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FITNESS MEASURES IN FEMALE HOUSE SPARROWS: NO CORRELATION WITH THE EXPRESSION OF TWO PLUMAGE ORNAMENTS

ABSTRACT

Male birds often possess conspicuous or colourful plumage traits which are thought to function either in mate choice or as status signals which indicate their competitive ability. Many studies have confirmed that the size or expression of these traits is positively correlated with their success at attracting mates, their social dominance, or their fitness. However, relatively few studies have examined plumage variation in females, likely because it is much less pronounced than in males. We examined whether female plumage is associated with fitness measures in the house sparrow (*Passer domesticus*). Male house sparrows have a conspicuous throat patch of black feathers that has been correlated with social dominance and fitness, and females also possess a variably-coloured throat patch, although the variation is much more subtle than in males. However, neither the timing of breeding nor reproductive performance was associated with throat patch colouration of female sparrows in any of three continuous study years, nor was it related to female age. The size of the other obvious female plumage trait, the wing bar, also did not predict fitness. We conclude that female plumage variation is not under sexual selection in the house sparrow.

Keywords: Female, house sparrow, plumage, status signal, fitness

INTRODUCTION

In many bird species, males display a range of colourful or contrasting plumage traits (Hill and McGraw 2006). These characters are thought to have evolved through female choice, where females prefer to mate with males displaying larger or more elaborate traits because this indicates that they are of superior genetic or physiological quality (Andersson 1994). Alternatively, the traits may have evolved as 'status signals', which indicate their bearer's competitive ability in social interactions over food or other resources (Rohwer 1975, Searcy and Nowicki 2005).

Although many studies have found positive correlations between the expression of male plumage traits and fitness measures (Searcy and Nowicki 2005) relatively few

such studies have been performed in females (though for notable exceptions see Hill 1993, Siefferman and Hill 2005, and also the review by Amundsen and Pärn 2006). This is probably because female birds usually display little, if any, plumage variation (Amundsen 2000), but may also reflect the traditional portrayal of mate choice as a unidirectional process.

While females are expected to maximize their reproductive success by mating with the highest quality males (Andersson 1994), males should also be under selection to mate with the highest quality females (Amundsen and Pärn 2006). High-quality females could initiate egg production earlier in a season, produce a greater number of clutches per season, lay larger clutches containing eggs with more resources, and provide better parental care to offspring. Moreover, males would also benefit by pairing with older females since in several bird species these outperform females that are in their first breeding season (Sæther 1990, Hatch and Westneat 2007). This suggests that females would benefit by possessing plumage signals that advertise their quality or age to potential mates as well as their competitive ability to other females.

We tested whether females exhibit plumage signals of quality or age in the house sparrow (*Passer domesticus*), a small (ca. 25g), sexually dimorphic passerine common around urban and suburban areas throughout most of the world (Anderson 2006). Male house sparrows possess a suite of colorful traits including a conspicuous 'bib' of black feathers which extends across their throat and upper breast (Anderson 2006). Studies of both free-living and captive sparrows have consistently found that males with large bibs are dominant over those with small bibs, and also over females (see Nakagawa et al. 2007 for a meta-analysis). The male wing bar may also be a status signal, since wing bar conspicuousness was positively correlated with dominance rank in captive house sparrows (Bókonyi et al. 2006).

Female house sparrows also show variation in the appearance of their throat plumage (IRK Stewart, personal observation). Some females have a distinct pale throat while some have a distinct dark throat which occasionally contains a small patch of melanistic feathers similar to those which comprise the male bib. Others have an indistinct brown throat which is the same color as the adjacent upper breast and neck sides (see Figure 1). We first hypothesized that throat color variation among females was related to their age, based on the observation that juvenile female house sparrows have a pale or even white throat while that of juvenile males is dusky (Anderson 2006). We predicted that juvenile females retain this pale throat during their first moult such that adult females with pale throats were in their first breeding year, while those with brown or dark throats were in at least their second breeding year. We then hypothesized that throat colouration of females is a comparable trait to bib size in males and acts as an indicator of social dominance or individual quality. Females with dark throats would thus be the equivalent of males with large black bibs, and so we predicted that females with dark throats would begin breeding earlier and have higher seasonal fitness than females with brown throats, who would in turn outperform females with

pale throats. Finally, we hypothesized that wing bars in females also function as status signals and predicted that females with larger wing bars would be socially dominant over those with small wing bars, and thus would acquire a mate and begin breeding earlier in the season.

MATERIALS AND METHODS

We collected morphological and reproductive data from female house sparrows during three successive breeding seasons (2007-2009) at a nest box colony located at the University of Kentucky's Agricultural Experiment Research Station. The study site is an approximately 5 km² area of horse pasture with mixed crops on the outskirts of Lexington, Kentucky, USA (38° 06' N, 84° 29' W). 50 nest boxes were erected on the sides of four barns used for storage and temporary housing of livestock.

Adult house sparrows were captured throughout each breeding season and the intervening winters using seed-baited cage traps, mist-nets and nest-box traps, and each bird was fitted with a metal leg band (United States Geological Service) and a unique combination of three coloured plastic leg bands for individual identification. Some of the adults had been banded at the study site in previous years as nestlings, juveniles or adults and so their exact age was known, although most individuals were unbanded when first captured so their age was unknown.

All captured females were placed flat on their back against a piece of white paper with their bill facing forward (see Figure 1) then their head and upper breast was photographed from a distance of about 10 cm using the automatic setting of a digital camera (Canon Powershot A540). All photographs were taken in the same room of an office building at the field site and under the same lighting conditions. The photographs were later imported into a computer and enlarged, then used to place females into one of the following three categories based on their throat colouration: 1) pale throat (a distinct throat, noticeably paler than the upper breast feathers), 2) brown throat (throat indistinct, the same colour as the upper breast feathers) and 3) dark throat (Type I: a distinct dark throat, noticeably darker than the upper breast feathers, and Type II: a brown throat containing a small patch of black feathers, see Figure 1). We assessed the repeatability of throat colour categorization by randomly selecting 10 females from each year then rescoring their photographs without knowledge of their previous score. 26 of the 30 rescored females were placed into the same throat colour category. Of the four mismatches, three were first scored as pale-throated but later scored as brown-throated, and one was first scored as dark-throated but later scored as brown-throated. Hence our categorization of throat colouration was not perfectly repeatable but we decided that it was sufficiently robust to be useful and proceeded with the analyses. Most of the females that we scored ($n = 125$) were captured during the breeding season (1 March – 31 August) although some ($n = 34$) had been caught outside this period (10 October – 28 Feb). This could introduce a bias if the appearance

of throat feathers changes according to how recently they were produced, perhaps because of abrasion or accumulated dirt. However, the proportion of females in each throat color category did not differ between those caught during the breeding season and those caught outside of it ($\chi^2 = 4.61$, $df = 2$, $P = 0.10$) and so they were pooled for the analysis. Note that none of the birds were in the process of moulting when they were scored and all photographs were scored by the same observer (IRKS).

In house sparrows, both sexes have a wing bar formed by 7-8 median secondary covert feathers. The wing bar feathers have a dark base, which is mostly hidden by feathers which overlap it from above, and a pale tip (Figure 2). One researcher (IRKS) measured the length of the pale tip of the second wing bar feather of both males and females using calipers. Data taken from birds recaptured within a moult year showed that wing bar length measurements were repeatable for both males ($r = 0.66$, $F_{21,22} = 4.98$, $P < 0.01$) and females ($r = 0.44$, $F_{20,23} = 2.59$, $P = 0.015$) (Lessells and Boag 1987).

Reproductive data for each female was gathered starting in mid-March of each year. Nest boxes were checked every three days to determine the date on which the first clutch of the year was initiated, and then checked every two or three days until either the nest attempt failed or the nestlings were banded (10 days after hatching). House sparrows at our site are multi-brooded, so the monitoring process was continued until the end of the breeding season (mid-August). Females were assigned to a particular nest box if they were repeatedly observed entering it or standing on or beside it. In a small number of cases, the identity of females which had produced successful clutches but were either unbanded or unidentified was later ascertained in the laboratory by comparing the genotypes of the resulting offspring at three or more microsatellite loci against the genotype of the female known to have laid the subsequent clutch in the same nest because she was captured and banded later in the season (see Stewart et al. 2006 for methods). We compared fitness measures of females of different throat colour categories using ANOVA if the data were parametric and a Kruskal-Wallis test if they were not. We tested whether the frequency distribution of females of the different throat colour categories deviated from randomness using a Fisher's exact test.

RESULTS

Throat coloration

Clutch initiation date did not vary with throat colour in any of the three study years ($F_{2,26} = 0.19$, $P = 0.83$ in 2007; Kruskal-Wallis $H = 1.78$, $df = 2$, $P = 0.41$ in 2008; Kruskal-Wallis $H = 3.35$, $df = 2$, $P = 0.19$ in 2009, see Table 1). Seasonal reproductive success did not vary with throat colour in any of the three study years ($F_{2,26} = 0.18$, $P = 0.84$ in 2007; $F_{2,38} = 1.61$, $P = 0.21$ in 2008; $F_{2,20} = 0.19$, $P = 0.83$ in 2009, see Table 1).

When pooling data from all three years, we had throat colour scores from 31 females known to be in their first breeding season based on their banding history. Of

Table 1. Variation in two indices of reproductive performance in relation to throat colouration of female house sparrows in Kentucky a) Julian first egg date b) Seasonal reproductive success (total number of fledglings produced per year). Each cell contains the mean \pm standard error and the sample size in parentheses

a)

Year	Pale Throat	Brown Throat	Dark Throat
2007	112.8 + 16.7 (6)	122.1 + 6.9 (13)	123.5 + 13.4 (10)
2008	109.3 + 3.0 (17)	108.3 + 3.2 (12)	104.0 + 1.9 (12)
2009	113.0 + 9.6 (12)	111.3 + 3.3 (7)	121.8 + 8.1 (4)

b)

Year	Pale Throat	Brown Throat	Dark Throat
2007	7.2 + 2.0 (6)	6.4 + 1.1 (13)	7.4 + 1.4 (10)
2008	4.8 + 0.9 (17)	7.0 + 1.1 (12)	7.1 + 1.4 (12)
2009	7.0 + 0.8 (12)	6.9 + 1.1 (7)	6.0 + 1.2 (4)

these 31 first-year females, 19 had dark throats, 11 had brown throats, and 10 had pale throats (Fisher's exact test $P = 0.51$). We also had throat colour scores from 33 females known to be in at least their second breeding season based on their banding history. Of these 33 older birds, 12 had dark throats, 11 had brown throats and 10 had pale throats (Fisher's exact test $P = 0.95$). We had throat colour scores from 19 females who had been captured and photographed in more than one breeding season. 11 of these females remained in the same throat colour category while the remaining 8 were placed in a different category (Table 2).

Table 2. Throat colouration category of 19 female house sparrows examined in more than one breeding season in Kentucky

		Season 2		
		Pale	Brown	Dark
Season 1	Pale	3	0	2
	Brown	4	5	1
	Dark	1	0	3

Wing bar length

Female wing bar length was not correlated with clutch initiation date in any of the three study years ($r = 0.16$, $n = 25$, $P = 0.44$ in 2007; $r_s = 0.00$, $n = 40$, $P = 0.98$ in 2008; $r_s = -0.17$, $n = 22$, $P = 0.46$ in 2009). Female wing bar length did not change between seasons (Paired $t = 0.67$, $df = 29$, $P = 0.51$) and was significantly repeatable across years within females ($r = 0.40$, $F_{28,32} = 2.26$, $P = 0.014$). However, male wing bar length increased significantly between breeding seasons (Paired $t = 3.1$, $df = 41$, $P = 0.003$). Males had significantly larger wing bars than females ($t = 11.9$, $df = 169$, $P < 0.001$).

males 4.16 ± 0.90 (SD) $n = 108$, females = 2.63 ± 0.64 (SD) $n = 63$, using measurements obtained the first time an individual was captured).

DISCUSSION

Male house sparrows possess a bib of melanin-infused feathers on their throat and upper breast, the size of which is positively correlated with social dominance, and in some populations, with seasonal reproductive success and age (Nakagawa et al. 2007). Males also possess a white wing bar, the conspicuousness of which is positively related to social dominance (Bókony et al. 2006). We tested whether variation in the expression of the two comparable plumage traits present in female house sparrows, throat colouration and wing bar size, was similarly correlated with their fitness or age. We found that neither throat colouration nor wing bar size of females was related to their reproductive success or timing of breeding in any of the three study years and there was no evidence that either trait was related to their age.

We first analyzed female throat colouration with respect to first egg date after predicting that dark-throated females were socially dominant over other females and would therefore start breeding earlier. This could be because they had greater access to food during the previous winter and thus attained breeding condition sooner, or because they were better at acquiring a nest box and then defending it against other females. However, first egg date did not vary with throat colouration in any of the three study years, suggesting that either female throat colour is not related to social dominance, or that social dominance during the previous winter does not influence timing of breeding.

We found that throat colouration was not a fixed trait, since almost half of the females assessed in more than one year had a different throat colour in each. These data are consistent with throat colouration being condition-dependent rather than genetically determined. The factors that influence throat coloration in female house sparrows might be the same as those that affect it in males. Bib size in male house sparrows does not appear to have a nutritional component (though see Stewart and Westneat (2010) for a negative effect of dietary calcium) but is positively related to circulating testosterone level (Gonzalez et al. 2001, Laucht et al. 2011) and can be increased by testosterone supplements provided during molt (e.g., Buchanan et al. 2003) or in the yolk (Strasser and Schwabl 2004). Testosterone might therefore influence the throat colouration of female house sparrows as well as males. There is evidence for a similar relationship in female Button Quail (*Turnix suscitator*), where the size and colouration of the dark throat patch was positively related to circulating testosterone levels. At least one phenotypic trait of female house sparrows is sensitive to testosterone, since females injected with this hormone develop black bills (Pfeiffer and Kirschbaum 1941).

Although our study failed to find any association between female throat colouration and fitness indices we believe the significance of throat colouration variation among

females deserves further study. First, aviary experiments could examine the outcome of female dominance interactions in relation to their throat colour, and could assess these interactions during contests over food during the winter and also over nesting sites during spring. We predict that dark-throated females are dominant over brown-throated females, which in turn are dominant over pale-throated females. Second, females could be given testosterone implants during their annual autumnal moult to test whether females with higher testosterone levels are more likely to develop dark throats. Strasser and Schwabl (2004) injected house sparrow eggs with testosterone and found that the females which hatched from these eggs did not develop male-like bibs, although they did not assess the subtle variation described in the current study. Third, female throat colouration could be measured using more sophisticated methods such as a spectrometer and thus analyzed as a continuous variable using more powerful statistics. Finally, mate choice experiments could assess whether male house sparrows prefer to display in front of dark-throated females. In the rock sparrow (*Petronia petronia*) for example, both sexes strongly resemble the female house sparrow but possess a small yellow carotenoid-based patch at the base of their throat (Griggio et al. 2005) in the same place where Type II dark-throated female house sparrows develop their patch of black feathers (Figure 1d). Griggio et al. (2005) found that male rock sparrows preferred females with larger throat patches.

Wing bar size was not correlated with first egg date, suggesting that either the size of a female's wing bar was not related to their social dominance during the previous winter, or that timing of laying is not influenced by the outcome of winter time dominance interactions. The size and growth of wing bars showed a clear difference between the sexes, with wing bars being larger in males than females (see Bókony et al. 2008 for the same result), and increasing with age in males (as was also found by Laucht and Dale 2012) but not in females. The outward appearance of the wing bars also differs between the sexes. In males, the distal tip of the wing bar feather is bright white (Figure 2b), except during the autumn when the recently molted feathers have a brown tinge, and the base of the feather is very dark brown, such that the contrast between the base and the tip is striking (Bókony et al. 2006). By contrast, female wing bar feathers show much less contrast between their base and tip (Figure 2a) and remain brownish throughout the year, which further suggests that female wing bars do not function as signals.

In sum, we examined whether variation in the expression of two plumage traits found in female house sparrows covaries with fitness, since fitness is positively correlated with the expression of comparable traits in male house sparrows. We did not find that the traits were correlated with proxy or actual measures of female fitness. However, we maintain that subtle female traits such as those examined here are likely more widespread than currently believed and that indices of female morphology or quality should be considered alongside those of males in studies of reproductive success.

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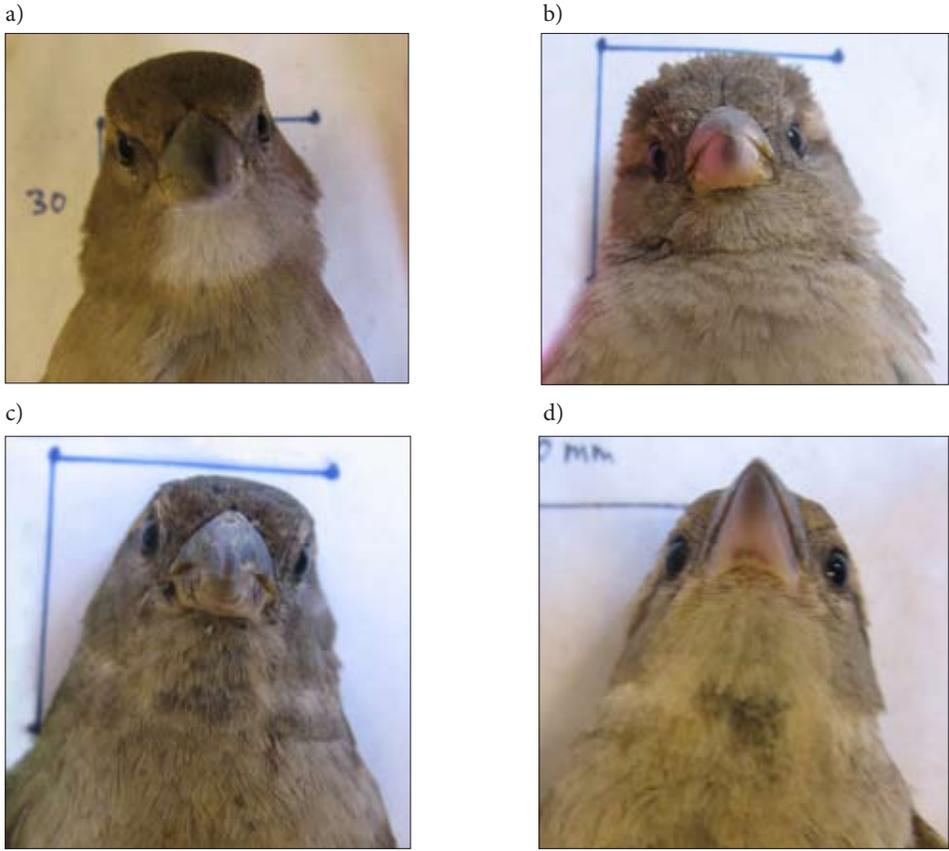


Fig. 1. Categories of throat color variation among female house sparrows in Kentucky a) Pale throat b) Brown throat c) Dark throat Type 1 – all throat dark d) Dark throat Type 2 – throat exhibits a distinct patch of very dark feathers

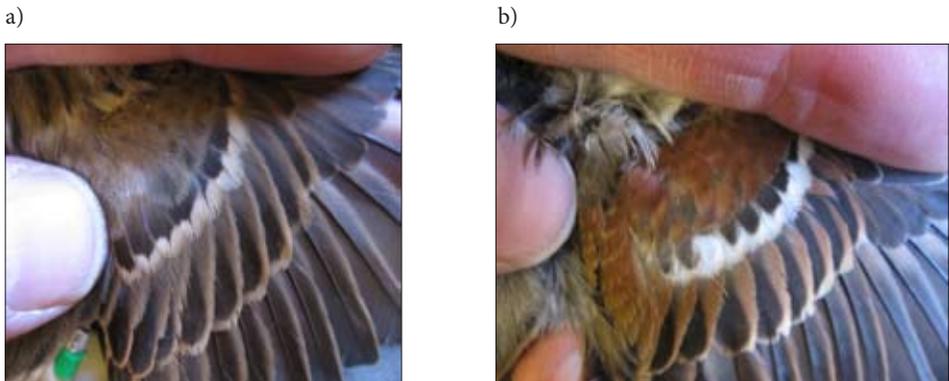


Fig. 2. The upper surface of the wing of a) a female house sparrow and b) a male house sparrow held open to display the wing bar