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Status badge-signalling in male but not in female Eurasian Tree Sparrows

Passer montanus

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Male ornaments, such as plumage coloration, frequently serve as signals. The signalling function of similar ornaments in females has, however, received much less attention despite the fact that conspicuousness of their ornaments is often comparable to those of males. In this study we tested the signalling function of a plumage trait present in both sexes in the Eurasian Tree Sparrow *Passer montanus*. The black throat patch has been repeatedly found to have a signal function in the closely

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related House Sparrow *Passer domesticus*, where only males bear the ornamental trait. However, the function of the black throat patch in the females of *Passer* species that have sexually monomorphic ornament expression has never, to our knowledge, been considered. We investigated the outcomes of aggressive encounters in foraging flocks of free-living Tree Sparrows, and assessed whether throat patch size and measurements of body size predicted fighting success in these flocks. We found that male throat patch size predicted fighting success against both male and female opponents. However, female throat patch size did not correlate with fighting success against either sex. Among the morphological traits studied, wing length was the best predictor of fighting success in females. Our findings suggest a status signalling function of throat patch size in males but not in females, although further experimental studies are necessary to corroborate these correlative results.

Keywords: badge-signalling, dominance, feeding competition, melanin, monomorphic ornaments.

Conspicuously coloured patches of feathers are often found to serve as signals in birds (e.g. Eaton & Lanyon 2003, Bókonyi *et al.* 2006, Senar 2006). While signalling and animal communication have been intensively studied, much less attention has been paid to inter-sexual differences in signal design and function (Amundsen 2000a, b, Kraaijeveld *et al.* 2007). Most investigations of animal communication have focused on male ornaments and have frequently disregarded female ornaments (Amundsen 2000a). In several species, however, both sexes possess conspicuous ornaments.

There are two not mutually exclusive hypotheses that explain signal design in relation to sex. First, the genetic correlation hypothesis (Lande 1980) argues that the traits in the two sexes are not inherited independently, so the selection acting on the ornaments of males can result in male-like ornaments in females. Although genetic correlation between the sexes may be widespread (Kraaijeveld *et al.* 2007, Poissant *et al.* 2010), it has rarely been shown to prevent sexes reaching their own sex-specific optima in ornament expression (e.g. Zebra Finch *Taeniopygia guttata* bill colour; Price 1996, reviewed in Kraaijeveld *et al.* 2007).

The second hypothesis is that female ornaments, like those of males, are maintained by direct selection (Price & Birch 1996). Both sexual selection and social selection may favour female ornamentation. In support of the sexual selection hypothesis, males have been observed to prefer highly ornamented females in various animal taxa (Clutton-Brock 2009, Tobias *et al.* 2012). Social selection, on the other hand, may favour female ornamentation if honest signals of competitive ability allow individuals to avoid frequent antagonistic interactions with conspecifics. Although the status signalling hypothesis (Rohwer 1975, Senar 2006) does not assume differences between the sexes – signalling competitive ability can be equally profitable both for males and females, and against both sexes – only a moderate number of avian studies have investigated its predictions in females (Kraaijeveld *et al.* 2007, Tobias *et al.* 2012). For instance, the facial colour patterns in Northern Cardinals *Cardinalis cardinalis* (Jawor *et al.* 2004), chest spottiness in Common Starlings *Sturnus vulgaris* (Swaddle & Witter 1995) and in Diamond Firetails *Stagonopleura guttata* (Crowhurst *et al.* 2012), black bib size in Sociable Weavers *Philetairus socius* (Rat *et al.* 2015) and multiple plumage traits in Harris's Sparrows *Zonotrichia querula* (Watt 1986) and Golden-crowned Sparrows *Zonotrichia atricapilla* (Chaine *et al.* 2011), were observed to predict dominance status and aggressive behaviour in females of these species. Bill colour in American Goldfinches *Spinus tristis* (Murphy *et al.* 2009b), orange breast coloration in Streak-backed Orioles *Icterus pustulatus* (Murphy *et al.* 2009a) and in Rock Sparrows *Petronia petronia* (Griggio *et al.* 2010), and UV/blue crown in Blue Tits *Cyanistes caeruleus* (Midamegbe *et al.* 2011), have also been suggested as acting as status signals in females, as these ornaments were observed to modulate female aggressiveness toward taxidermy models or conspecifics with manipulated signals.

Recent reviews have concluded that investigating intersexual signal design in taxa in which evolutionary transition has occurred between sexually monomorphic and dimorphic states of the ornament may be particularly important (Amundsen 2000b, Kraaijeveld *et al.* 2007, Hofmann *et al.* 2008, Clutton-Brock 2009). This kind of evolutionary transition is assumed to have happened in the genus *Passer*, and resulted in the apparently sexually monochromatic plumage of the Eurasian Tree Sparrow *Passer montanus*, in which both males and females possess a black throat patch. Its ancestor is assumed to have been dichromatic, having a black throat patch in males and having no throat patch

in females, as is the case in the species' closest extant relatives (e.g. Plain-backed Sparrow *P. flaveolus* and Russet Sparrow *P. rutilans*; Allende *et al.* 2001, Tibbetts & Safran 2009). Although the function of the male's black badge has been intensively studied in the closely related and dichromatic House Sparrow *Passer domesticus* (Nakagawa *et al.* 2007), we have very little information about the function of the throat patch in Tree Sparrows (Torda *et al.* 2004) or in any other *Passer* species.

The size of eumelanin-based black feather patches, like chest and throat patches in sparrows, are assumed to primarily act as status signals in birds (Hill 2006, Senar 2006). A comparative study found that the presence of these patches is strongly associated with sociality during the non-breeding season in both New World and Old World sparrows, supporting the idea that they have evolved as a result of social competition, and hence may be used as 'badges of status' (Tibbetts & Safran 2009). For instance, in male House Sparrows the size of the badge positively correlates with various aspects of fighting ability (Bókony *et al.* 2006) and predicts dominance toward both males (e.g. Møller 1988) and females (Liker & Barta 2001). Although some studies have found correlation between badge size of male House Sparrows and some aspects of reproductive behaviour (e.g. frequency of extrapair copulations or parental effort), the only relationship that was strong and robust across several studies in a meta-analysis was between badge size and fighting ability (Nakagawa *et al.* 2007).

To our knowledge, in *Passer* species other than the House Sparrow only one study has investigated the relationship between dominance and badge size. Torda *et al.* (2004) observed three flocks of Tree Sparrows under laboratory conditions but did not find consistent results. Throat patch size was strongly related to the individuals' dominance rank in one flock, but not in the other two flocks. Since the authors did not know the sex of the experimental birds, they concluded that intersexual differences in the relationship between dominance and throat patch size may contribute to the inconsistencies in their results. In a previous morphological study, we found that both mean size and variance of the throat patch is greater in male than in female Tree Sparrows (Mónus *et al.* 2011). This finding suggests that the role of the throat patch may differ between the sexes, because a more variable trait is likely more suitable in acting as a signal (Møller 1991, Delhey & Peters 2008).

We investigated the status signalling role of the throat patch in free-living male and female Eurasian Tree Sparrows. Signalling dominance status may be advantageous in this species because individuals forage in flocks of unstable composition during the winter (Mónus & Barta 2010) which usually results in frequent aggressive encounters over food resources (Rohwer 1975). We assessed whether throat patch size of males and of females predicts fighting success towards conspecifics, and whether the correlation between throat patch size and fighting success differs according to the sex of the opponents. This is a frequently overlooked aspect of the originally proposed status signal hypothesis (Rohwer 1975; but see Liker & Barta 2001, Hein *et al.* 2003). We also investigated other potential morphological correlates of fighting success in both sexes.

METHODS

Study site and species

This study was conducted on Tree Sparrows resident in the Botanical Garden of the University of Debrecen, Hungary, during the winter of 1999-2000. For a detailed description of the study site, see Barta *et al.* (2004). In the Garden, approximately 200-300 Tree Sparrows foraged regularly during the winter in groups of various sizes (ranges 1 to 70; pers. obs.). They usually foraged in grassy open parts of the Garden, but also readily used feeding stations. Preceding the experiment, in the autumn of 1999, 112 adult Tree Sparrows (54 males and 58 females) were individually marked using colour rings, and were sexed by PCR-based amplification of the sex-chromosome linked chromodomain helicase DNA binding protein 1 (CHD1; Griffith & Tiwari 1995) as described in Mónus *et al.* (2011). The sex identification procedure was repeated in 32 individuals, and 3 individuals that were recaptured in the next breeding season were sexed on the basis of morphological traits (Svensson 1992). No inconsistent results were found in sex identification.

Data collection

A 150 × 150-cm feeding platform was installed on the ground in an undisturbed corner of the Garden. After familiarization with the feeder, Sparrows used the closest bush (1.5 m from the feeder) to gather, and then initiated feeding trials in flocks from this bush (Barta *et al.* 2004, Mónus & Barta 2011). The observer (ZB) hid in a camouflaged tent 6 m from the feeder and used a video camera to record the behaviour of individual Tree Sparrows on the platform. Recordings were made on 13 mornings (between 07:00AM and 11:00AM) from mid-December 1999 to mid-January 2000, well after the birds had familiarized themselves with the activity of the observer in the hide. During recordings, the observer tried to locate and zoom the camera towards individually marked sparrows, so that colour rings could be recognized later from the recordings. Before and during recording, the observer regularly collected the remaining food from the platform and supplied small amounts (one teaspoon) of corn grit into twenty of the holes bored into a 12-by-12 grid in the feeding platform. This arrangement of the food produced a situation in which birds were forced to search for the seeds (Liker & Barta 2002, Barta *et al.* 2004).

Morphological measurements were taken when Sparrows were captured and marked. Body weight was measured by a Pesola spring balance to the nearest 0.5 g, tarsus length by calliper to the nearest 0.1 mm, wing length by ruler to the nearest 1 mm, each in a standardised holding position. The throat patch (badge) was photographed from the front view, including a ruler as a measurement reference. Throat patch size was defined by the area covered by black feathers measured from the digitalized photographs using Image J 1.24 for Linux software (see Fig. 1 of Mónus *et al.* 2011). Before releasing the birds, the throat patch was photographed again in 73 individuals; repeatability for our throat patch size measurement was 0.79 ($F_{72,73} = 8.33$, $P < 0.001$). Repeatabilities for wing length, body weight and tarsus length were 0.76, 0.64 and 0.59; respectively ($F_{33,34} > 3.87$, $P < 0.001$ for all cases; based on 34 recaptures). All repeatability values were calculated following Lessells and Boag (1987).

We collected 14–90 separate video recordings per observation day. During each recording, the experimenter continuously recorded the behaviour of Sparrows on the feeder without switching off the camera. Since the detailed analysis of Sparrow behaviour (see below) was very time consuming, we analysed a maximum of 30 randomly chosen recordings per day. Altogether, we analysed 378 video recordings in detail, each lasting from several seconds in length to about 1 minute. Based on their colour rings, we identified as many individuals as possible on the analysed recordings (1 to 12 individuals per recording; 4 individuals on average).

For each focal bird, we recorded the total number of aggressive encounters and the total number of non-aggressive encounters. Aggressive encounters were defined as occasions on which any obviously aggressive interaction (pecking, fighting, charging) occurred between the focal bird and another bird. Non-aggressive encounters were defined as occasions on which the focal bird met other birds at a food-containing hole (independently of whether the focal bird arrived before or after its flock mates), but no obviously aggressive interaction occurred between them. Aggressive encounters with unambiguous outcomes were categorized as a defence, if the encounter occurred when the focal bird was feeding (i.e. staying in a food patch), and as an attack if the encounter occurred when the focal bird was searching (i.e. moving on the feeder and searching for food patches). The focal bird was considered to unambiguously win a contest if it clearly supplanted its opponent, or to unambiguously lose a contest if it was clearly supplanted by its opponent. Of all aggressive encounters, 94% (1021 out of 1085) had an unambiguous outcome, and encounters with ambiguous outcomes were excluded from the analyses. Finally, we described competitive ability according to fighting success as a surrogate of dominance (Rohwer & Ewald 1981, Liker & Barta 2001, 2002). Fighting success was assessed as a binomial variable (see below) considering the total number of unambiguous aggressive encounters (a series of binomial events); in each of them the focal bird was either a winner or a loser. This measure, in contrast to the proportion of encounters won compared to the total number of unambiguous aggressive encounters, preserves the information deriving from the frequency values (Crawley 1993). Attack success and defence success were calculated and analysed in the same way as the fighting success, but only encounters categorized as attacks and as defences were included, respectively.

In total, we identified 51 individuals from the recordings; fighting success (based on 1 to 63 encounters per individuals; median = 11) was available for 47 individuals (four individuals were not observed to be involved in any aggressive encounters with an unambiguous outcome); sex identification was available for 16 males and 23 females (there was no sex identification for individuals that were colour ringed during the previous years). All data, including behavioural observations, morphological traits and sex identification, were available for 35 individuals (15 males and 20 females).

Data analysis

We carried out all statistical tests in the R interactive statistical environment (R Development Core Team, 2014). We analysed individual differences by fitting generalized linear models (*glm* function in R). In order to analyse the correlates of competitive ability (fighting success) we used a binomial error distribution where the total number of wins and losses of the individuals were entered as a response variable. The binomial error distribution allowed us to represent fighting success in our models with a series of binomial events (instead of a simple arithmetic mean), while each individual was included only once in the analyses. We analysed males and females separately, and fitted tarsus length, wing length, body weight and throat patch area in these models as predictor variables (Table 1). We checked for multicollinearity in these continuous variables. Pairwise Pearson correlations did not reach $r = 0.4$ in any cases, and variance inflation factors (VIF) were lower than 1.6 for all cases. Multicollinearity is widely considered to potentially affect the results if VIF values are greater than 10 (Kutner *et al.* 2004), so we did not exclude any of the above mentioned continuous predictors from the models. Overdispersion was accounted for by setting the *glm* family to *quasibinomial* (Venables & Ripley 2002); homoscedasticity and residual normality were checked visually.

In order to analyse whether the correlates of competitive ability were different when fighting against males or when fighting against females, we repeated the analyses using only those encounters in which the opponent was identified either as male or female (i.e. we built two separate models for fights with male and female opponents; Table 2). In these models, we analysed fighting behaviour of males and

females together, because sample sizes would have been very small for sex-specific models (not all individuals fought with opponents of both sexes, see Table 2). In addition to the four previously described morphological traits, we included the sex of focal individuals as an explanatory variable, and its interaction terms with each of the four continuous predictors. These interaction terms show whether there are sex related differences in the correlates of the competitive ability, hence these were our main interests when evaluating these models.

In order to analyse the effect of morphological differences between opponents on the outcome of encounters, we used the dyads in which both opponents were identified (Table 3). We fitted binomial glms with the number of wins and losses of one member of the dyad toward the other member of the dyad as a response variable. As predictor variables, we entered the differences in throat patch sizes, tarsus lengths, wing lengths and body weights between the opponents in these models. Each dyad was considered only once; male-male dyads, female-female dyads and mixed-sex dyads were analysed separately.

When we analysed log-normally distributed variables (e.g. number of aggressive encounters per unit time), the *glm* family was set to *Gamma* specifying a *log* link (Venables & Ripley 2002). We used the appropriate test statistic according to the model family (the *F*-test when *glm* family was set to *quasibinomial*, and the χ^2 -test when it was set to *binomial* or *Gamma*; Venables & Ripley 2002). We report ANOVA tables with type III sum of squares and unstandardized regression coefficients \pm SEs throughout. Pearson *r* effect sizes were calculated from *t*-statistics of regression coefficients (see equation 11 in Nakagawa & Cuthill 2007).

RESULTS

Aggressive behaviour and dominance relationships

We analysed 217 minutes of recordings of the 51 Sparrows individually identified on the feeder. During this time, we observed 1021 aggressive encounters with an unambiguous outcome, 512 of which were attacks and 509 defences. In the cases of individuals for which both attacks and defences

were registered, attack success and defence success were positively correlated (Spearman rank correlation correlation: $r_s = 0.620$, $P < 0.001$, $n = 40$).

Birds with higher fighting success were involved in more aggressive encounters per unit time ($n = 47$, deviance = 167.270, $F_{1,45} = 32.968$, $P < 0.001$, $\beta = 25.002 \pm 5.725$). This strong positive relationship remained significant when calculating fighting success and the rate of aggressive encounters from independent data (attack success vs. aggressive encounters per unit time during feeding time: $n = 46$, deviance = 68.103, $F_{1,44} = 20.251$, $P < 0.001$, $\beta = 25.678 \pm 7.014$; defence success vs. aggressive encounters per unit time during searching time: $n = 42$, deviance = 79.494, $F_{1,40} = 20.872$, $P < 0.001$, $\beta = 11.277 \pm 2.927$). Birds with higher fighting success were involved in fewer non-aggressive encounters per unit time during the total observation time ($n = 47$, deviance = 89.870, $F_{1,45} = 13.932$, $P < 0.001$, $\beta = -21.707 \pm 6.120$). The proportion of encounters initiated by the focal bird (i.e. the number of attacks compared to the total number of both attacks and defences) did not differ between males and females (males: $54.9 \pm SE: 3.72 \%$; females: $50.4 \pm SE: 3.95 \%$; binomial *glm* for the frequencies of attacks and defences: $n = 36$, $\chi^2_1 = 1.028$, $P = 0.311$, $\beta = -0.137 \pm 0.136$), and was not significantly affected by the measured morphological traits ($n = 44$, $\chi^2_1 < 0.880$, $P > 0.348$, for all traits). Fighting success did not differ significantly between males and females (males: $36.9 \pm SE: 7.86 \%$; females: $17.2 \pm SE: 4.65 \%$; after controlling for the measured morphological traits: $n = 35$, deviance = 8.867, $F_{1,29} = 1.340$, $P = 0.256$).

Out of the aggressive encounters with an unambiguous outcome, we recorded 219 encounters between 149 dyads of 42 known individuals, i.e. where both fighting birds were identified. Only 47 dyads were observed to fight more than once (2 to 4). The outcomes of these repeated fights within dyads were consistent in most cases, i.e. the same individual won each of the multiple fights in 39 out of the 47 dyads (83%). Unfortunately, these observations are far from sufficient to reconstruct the real dominance structure among these 42 individuals, because for many possible dyads there were no recorded encounters (712 out of the possible 861 dyads).

Morphological correlates of fighting success

When analysing all interactions – towards conspecifics of both known and unknown sex – fighting success in males was significantly correlated with wing length, body weight and throat patch size.

Notably, throat patch size was the only trait that was significant without controlling for the other variables ($F_{1,13} = 5.518$, $P = 0.035$; for all other traits without controlling for other variables $F_{1,13} < 0.993$, $P > 0.337$). In males, fighting success correlated positively with throat patch area (Fig. 1a) and correlated negatively with wing length (Fig. 1b) and body weight. In females, however, fighting success was significantly related only to wing length (Table 1), but unlike males, individuals with longer wings had greater fighting success (Fig. 1b).

When analysing only those interactions in which the sex of the opponent was known, a similar pattern was found. When fighting against males, the effect of throat patch area remained the same as in the analyses of all interactions: throat patch size correlated positively with fighting success in males but not in females (i.e. there were significant interactions between throat patch size and sex of focal bird; Table 2 and Fig. 2a). Fighting success did not significantly correlate with wing length in either sex (no wing-length by sex interaction; Table 2, Fig. 2c) and correlated negatively with body weight (no body-weight by sex interaction; Table 2). When fighting against females, in common with the analyses of all interactions, wing length and throat patch area affected fighting success in a sex-specific way (significant trait by sex of focal bird interaction terms in Table 2; Figs. 2b and 2d). However, body weight was not a significant predictor of fighting success against females (Table 2).

Where both members of the dyad were known, the following morphological differences between the two opponents predicted the outcomes of aggressive encounters (Table 3). In male-male dyads, males with greater throat patch size and smaller body weight than their opponents tended to win the encounters more frequently. In female-female dyads, females with the greater wing length tended to win more frequently than their smaller winged opponents (a marginally non-significant effect). Within mixed sex dyads, neither of the morphological traits predicted the outcomes of the encounters. Note, however, that in mixed sex dyads we would expect significant effects only if a trait predicts fighting success similarly in both sexes.

DISCUSSION

In a previous behavioural study, it was suggested that the signalling role of the throat patch in this apparently sexually monochromatic species may differ between the two sexes (Torda *et al.* 2004).

Intersexual differences in the mean and variance of throat patch size also pointed towards this possibility (Mónus *et al.* 2011). Here, we tested this idea further by studying the morphological correlates of aggressive interactions among free-living Tree Sparrows of known sex.

Among the measured morphological traits, throat patch size was a consistent predictor of fighting success of males against both male and female opponents (Table 2): male Sparrows with a larger throat patch won more aggressive encounters against their flock mates than did males with a smaller throat patch. In contrast, throat patch size in females was not a significant predictor of fighting success in any of the analyses. The best predictor of fighting success in females was wing length: females with longer wings won more fights against their opponents.

As fighting success and dominance rank are highly correlated in species foraging in winter flocks of unstable composition (Rohwer & Ewald 1981, Liker & Barta 2001), our correlative results suggest that throat patch size in male Tree Sparrows may function as a status signal, whereas the throat patch size in female Tree Sparrows may lack a status signalling function. Further experimental testing, for example by controlled experiments in an aviary or by using taxidermy models with manipulated traits (Murphy *et al.* 2009b, Crowhurst *et al.* 2012) should be performed in the future in order to more fully test our conclusions. The suggested intersexual differences in the role of throat patch size may explain why Torda *et al.* (2004), investigating Tree Sparrows of unknown sex, found different results in different experimental flocks. Without taking into account the sex-composition of the flocks, they found a positive correlation between dominance and throat patch size in one flock, and found no correlation in the other two. Presumably the flock in which there was a relationship between throat patch size and fighting success consisted mainly of males, while in the two other flocks the sex ratio was more even, or even female skewed.

Our findings are in accord with a study on a Tree Sparrow population in Japan (S. Matsui, pers. comm.), in which a positive correlation between throat patch size and haematocrit value was documented in the case of males but not in females, suggesting that the throat patch of males may signal some aspects of male quality (e.g. oxygen transport ability). Previously, we found that in Tree Sparrows the variance of throat patch size was greater in males than in females, while the variance of other traits did not differ between the sexes (Mónus *et al.* 2011). This finding also supports a possible sexual difference in the function of throat patch size in the Tree Sparrow (Mónus *et al.* 2011), since greater variance in the size of a trait may be expected when the size of the trait functions as a signal (Møller 1991, Delhey & Peters 2008).

Our results are also in accord with those reported in the House Sparrow. Liker and Barta (2001) reported that badge size was the only significant predictor of the dominance rank of males against both sexes, while the dominance rank of females correlated with body weight. We have no information on whether female Tree Sparrows use their throat patch as a signal in a different context, for example toward males in order to signal some aspects of their quality during pair formation. Many signals have been observed to function in multiple contexts (dual utility hypothesis; Berglund *et al.* 1996, Griggio *et al.* 2010). In species with socially monogamous mating systems and biparental care, such as the Tree Sparrow, both males and females may be selected to be choosy and to exhibit quality signals during mate choice (Daunt *et al.* 2003, Griggio *et al.* 2010). Unfortunately, recent studies that have investigated within-pair and extra-pair sexual behaviour in Tree Sparrows have not reported whether there is a relationship between sexual behaviour and throat patch size (Heeb 2001, Cordero *et al.* 2002, Seress *et al.* 2007).

The throat patch in females may be adaptive if it has a function that makes its bearer more successful. However, our results do not support the expected status signalling function of throat patch size in female Tree Sparrows. As an alternative to size, the blackness of the throat patch may have a signalling function (e.g. Catoni *et al.* 2009), which would be worth testing in future studies.

Furthermore, both males and females may benefit by looking similar to the other sex at first sight (a

phenomenon referred as intraspecific sexual mimicry), and may thereby avoid some unnecessary aggression, or may accrue some other social or sexual benefit (Clutton-Brock & Huchard 2013).

However, it seems more reasonable to assume that individuals are capable of easily recognizing the sex of the opponent, since foraging sparrows seem to differentiate among individuals and consider only the throat patch size of males but not of females. Future work is needed to assess the mechanism and reliability of sex recognition in wild Tree Sparrow flocks.

Several studies have demonstrated that mutual ornaments may be used as status signals by both sexes (e.g. Jones & Hunter 1999, Kraaijeveld *et al.* 2004, Alonso-Alvarez *et al.* 2004, Midamegbe *et al.* 2011; reviewed in Kraaijeveld *et al.* 2007, Tobias *et al.* 2012). However, there are few studies that, in common with our work, have found evidence of intersexual differences in status signalling in the case of sexually monomorphic ornaments (reviewed in Murphy *et al.* 2014). We have very limited knowledge on the cause of these intersexual differences, so one can only speculate in order to find reasonable explanations. It may be that females use their ornaments in signalling contexts unrelated to foraging competition, or may signal status with multiple ornaments simultaneously, that other ornaments may supersede the information conveyed by throat patch size, or that the function of the ornamental trait may change over time or space (Tarvin & Murphy 2012, Murphy *et al.* 2014).

Whereas signalling competitive ability seems to be equally profitable for males and for females (Rohwer 1975), our results, although based on observational rather than experimental data and so are only suggestive, raise the intriguing question of what prevents female Tree Sparrow from using the throat patch size as a status signal. Honest signals are thought to involve costs to their bearer, but costs may affect males and females differently (Tibbetts 2014), as also may advantages (Tobias *et al.* 2012). Ornaments in females may be limited more often by the costs to fecundity rather than to survival (Clutton-Brock 2009). Black feather patches are widely thought to be testosterone-regulated (Bókonyi *et al.* 2008; but see McGraw 2008); an elevated level of testosterone, in turn, may negatively affect fecundity in females (Packer *et al.* 1995, Clutton-Brock 2009, Rosvall 2013). Even if females possess black throat patches, using an androgen controlled signal may be too costly for them (but see Eens *et*

al. 2000, Vitousek *et al.* 2013, Pham *et al.* 2014). Alternatively, it may be that female Tree Sparrows lack the pathway which links throat patch size expression and competitive ability. Although testosterone was shown to modulate female aggressiveness in birds (e.g. Zysling *et al.* 2006, Cain & Ketterson 2012), little is known about the physiological mechanisms mediating honest status signalling in females (Ketterson *et al.* 2005, Møller *et al.* 2005, Pham *et al.* 2014).

The reason for the negative correlations of male fighting success with wing length and body mass is not clear. These relationships, however, were not consistent throughout all analyses, and reached significance only after controlling for other morphological traits. Note also that body size is not a good predictor of fighting success in male House Sparrows (Liker & Barta 2001). Given the obviously small variability of male wing length in our sample (Fig. 1b), it is possible that the pattern observed does not reflect a biologically meaningful effect. In the case of body weights controlled for body size and throat patch size, negative relationship with fighting success may arise if more competitive individuals among birds with similarly sized throat patches maintain lower levels of fat reserves. Such strategic body mass regulation has often been observed due to mass-dependent predation (e.g. Krams *et al.* 2010). Alternatively, individuals with relatively lower body weight (i.e. poorer condition) among birds with similarly sized throat patches may be more motivated to compete for food, and hence may forage more aggressively and may win more encounters (e.g. Lendvai *et al.* 2004, Preiszner *et al.* 2015).

In summary, our study suggests that male Tree Sparrows may use their black throat patch as a status signal in free living flocks, whereas female throat patch size is be unrelated to their fighting behaviour. Further work needs to investigate the causes of intersexual differences in the function of monomorphic ornaments, and experimental testing of the function of the black throat patch both in male and female Tree Sparrows may enhance our understanding of the function and evolution of monomorphic ornamental traits.

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Table 1. The effects of the measured morphological traits on the fighting success of Tree Sparrows, shown separately for the two sexes. Results are from binomial generalized linear models.

	<i>df</i>	deviance	<i>P</i> -value of <i>F</i> -test	<i>B</i> ± <i>SE</i>	Effect size (<i>r</i>)
Males (<i>n</i> = 15; number of encounters = 407)					
tarsus length	1	19.041	0.060	1.025 ± 0.496	0.55
wing length	1	33.439	0.019	-0.881 ± 0.344	-0.63
body weight	1	36.925	0.015	-0.925 ± 0.334	-0.66
throat patch area	1	86.402	0.001	9.078 ± 2.390	0.77
residuals	10	42.479			
Females (<i>n</i> = 20; number of encounters = 468)					
tarsus length	1	5.421	0.293	-0.627 ± 0.573	-0.27
wing length	1	34.499	0.015	0.616 ± 0.278	0.50
body weight	1	0.025	0.942	-0.025 ± 0.336	-0.02
throat patch area	1	0.939	0.656	-0.830 ± 1.839	-0.12
residuals	15	68.353			

Table 2. The effects of morphological traits and sex on the fighting success of Tree Sparrows according to the sex of their opponents. Results are from binomial generalized linear models; all non-significant interactions term were omitted ($P > 0.30$ for all omitted terms).

	<i>df</i>	deviance	<i>P</i> -value of <i>F</i> -test	<i>B</i> ± <i>SE</i>	Effect size (<i>r</i>)
Against males					
<i>number of individuals</i> = 25 (12 males, 13 females); <i>number of encounters</i> = 150					
tarsus length	1	2.837	0.162	0.793 ± 0.553	0.32
wing length	1	1.939	0.243	0.243 ± 0.224	0.25
body weight	1	8.481	0.021	-0.803 ± 0.329	-0.50
throat patch area	1	6.149	0.045	4.529 ± 2.226	0.43
SEX _(female)	1	7.960	0.025	6.194 ± 2.617	0.13
SEX _(female) *throat patch area	1	9.044	0.018	-6.929 ± 2.760	-0.51
residuals	18	23.965			
Against females					
<i>number of individuals</i> = 30 (11 males, 19 females); <i>number of encounters</i> = 172					
tarsus length	1	0.014	0.941	-0.050 ± 0.668	-0.02
wing length	1	23.071	0.006	-1.286 ± 0.514	-0.47
body weight	1	0.101	0.842	0.072 ± 0.359	0.04
throat patch area	1	8.216	0.083	7.066 ± 4.333	0.33
SEX _(female)	1	26.920	0.003	-121.11 ± 44.60	-0.50
SEX _(female) *wing length	1	29.877	0.002	1.794 ± 0.637	0.51
SEX _(female) *throat patch area	1	12.047	0.039	-9.095 ± 4.524	-0.39
residuals	22	54.794			

Table 3. The effects of morphological differences between opponents of known sex on the outcomes of aggressive encounters in Tree Sparrows. Results are from binomial generalized linear models (for details see *Statistical Analyses*).

	<i>df</i>	deviance	<i>P</i> -value of <i>F</i> -test	<i>B</i> ± <i>SE</i>	Effect size (<i>r</i>)
Male-male dyads					
<i>number of dyads</i> = 23; <i>number of encounters</i> = 32					
tarsus length ^a	1	2.944	0.101	1.062 ± 0.659	0.35
wing length ^a	1	0.424	0.520	0.269 ± 0.407	0.15
body weight ^a	1	8.902	0.008	-1.246 ± 0.518	-0.49
throat patch area ^a	1	7.466	0.013	5.655 ± 2.476	0.47
residuals	18	17.693			
Mixed sex dyads					
<i>number of dyads</i> = 52; <i>number of encounters</i> = 81					
tarsus length ^a	1	0.000	0.994	-0.004 ± 0.515	-0.00
wing length ^a	1	0.071	0.830	0.034 ± 0.160	0.04
body weight ^a	1	2.574	0.200	-0.439 ± 0.349	-0.22
throat patch area ^a	1	0.327	0.645	-0.727 ± 1.572	-0.08
residuals	47	71.493			
Female-female dyads					
<i>number of dyads</i> = 29; <i>number of encounters</i> = 40					
tarsus length ^a	1	0.472	0.580	-0.465 ± 0.833	-0.11
wing length ^a	1	5.849	0.060	0.535 ± 0.346	0.30
body weight ^a	1	1.187	0.382	0.314 ± 0.367	0.17
throat patch area ^a	1	2.199	0.237	-2.639 ± 2.270	-0.23
residuals	24	35.912			

^a – Differences in the trait between fighting opponents

Figure legends

Fig. 1. Fighting success of free-living Tree Sparrow males ($n = 15$) and females ($n = 20$) in relation to a) area of their throat patch and b) wing length. Lines are predicted regression lines from generalized linear models after controlling for the measured morphological traits.

Fig. 2. Fighting success of free-living Tree Sparrows against male (a, c) and female (b, d) opponents in relation to (a, b) the area of their throat patch and (c, d) the wing length. Lines are predicted regression lines from generalized linear models after controlling for the measured morphological traits.





