We suggest some factors that may contribute to the observed differences among flocks in the association between badge size and dominance rank.

Key words: tree sparrow, Passer montanus, badge size, dominance hierarchy, status signalling

## INTRODUCTION

The Eurasian tree sparrow (*Passer montanus*) is a common breeding bird in most part of its range. Although many aspects of the breeding ecology and social behaviour of the species are thoroughly investigated (e.g. CRAMP & PERRINS 1994, SUMMERS-SMITH 1995), much less is known about the sparrows' behaviour in winter flocks. Earlier studies showed that tree sparrows typically form flocks after the breeding seasons which persist until the next spring, and the members of these flocks usually forage and roost together (CRAMP & PERRINS 1994). Foraging flocks may consist of up to 1000 birds in favourable areas, although these large flocks may brake up into smaller groups when food become scarce, e.g. during periods of snow cover. Foraging birds often interact aggressively, and both threat dis-

plays and direct physical attacks are used for acquiring food and defending food patches against conspecifics (CRAMP & PERRINS 1994, SUMMERS-SMITH 1995). Although the spatial position of foraging birds suggest that males may be dominant over females (CRAMP & PERRINS 1994), it has not been investigated whether group members form stable dominance relationships in the flocks.

Furthermore, it is also not clear whether the conspicuous black throat patch (the badge) of tree sparrows may have a signal function, e.g. in a similar way that the badge of males signals social status in the closely related house sparrows (*Passer domesticus*). According to the predictions of the status signalling hypothesis (ROHWER 1975), the dominance rank of male house sparrows is positively correlated with the size of their badge, and the frequency of aggressive interactions seems to decrease with increasing differences in the opponents' badge size (MØLLER 1987, SOLBERG & RINGSBY 1997, LIKER & BARTA 2001, GONZALEZ *et al.* 2002). Such badge signalling system may be profitable for members of a flock because it may reduce the costs associated with intraspecific competition for valuable resources such as food, roosting sites or nest sites. Without status signalling, individuals should often compete by direct physical interactions (e.g. escalated fights), at least in groups where group members are not able to recognise individually all of their opponents (ROHWER 1975, MAYNARD SMITH & HARPER 1988). Frequent fights may be costly because they need time and energy, and the risk of getting wounded may also be large.

Badge size is expected to have a status signal function in tree sparrows for several reasons. First, the house sparrow (that use badge size for status signalling) and the tree sparrow are closely related species (hybrids with intermediate plumage coloration have been reported; SUMMERS-SMITH 1995), thus the biological mechanisms underlying both fighting behaviour and signal variability may be similar in these species. Second, tree sparrows often feed and roost in large, fluctuating flocks during the non-breeding season (CRAMP & PERRINS 1994, SUMMERS-SMITH 1995), that makes it difficult for a bird to recognise all flock members individually. Third, aggressive interactions are frequent during winter, e.g. among feeding birds (TORDA, LIKER & BARTA, unpubl. data). Because in tree sparrows both sexes have the black throat patch without clear sex differences during the non-breeding season (SVENSSON 1992, CRAMP & PERRINS 1994), the badge may have the same function (e.g. status signalling) in both sexes.

The aims of this study were to investigate whether (1) tree sparrows form dominance hierarchies in their winter flocks, and (2) whether the size of the black throat patch of birds is correlated with their dominance ranks, i.e. may have a status signal function. Specifically, we tested the following two predictions of the status signalling hypothesis: (i) individuals with large badge size should have higher

dominance than small-badged individuals, and (ii) fights should occur more often between individuals having similar badge sizes than between opponents with different badges. We investigated these predictions in small captive flocks (the same approach was successfully used to investigate status signalling, for example, by MØLLER 1987, SOLBERG & RINGSBY 1997, LIKER & BARTA 2001, GONZALEZ *et al.* 2002).

## METHODS

Tree sparrows were captured with mist nets at the Dóra-farm Experimental Station of the Szent István University, 30 km south-east from Budapest, on 28 September and 4 October 1999. After capturing the birds, we measured their body weight to the nearest 0.1 g, tarsus length and beak length to the nearest 0.1 mm, and wing length to the nearest 1.0 mm. We took digital photographs from each individual with an Olympus 2000 camera. For these photographs we held birds in standardised posture (body extended and bill pointing up in right angle with the body) over a standard background. Visible badge sizes were measured from these digital images by the ScionImage software. This measure of badge size was significantly repeatable in a sample of 14 birds for which we took a second photograph at the end of the study (repeatability: 52%, $F = 3.2$, $P = 0.013$; LESSELLS & BOAG 1987). Note that the mean visible badge area increased significantly between the two measurements due to the wearing of the pale tips of bib feathers that partially cover the badge after moult (mean±SD, first: $85.1 \pm 20.1$ mm$^2$, second: $97.5 \pm 17.4$ mm$^2$; paired t-test: $t = 3.79$, $P = 0.002$), which might have reduced the true value of repeatability. We used the first measurement of the badge (i.e. that we measured at the beginning of the study) in all analyses. We lacked the image for one bird in flock B (see below), so this bird was not used in the badge size analyses. Birds were ringed with a metal ring and two colour rings. We also painted small red or white markings on the top of the head or on tail feathers to facilitate quick individual recognition for the observer during behavioural observations. These markings did not affect the dominance ranks of individuals (Kruskal-Wallis tests, colour of marking: $\chi^2 = 0.1$, $P = 0.609$; location of marking: $\chi^2 = 0.03$, $P = 0.857$, $n = 29$).

Birds were transferred to the campus of Szent István University, where individuals were divided randomly into three flocks (flock A, B and C). Birds were not sexed or separated by age before constructing these experimental flocks, because we did not find any morphological clues that reliably separate age or sex classes in autumn (SVENSSON 1992, CRAMP & PERRINS 1994). Flock A initially consisted of ten individuals, but one individual died in the middle of the study (four weeks after the start of observations). Because the dominance hierarchy changed after the death of this bird, we divided the study period into two intervals for this flock: flock A1 with ten birds and flock A2 with nine birds. Then, in analyses including dominance ranks, data were analysed separately for these two subsets of observations. Flock B consisted of ten individuals throughout the study. Flock C contained ten birds at the beginning and one bird died on the first week of study. Because this bird only had two fights by then, these records were omitted from the study, and data from nine individuals were analysed in flock C. The flocks were kept in indoor aviaries, each of which measured 2 m × 1.5 m × 2 m. Artificial light (10 : 14 hr light:dark periods), *ad libitum* water and food were provided between the observations. Each of the aviaries contained an approximately 1.5 m tall roosting tree, a water dish and a sand dish. Feeding took place on a 0.8 m × 0.8 m-sized feeding-table, which contained 64 (8 × 8) small holes for presenting food (a mixture of millet seed and canary seed-mixture, enriched with vitamins). The individuals' weight did not change during the study period (mean±SD, weight at capture:

21.93±1.22 g, weight at the end of the study: 21.96±2.05 g; paired t-test: t = 0.08, P = 0.935). Birds were released after the experiment at the site of capture on 10 December 1999.

In the evening before the days of observations, we removed food from the aviaries. Food was provided again next day, right before the observations, by placing seeds into 2 holes in the middle of the feeding-table. We then recorded dyadic fights on the table. Two types of aggressive interactions were recorded. (1) Threat displays, with no physical contact between the individuals, when opponents used calls and various visual signals to scare away the other (e.g. fig 6.3. and fig 6.4. in SUMMERS-SMITH 1995). (2) Fights, with physical contact, when birds pecked the opponents' foot, head or tail, or even held tight for a longer time. We recorded all those aggressive interactions in which both birds were identifiable and we could determine the outcome of the encounter. The minimal requirement for winning was to chase away the opponent from the actual feeding-hole, though sometimes the loser even left the feeding-table. We also noted which bird initiated the encounter. Behaviour of the birds was observed through a one-way window. Two observations were done on each flock every week, choosing the order of observations randomly among flocks. Each observation session lasted until the birds showed activity on the feeder (ca. 20 minutes). We recorded 401 aggressive interactions in flock A, of which 192 were collected during the first interval (A1) and 209 during the second one (A2). 441 and 343 aggressive interactions were recorded in flock B and flock C, respectively. All observations were done by G.T.

Dominance relationship was determined for each pair of individuals by the outcomes of repeated interactions (threats and fights combined): an individual was considered dominant in the dyad if it won more than 50% of the aggressive encounters, and the other member was considered subordinate. Dominance rank of individuals within the flocks was determined by DE VRIES (1998) 'I and IS' algorithm. The significance of linearity of the hierarchies was tested by a randomisation test developed by DE VRIES (1995). We used 10,000 repeats to estimate the significance level for the unbiased Landau's linearity index (h'). We used non-parametric correlations to test for associations between badge size and the rank and body size of birds. However, since ranks within a flock cannot be treated as independent data points, we also tested the correlation between badge size and dominance rank by using a randomisation test (R statistical computing environment, boot function [(R DEVELOPMENT CORE TEAM 2003]). As highest ranking individuals were coded with the largest numbers in the rank order (i.e. 9 or 10) and the most subordinate with the lowest (1), positive correlation coefficients involving dominance rank indicate dominants having higher values than subordinates for the variables examined. To compare frequencies of aggressive interactions between groups of dyads with various badge size differences, we used Mantel's randomisation test with 10,000 repetitions, and calculated Kruskal-Wallis $\chi^2$ values and the corresponding P values by this test (MANLY 1991). In multiple statistical tests, Bonferroni correction was applied to adjust significance levels (CHANDLER 1995). Mean±SD and two-tailed probabilities are given throughout.

## RESULTS

The average number of aggressive interactions (threats plus fights) an individual was involved in did not differ between the flocks: birds had 85.4±23.2 aggressive interactions in flock A (38.4±14.9 during the A1 period, and 46.4±20.1 during the A2; n = 10 and 9 birds, respectively), 88.2±36.2 in flock B (n = 10), and 80.3±31.8 in flock C (n = 9; Kruskal-Wallis test: $\chi^2$ = 0.5, df= 2, P = 0.777). There was no difference between the flocks in the relative frequencies of threats and

**Table 1.** Dominance hierarchies in the studied tree sparrow flocks. h'= Landau's unbiased linearity index, I = number of inconsistencies (loops), IS = strength of inconsistencies, P = significance of the linearity index according to DE VRIES (1995) randomisation test, n = number of individuals

| Flock | h' | I | IS | P | n |
|---|---|---|---|---|---|
| A1 | 0.472 | 4 | 24 | 0.073 | 10 |
| A2 | 0.442 | 4 | 18 | 0.161 | 9 |
| B | 0.915 | 0 | 0 | 0.000 | 10 |
| C | 0.700 | 4 | 12 | 0.010 | 9 |

fights (threat/fight ratios, flock A: 0.257, flock B: 0.251, flock C: 0.309; chi-square test: $\chi^2 = 3.4$, df = 2, P = 0.179).

Significantly linear dominance hierarchies were found in two flocks. Dominance relationships of birds in flock B formed a completely linear dominance hierarchy, and in flock C birds established a close to linear dominance hierarchy (Table 1). The hierarchy was not significantly linear in flock A, either with 10 (flock A1) or 9 (flock A2) individuals (Table 1). Higher ranking individuals initiated a higher proportion of their aggressive interactions than lower ranking individuals in flock A1 (Spearman rank correlation, $r_s = 0.63$, P = 0.05, n = 10), flock A2 ($r_s = 0.97$, P < 0.001, n = 9) and flock B ($r_s = 0.95$, P < 0.001, n = 10), whereas dominance ranks were unrelated to the proportion of fights initiated by the individuals in flock C ($r_s = 0.48$, P = 0.187, n = 9).

There were no significant differences in mean badge size among the flocks (A: 83.8±14.3 mm², B: 82.4±23.2 mm², C. 88.5±15.5 mm²; Kruskal-Wallis test, $\chi^2 = 0.36$, df = 2, P = 0.834). Badge size was significantly related to dominance ranks in flock B: higher ranking (i.e. more dominant) individuals had larger badge size than lower ranking individuals (Table 2, Fig 1; randomisation test: P < 0.05, based on 1000 bootstrap replicates). Badge size was unrelated to dominance ranks in other flocks (Table 2; randomisation tests: P > 0.05 in all cases, based on 1000

**Table 2.** Spearman's rank correlations between morphological characteristics of birds and their dominance ranks ($r_s$ values are given). A positive correlation coefficient indicates dominants having higher values for the trait than subordinates. Bonferroni correction was used to adjust significance levels for five comparisons, * indicates P < 0.05 at the adjusted significance level

| Flock | Badge size (mm²) | Weight (g) | Tarsus length (mm) | Wing length (mm) | Beak length (mm) | n |
|---|---|---|---|---|---|---|
| A1 | –0.236 | 0.190 | 0.524 | –0.178 | –0.024 | 10 |
| A2 | –0.533 | 0.169 | 0.277 | –0.009 | 0.017 | 9 |
| B | 0.800* | 0.521 | 0.006 | 0.445 | –0.182 | 9 |
| C | 0.133 | 0.025 | 0.276 | –0.114 | 0.405 | 9 |

bootstrap replicates). Other morphological traits of the birds such as body mass, wing, tarsus and beak length were unrelated to their dominance ranks (Table 2).

To investigate whether the frequencies of aggressive interactions were related to within-dyad badge size differences, we divided birds into two badge size classes within each flock: (1) lower than average badge size, (2) average or larger than average badge size. Then, within each flock, we calculated aggression frequencies for three types of dyads: (1) two large-badged opponents (LL dyads), (2) one large-badged and one small-badged opponents (LS dyads), and (3) two small-badged opponents (SS dyads). Frequencies were compared among these dyad types by Mantel randomisation tests. We found a significant heterogeneity in aggression frequencies in flock B: the average number of aggressions per dyad was highest in LL dyads, intermediate in SS dyads, and lowest in LS dyads (Table 3). The frequencies of fights were unrelated to badge size differences in other flocks.

## DISCUSSION

In this study we investigated the aggressive behaviour of tree sparrows in small captive flocks. Our results showed that individuals frequently interacted by threat displays and fighting when they foraged on concentrated food patches. We found that individuals established dominance hierarchies by the outcomes of ag-
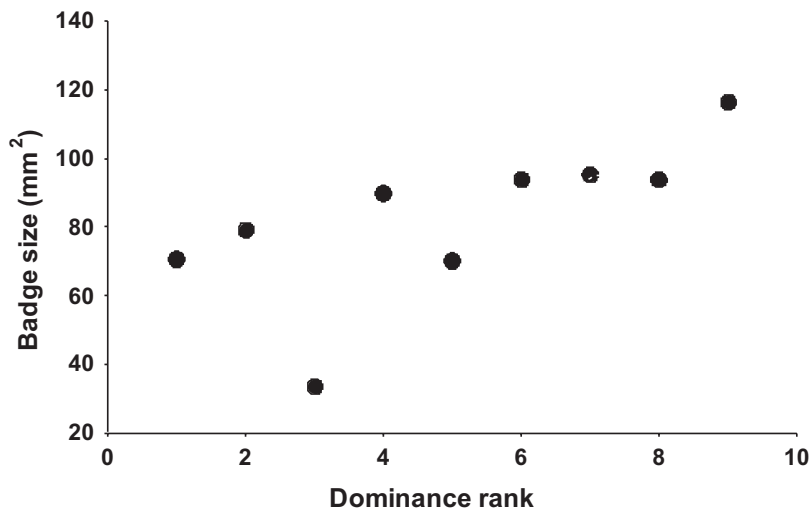


**Fig. 1.** The relationship between badge size and dominance ranks in flock B (n= 9 birds, for statistics see Table 2). The most subordinate individual has rank 1

**Table 3.** Mean number of fights (± SD) in dyads with different badge size differences. Dyad types: SS = two small-badged individuals, LS = a small-badged and a large-badged individual, LL= two large-badged individuals. Kruskal-Wallis $\chi^2$ values and the corresponding P values were calculated by Mantel's randomisation test, n is the number of dyads per dyad types

| Flock | Dyad type | No. fights/dyad (mean ± SD) | $\chi^2$ | P | n |
|-------|-----------|------------------------------|----------|------|-----|
| A1 | SS | 3.9±2.9 | 0.1 | 0.962 | 15 |
| | LS | 4.3±3.2 | | | 24 |
| | LL | 5.0±4.7 | | | 6 |
| A2 | SS | 6.7±5.9 | 0.5 | 0.829 | 15 |
| | LS | 5.4±3.8 | | | 18 |
| | LL | 3.7±1.5 | | | 3 |
| B | SS | 7.8±5.9 | 5.2 | 0.039 | 6 |
| | LS | 6.8±5.5 | | | 20 |
| | LL | 11.8±6.2 | | | 10 |
| C | SS | 7.9±5.5 | 0.132 | 0.953 | 10 |
| | LS | 8.5±4.9 | | | 20 |
| | LL | 15.5±15.1 | | | 6 |

gressive interactions in two of the three studied flocks. The hierarchies were linear or close to linear in these two flocks, i.e. the dominance relationships were transitive in most cases. Dominant tree sparrows also appeared to be the most aggressive birds in the flocks, i.e. initiated fights more frequently than subordinate individuals. These characteristics of the dominance relationships between wintering tree sparrows are very similar to those found in house sparrow flocks (HEGNER & WINGFIELD 1987, MØLLER 1987, SOLBERG & RINGSBY 1997, LIKER & BARTA 2001). Thus the social organisation of flocks may be similar in the two species during the winter, at least where tree sparrows form small flocks (see Introduction).

Our results did not support unambiguously, however, that the badge has the same adaptive function, i.e. status signalling, in tree sparrows and house sparrows. On the one hand, we found a strong correlation ($r_s = 0.8$) between badge size and the dominance rank in one flock, whereas no other measurements of the birds were related to dominance ranks. The 'like-versus-like' prediction of the status signalling hypothesis (ROHWER 1975, SENAR 1999) was also supported in that flock: fighting frequency increased with increasing similarity of the badges, and fights were most common between opponents having large badges. These results are similar to those found in male house sparrows where the status signalling function of the badge has been well supported (MØLLER 1987, SOLBERG & RINGSBY 1997, LIKER & BARTA 2001, GONZALEZ *et al.* 2002). On the other hand, in two out of

three flocks we did not find a relationship between badge size and dominance rank, or between badge size differences and fighting frequencies.

One interpretation of the differences may be that we found a significant association between badge size and dominance rank in one of the three flocks by chance, and badge size may not be involved in signalling dominance status. However, such inconsistencies among flocks are not uncommon in those species where status signalling by plumage has been showed, and may be related to differences in flock composition. For example, in Harris' sparrows (*Zonotrichia quereula*), the amount of black coloration correlated with status in flocks that included both males and females and individuals from different age groups (ROHWER 1975). This relationship was not found, however, in flocks that included only one sex from one age group, and it has been suggested that colour differences in this species may signal coarse differences in fighting ability between age and sex classes (JACKSON *et al*. 1988). Some observations suggest that dominance may also be sex-related in tree sparrows, with males being dominant over females (CRAMP & PERRINS 1994). In our study, we were not able to separate birds by age or sex, so the small flocks may differ in sex or age composition by chance. If tree sparrows' badge size mostly play a role in status signalling between age or sex classes, than differences in sex or age composition might have resulted in the observed differences among the flocks.

Second, familiarity with flock mates may also be important. For example, SOLBERG and RINGSBY (1997) found only weak relationships between status and badge size in male house sparrows that were captured from small and isolated populations. They suggested that in flocks where individuals are familiar to each other prior experience rather than badge size may be the most important indicator of the fighting ability of opponents. Similarly, LEMELN and WALLIN (1993) found in great tits (*Parus major*) that breast stripe predicted the outcome of fights only when the opponents had no prior experience with each other. In our study we could not control the familiarity of flock mates. As birds were usually captured in groups, experimental flocks might have included several birds that were familiar to each other, potentially decreasing the chance that status signalling had a detectable effect on dominance ranks.

Finally, the stability of dominance relationships may also affect the strength of correlations between dominance rank and badge size. In flocks where dominance relationships are not stable between the opponents (i.e. reversals are frequent, and linearity of the hierarchy is low), the calculated rank of birds within the hierarchy may not reflect accurately their relative fighting ability. In such flocks only weak relationships can be expected between dominance rank and badge size even if badge size is associated with fighting ability. According to this, we found a

significant relationship between badge size and rank in the flock where birds formed a completely linear hierarchy, and the strength of correlation decreased with decreasing linearity of the hierarchies (i.e. with increasing number of 'loops' in the dominance relationships, see Table 1 and 2).

In conclusion, we found that dominance relationships in wintering tree sparrows flocks may form linear hierarchies, at least when they are in small groups. Our study provided inconsistent results with respect to status signalling by badge size. We suggest that birds with known age and sex should be used in further studies to increase the chance of corroborating the status signal function of badge size in tree sparrows.

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