Co-evolution of plumage characteristics and winter sociality in New and Old World sparrows

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Abstract

Understanding the evolution of phenotypic diversity, including the stunning array of avian plumage characters, is a central goal of evolutionary biology. Here, we applied a comparative analysis to test factors associated with the origin and maintenance of black chest and throat patches, which in some taxa are referred to as 'badges-of-status'. Specifically, we tested whether the evolution of black colour patches in Old and New World sparrows is consistent with a signalling function during the nonbreeding season or breeding season. We found no positive associations between patch evolution and polygyny or summer sociality. Instead, patch evolution is significantly associated with sociality during the nonbreeding season. Additionally, unlike typical plumage characteristics under sexual selection, these patches are visible throughout the nonbreeding season. Further, the pattern of patch dimorphism uncovered in this study does not match expectations for a trait that evolved in a reproductive context. In particular, patch dimorphism is not associated with polygyny or the presence of extra-pair mating although other types of plumage dimorphism are strongly associated with nonmonogamous mating systems. Overall, patterns of patch evolution suggest that they are more strongly associated with social competition during the nonbreeding season than sexual competition during the breeding season. These results clarify why some previous work has uncovered puzzling relationships between black plumage patches and reproductive behaviour. We discuss these findings in the context of signal theory and previous work on badges-of-status.

Introduction

The remarkable diversity of animal colouration has produced interest in the selective pressures that underlie this variation. Avian colouration is particularly variable and multiple studies have found that sexual selection has played an important role in plumage evolution (Andersson & Simmons, 2006; Price *et al.*, 2007). Although sexual selection is a key factor in the evolution of many avian plumage ornaments (Safran *et al.*, 2005; Tarof *et al.*, 2005), the evolution of these traits for communication in nonreproductive contexts is another possible explanation. One of the more controversial plumage traits is the black chest and throat patches found in Old and New World sparrows (Families Paridae and Emberizidae, respectively) that have been termed 'badges-of-status' (Rohwer, 1975; Senar, 2006). In the context of this study, we adopt the neutral terminology 'patch', rather than 'badge-of-status' to refer to these traits, removing the assumption that these traits are status- or quality-related signals.

The function of patches has been a source of controversy since they were first described by Rohwer in the 1970s. For example, Rohwer hypothesized that the black chest patches in Harris sparrows (*Zonotrichia querula*) were signals of competitive ability used to settle minor dominance contests in wintering flocks (Rohwer,

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1975). Similar black ventral plumage patches are prominent in other Old and New World sparrow taxa (Fig. 1). Research on the signal value of patches and the contexts in which they are used has been ambiguous, with evidence that these traits may play a role in dominance (Rohwer, 1975), territoriality (Veiga, 1993), or mate selection (Møller, 1988, 1990; reviewed in Senar, 2006).

The prevalence of melanin-based ventral patches in the Old and New World sparrow clades suggests that they have an important role in avian behaviour, even though their precise function remains uncertain. Thus far, most

Fig. 1 Photo montage of New and Old World sparrow species, illustrating traditional, throat patches and nontraditional cap and crown patches. (a) *Junco phaeonotus*, (b) *Spizella passerina*, (c) *Emberiza elegans*, (d) *Passer domesticus*, (e) *Amphisopza bilineata*, (f) *Passer melanurus*, (g) *Zonotrichia leucophrys* and (h) *Emberiza cirlus*. Nontraditional patch (g); traditional patch (c–f, h); no badge (a, b). (a) © Jeff Mitton, (b–h) no copyright.

Table 1 Predicted patterns of trait evolution according to functions during nonbreeding and breeding contexts. Our results are indicated in boldface.

	Predicted patterns	
	If function primarily in a reproductive context	If function primarily in a nonreproductive context
Association between patch and nonreproductive context?	No	**Yes**
Patch and reproductive context?	Yes	**No**
Association between patch and social and genetic mating system?	Yes	**No**
Dimorphism in patch?	**Yes**	No

research has focused on the current function of these patches. Here, we study the patches from a different perspective by using a comparative approach to assess the behavioural characteristics that are associated with the origin and maintenance of these traits. We test whether the pattern of evolution in patches suggest that these traits have been more strongly associated with intra- or inter-sexual competition during the breeding season or aggressive competition for limiting resources during the nonbreeding season. Table 1 outlines the predictions for each hypothesis. Specifically, we test whether the evolution of black chest and throat patches in the sparrows is associated with key predictors of signal function in breeding and nonbreeding contexts: summer sociality, winter sociality, polygyny and sexual dimorphism. A consistent co-evolutionary association between patches and winter sociality suggests the patches may be involved in interactions during the nonbreeding season, whereas a consistent co-evolutionary association between patches and summer sociality, sexual dimorphism, and/or polygyny suggests that these traits may have evolved in a reproductive context.

Methods

We used the Old and New World sparrow topologies portrayed in the oscine passerine supertree published by Jonsson & Fjeldsa (2006) because it is the most recent and comprehensive phylogeny of the New and Old World sparrows. Although it does not contain all of the recognized taxa in the Old and New World sparrow clades, it combines the most recent systematic relationships published for the Passeridae and Emberizidae avian families, including a recent phylogeny for the Old World sparrows (Allende *et al.*, 2001). Because we use topology alone, and not branch lengths, our inferences are conservatively limited to evolutionary relationships and not time since divergence.

To score visual characters for this analysis (see Table 2), we consulted avian collections in the Museum of Natural History at the University of Colorado and the Museum of Natural History at the University of Michigan. We visually analysed 30 species in the museum collections. In all cases, the museum data were concordant with data collected from published images. As such,

and to be consistent, we scored plumage phenotypes using published photographs or illustrations from taxonomic monographs (e.g. Clement *et al.*, 1993; Byers *et al.*, 1995). To collect data on sociality and mating systems, we consulted the primary literature, when available, and published natural history accounts (e.g. the Birds of North America) and taxonomic monographs (e.g. Summer-Smith, 1988; Clement *et al.*, 1993; Cramp & Perrins, 1994; Byers *et al.*, 1995). We used published evidence of social polygyny as indicative of the presence or absence of a nonmonogamous social mating system. If polygyny was observed, we categorized the species as 'occasionally polygynous'. We analysed associations between plumage-based traits and genetic measures of paternity, where available. Sexual dimorphism was assessed using only plumage-based characteristics. Definitions of these traits and how they were analysed are indicated in Table 2. Citations are in the Supporting Information (Appendix S1). Throughout, we use the term 'patch' to indicate patches of colour on the breast and throat; when we refer to other patches (e.g. crown and cap), we mention this explicitly.

We analysed the data using the concentrated changes test (CCT) to control for possible similarities among closely related species due to common ancestry. CCT is a common analytical methodology used to find associations between discrete characters, taking evolutionary relationships on a phylogenetic tree into consideration (e.g. Maddison, 1990; Lorch & Eadie, 1999; Tibbetts, 2004; Rubenstein & Lovette, 2007). CCT tests whether changes in badge characteristics (y; dependent variable) are significantly associated with sociality either in a breeding or nonbreeding context (x; dependent variable) by assessing whether gains and losses of badges are equally likely on every branch or whether they are significantly associated with particular behaviours. For example, the CCT tests whether sociality corresponds with the evolution of badges (if gains of patches are associated with sociality) and/or the maintenance of the patch (if losses of patches are associated nonsociality).

The number of gains and losses of patches was estimated by MESQUITE (v. 1.12, http://mesquiteproject.org), using the most parsimonious reconstruction of character evolution (Fig. 2). The CCT was run in

Table 2 Definitions of binary characters used in analyses.

Description of binary characters	Definition
Patch present?	We indicated that a patch was present in species with large black patches of colour on the crown, throat, or breast. Black breast colour is traditionally studied, so we refer to breast patches as 'traditional' patches. In a subset of analyses, we explore the possible relationship between black patches of colour in the crown and throat and refer to cap/crown patches as 'nontraditional' patches
Breast patch only present?	We indicated that a breast patch was present only in species with large, black patches of colour on the throat and breast regions
Patch present year-round?	Because most species moult their contour feathers once per year, we indicated whether or not the patch was present year-round (winter and summer) or just summer. A 'no' always indicates that the patch is only visible in the summer and not visible during the winter
Social during the nonbreeding season?	We recorded a species as social during the nonbreeding season if there was evidence of flocking or loose flocking behaviour of conspecifics
Social during the breeding season?	We recorded a species as social during the breeding season if we found evidence of group breeding ($\geq$ two pairs or more breeding in close spatial proximity)
Evidence of social polygyny	We recorded a species as polygynous if we found information related to nonmonogamous social mating systems. As such, a species is recorded as being polygynous if we found evidence of any polygyny in social mate choice
Evidence of extra-pair mating	We recorded the presence or absence of extra-pair mating using published genetic analyses of paternity
Dimorphic?	We characterized a species as sexually dimorphic if there was available visual and quantitative data on sex differences in plumage. Dimorphism was not contingent on sex differences in the patch trait alone, as nonbreast, throat, and head patch characteristics such as wing bars, crown stripes, and other aspects of plumage were also considered

MESQUITE using 10 000 replicate simulations with the ancestral state unspecified and actual changes only considered (e.g. Rubenstein & Lovette, 2007). The Pagel 94 algorithm in Mesquite analyses differences in the likelihood of independent vs. correlated models of evolution where P-values below 0.05 indicate a significant association between traits of interest. Accordingly, large differences between the likelihood of independent and correlated patterns of evolution (reported as 'differences in likelihoods' in our results) reject the null hypothesis of the independent association of two binary traits. Below, we report both the P-value associated with each analysis and the differences in the likelihoods of independent and correlated models of evolution.

Results

Patch evolution and sociality

Patch evolution is significantly associated with winter sociality (Fig. 3). The probability that the observed association between winter sociality (x) and patches (y) would occur by random chance was $P < 0.001$, difference in likelihoods = 8.47). The results are similar after broadening our definition of patches to include patches on the cap and crown (see Table 2, for definitions of characters and Fig. 1 for pictures) such as the wide black crown stripes found in white-crowned sparrows ($P < 0.001$, difference in likelihoods = 11.52).

With the exception of one species, taxa exhibit plumage patches year-round. In the snowfinch, *Montifringilla nivalis*, males express a black breast patch during the

summer, but this trait is absent during the entire winter (Clement *et al.*, 1993). When this species is excluded from the analysis, the relationship between winter sociality and black breast patches remains significant ($P < 0.001$, difference in likelihoods = 8.20). Further, house sparrows *Passer domesticus* have an unusual moult pattern of their black breast patches because these plumages are coated by grey tips when they are first developed; these tips wear throughout the winter and spring to reveal their underlying black contour feathers. Although patches are often visible in house sparrows year-round, this trait grows larger between winter and spring. As such, we estimated the effect of this taxon by removing it from our analysis of patch presence and nonbreeding sociality. The results to be similar both with (see above) and without this species ($P < 0.001$, difference in likelihoods = 7.60), implying that the unusual moult pattern of house sparrow patches does not significantly affect our results.

We found no significant association between summer sociality (x) and patches (y) ($P = 0.20$, difference in likelihoods = 2.80). Similarly, there was no association between summer sociality and patches after including taxa with black cap, crown, and breast patches ($P = 0.43$, difference in likelihoods = 2.01).

Interestingly, summer sociality and winter sociality are not correlated. Some species with summer sociality have winter sociality, but many species with winter sociality are not social during the summer, including most of the Emberizid (New World) sparrows in our data set (Fig. 2) ($y =$ winter sociality, $x =$ summer sociality, $P = 0.15$, difference in likelihoods = 3.03; $y =$ summer sociality,

1 ■ Cap/crown patch
   ■ Chest patch
   □ No patch

2 ■ Winter sociality
   □ No winter sociality

3 ■ Summer sociality
   □ No summer sociality

4 ■ Sexual dimorphism
   □ No sexual dimorphism
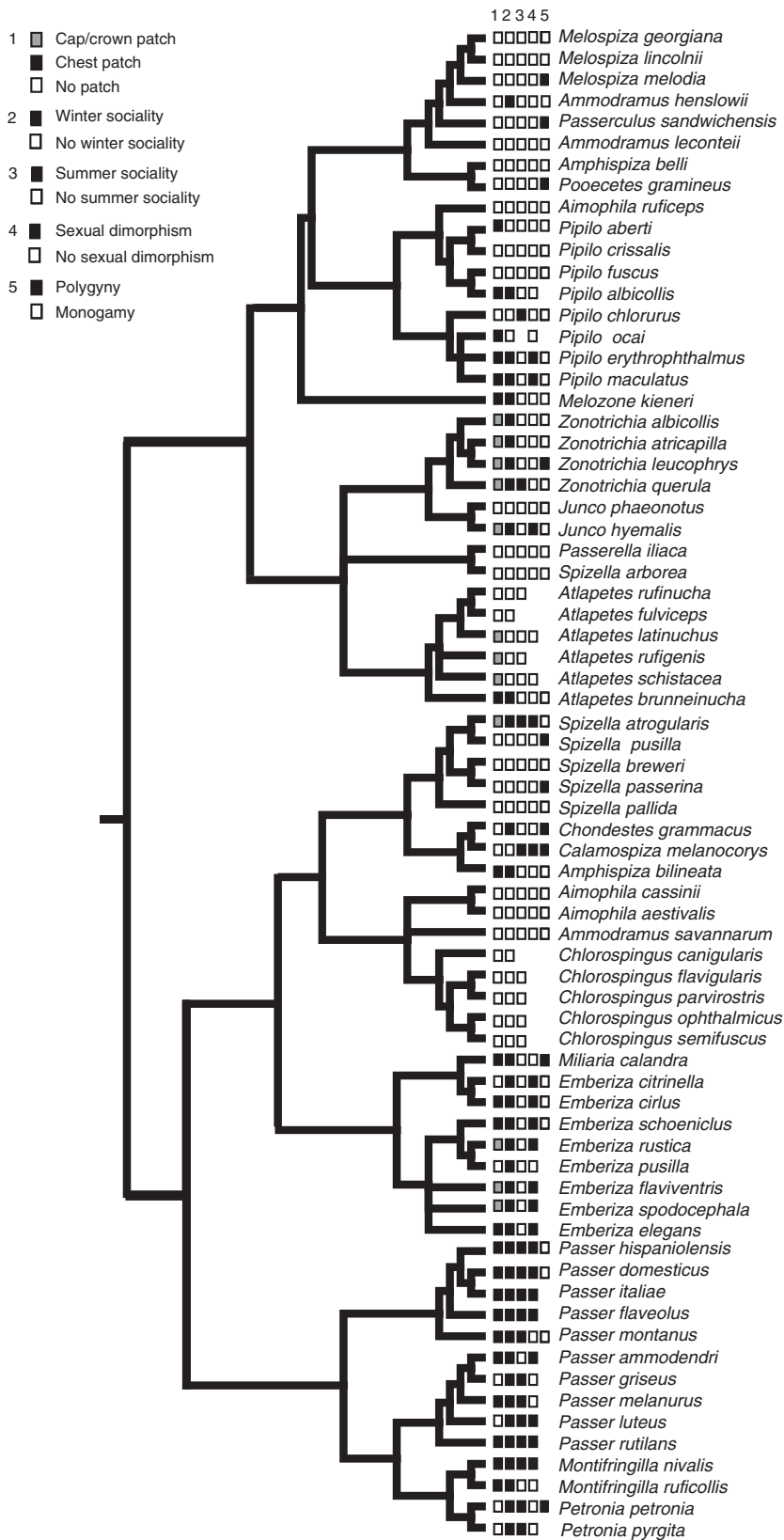
5 ■ Polygyny
   □ Monogamy

Fig. 2 The distribution of behavioural and morphological traits in clades of the Old and New World sparrows. Jonsson & Fjeldsa's (2006) tree is used. All Old World Sparrows are all in the genus *Passer*, *Montifringilla* and *Petronia*. Columns are numbered left to right (1 = black patch, 2 = winter sociality, 3 = summer sociality, 4 = dimorphism, 5 = polygyny). No box indicates that the data were unavailable.
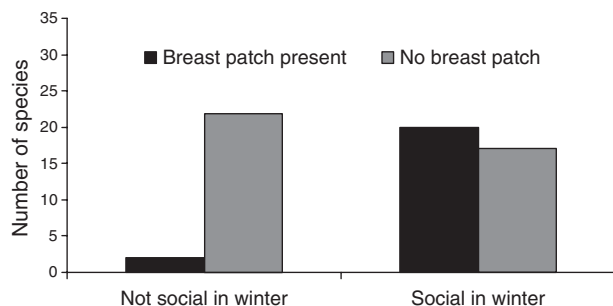
Fig. 3 Number of species with and without breast patches in association with different social systems in the nonbreeding season. Among taxa with breast patches, there is a greater likelihood of an association with winter sociality.

x = winter sociality, $P = 0.13$, difference in likelihoods = 3.20).

Patch evolution and social mating system

There is a significant inverse association between mating system and patch evolution. The probability that the observed association between polygyny (x) and patches (y) would occur by random chance was $P = 0.03$ (difference in likelihoods = 3.26). Interestingly, this significant association between patch and mating system is generated by the pattern that only one of the taxa with patches in our data set are polygynous (see Fig. 4). There was no association between polygyny and patches of colour when cap and crown badges are grouped with breast patches ($P = 0.09$, difference in likelihoods = 2.97).

Patch evolution and sexual dimorphism

We found a significant association between sexual dimorphism (in all plumage-based characteristics) and the presence/absence of patches ($P < 0.01$, difference in likelihoods = 5.73, Fig. 5). When considering only species *with* breast patches separately, they are as likely to be sexually dimorphic as they are monomorphic (Fig. 5). The
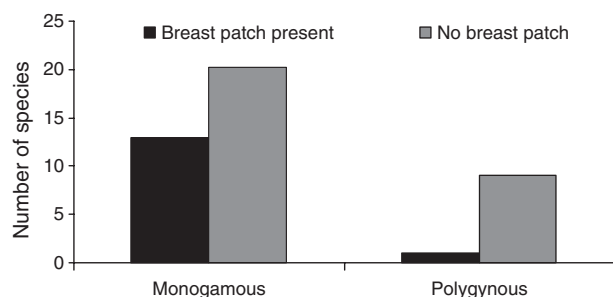

Fig. 4 Number of species with and without breast patches in association with polygynous and monogamous mating systems. Only one species in our study with a breast patch has a socially monogamous mating system.

relationship between sexual dimorphism and patch evolution is similar after including cap and crown patches in the analysis ($P < 0.01$, difference in likelihoods = 6.60).

Sexual dimorphism and mating system

The significant relationship between sexual dimorphism and patches initially suggests that these traits could be associated with a function during the breeding season (e.g. are under sexual selection). If the sexual dimorphism is consequence of sexual selection, polygynous species are expected to be more sexually dimorphic than monogamous species. In fact, contrary to predictions of a trait that is important in a breeding context, there is no association between dimorphism and polygyny across the taxa in our data set ($P = 0.20$, difference in likelihoods = 2.06). There is also no relationship between dimorphism and polygyny within species with cap, crown, or breast patches ($P = 0.24$, difference in likelihoods = 0.92). Remarkably, all species except for one with sexually dimorphic black breast patches are socially monogamous (shown in Fig. 5), suggesting that this type of dimorphism is unlikely to be associated with sexual selection. Overall, dimorphism in black breast patches is unrelated to mating system and unlikely to be a result of sexual selection. In contrast, within taxa lacking black patches, for example *Melospiza melodia*, the relationship between dimorphism and polygyny is highly significant ($P < 0.001$, difference in likelihoods = 9.06). Therefore, plumage dimorphism in traits other than patches is significantly associated with mating system and is likely to have evolved as a consequence of sexual selection. These results suggest that black chest, throat, and crown patches have experienced different selective pressures within the sparrows than other types of plumage colour. Specifically, other types of plumage colour dimorphism appear to have evolved as a consequence of sexual selection while dimorphism in black colour patches does not appear to be associated with sexual selection.
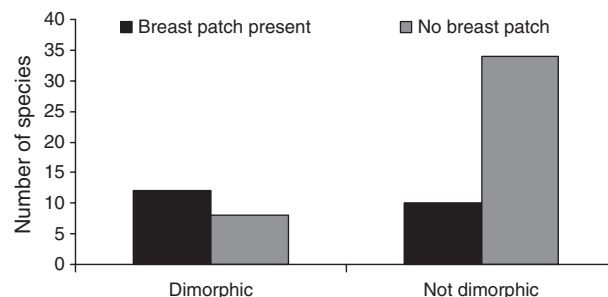

Fig. 5 Number of species with and without breast patches in association with total sexual dimorphism of plumage characteristics. Species with breast patches are equally likely to have sexually dimorphic plumage characteristics as they are to have sexually monomorphic plumage characteristics.

Patch evolution and genetic mating system

We analysed the association between extra-pair mating and colour patches in a smaller subset of taxa (n = 13) for which extra-pair paternity data is available. Although the sample size is small, these results mirror our analyses with social polygyny. We found no association between the presence of extra-pair mating (x) and patches (y; P = 0.16, difference in likelihoods = 1.65) and the presence of extra-pair mating (x) and all black patches (including black throat, crown, and cap patches; P = 0.27, difference in likelihoods = 1.38). The presence of extra-pair mating (x) was not associated with sexual dimorphism (y; P = 0.80, difference in likelihoods = 0). Interestingly, the presence of extra-pair mating was positively associated with dimorphism in taxa without black patches (P = 0.006, difference in likelihoods = 9.18); whereas we found no association between the presence of extra-pair mating and dimorphism when we limited our analysis to taxa with black patches (P = 0.27 difference in likelihoods = 0.42). Because we have quantitative data for the prevalence of extra-pair mating, we also explored relationships between the presence and absence of black patches as a function of % extra-pair paternity (using two-sample T-tests to explore mean differences in paternity for taxa with and without patches). Similarly, these results are concordant with our data on social polygyny (mean % paternity recorded in six taxa with black patches = 34.93, mean % paternity recorded for seven taxa without black patches = 37.96; unequal variance T = −0.234; Satterthwaite d.f. = 10.94, P > 0.81).

Discussion

Black colour patch function in a breeding context

We found no association between the evolution of black ventral patches and social polygyny, or summer sociality, suggesting that reproductive signalling is not a primary factor favouring the evolutionary origin and maintenance of these plumage-based traits (Table 1). Although the data available for exploring genetic mating systems are limited, the genetic data mirror those from our larger data set on social mating systems. Collectively, the results suggest that patches have not evolved solely for communication in a reproductive context. Instead, our results suggest that the melanin-based chest and throat patches of colour, often termed badges-of-status, may be associated with a signalling function in a nonbreeding context.

Although some species in the Old and New World sparrow clades are sexually dimorphic, patch dimorphism does not match the expectations for sexually selected plumage dimorphism. In particular, dimorphism in black chest and throat patches is quite different from other types of plumage dimorphism within the sparrows. First,

in the majority of taxa we studied, the colour patches are visually apparent throughout the whole year. Their year-round expression contrasts with many songbirds whose sexually dimorphic colour is often diminutive or absent during the nonbreeding season (e.g. the seasonal plumage differences in many warblers (Sibley, 2001). Second, our comparative data suggest that different selective pressures underlie plumage dimorphism in black colour patches and other colour-based plumage traits. If dimorphism in patches is primarily a consequence of mate competition, it should be particularly likely to occur in polygynous species. However, there is no relationship between plumage dimorphism and polygyny across all the sparrows and within sparrows with black plumage patches. In fact, only one of the species with black breast patch dimorphism has some polygyny. In contrast, within sparrows lacking black plumage patches, plumage dimorphism is strongly associated with polygyny. Therefore, dimorphism in other plumage traits appears to be associated with the heightened sexual selection of polygyny. Previous comparative studies also suggest that sexual selection has not played a strong role in the evolution of patches, as Badyaev & Hill (2000) found that melanin-based ornaments tend to be less dimorphic that carotenoid-based ornaments. Therefore, our results suggest that dimorphism in black plumage patches may be a consequence of ecological or social selection rather than sexual selection. For example, one potential explanation is that females may lose black colour patches because they are under stronger selection to be cryptic than males, especially during incubation (Slatkin, 1984; Galeotti et al., 2006).

The observation that black colour patches are often sexually dimorphic may be one important reason for the persistent view that their evolution is linked with sexual selection. After all, sexual dimorphism is often a consequence of sexual selection. However, many other selective pressures (Slatkin, 1984), including reduced competition for food between males and females (Temeles et al., 2000) may favour dimorphism. As the results of this comparative study suggest that sexual selection is unlikely to be the prime factor underlying dimorphism in black colour patches, additional studies are important to establish the factors that mediate the evolution of this plumage dimorphism.

Although the role of sexual selection in the evolution of black patches has been an ongoing focus of research, empirical results have been inconsistent. These traits are sometimes referred to as sexually selected traits and some studies have shown that birds with larger black patches have higher reproductive success, better territories, and more extra-pair offspring than individuals with smaller black patches (Møller, 1988, 1990). However, other studies failed to find similar relationships (Stewart et al., 2006; Whitekiller et al., 2000; reviewed in Senar, 2006). Concordant with our results, Nakagawa et al. (2007) used a meta-analysis to synthesize house

sparrow research, finding that house sparrow chest patches are not consistently associated with extra-pair mating success, reproductive success, or territory quality. Although they are not consistently associated with mating success, it is not surprising that some studies have found a correlation between chest patches and aspects of quality typically associated with sexual selection. Aspects of quality are often correlated such that individuals with good agonistic abilities may also be in good physical condition and attractive to females (Berglund *et al.*, 1996; Hunt *et al.*, 2009 but see Qvarnström & Forsgren, 1998). Overall, data on the evolutionary history and current function of patches suggest that these plumage traits have not evolved as a consequence of mate competition during the breeding season.

Black colour patch function in a nonbreeding context

Our results suggest that the evolution of black plumage patches is significantly associated with sociality during the nonbreeding season. Species that form social winter flocks were more likely to gain and less likely to lose these colour patches than species that do not flock during the winter. Therefore, nonbreeding sociality is likely to be a key selective pressure associated with the evolution and maintenance of these plumage traits.

The significant association between black plumage patches and nonbreeding sociality is unlikely to be a product of mate selection during the winter. In both clades of sparrows, there is little room for sexual selection to occur in a nonbreeding context, as it does in waterfowl (Sibley, 2001). Sparrow pair formation typically occurs immediately before the breeding season rather than during the winter (Griggio *et al.*, 2005). In at least one well-studied species, males and females actually spend the winter in different habitats, leaving little opportunity for mate-selection activities before arrival to breeding grounds (Ketterson & Nolan, 1976).

The importance of winter sociality in patch evolution matches Rohwer's (1975) original concept of badges as signals of agonistic ability used during minor dominance contests within flocks. Empirical research on the melanin patches throughout the sparrows generally supports the role of these traits in agonistic competition. In many of the taxa included in this comparative study, black colour patches are correlated with the dominance and/or body size of their bearer (corn bunting *Miliaria calandra*, Maynard-Smith & Harper, 1988; house sparrow *Passer domesticus*, Maynard-Smith & Harper, 1988; siskin *Carduelis pinus*, Senar *et al.*, 1993; *Junco hyemalis*, Balph *et al.*, 1979; harris sparrow *Zonotrichia querula*, Watt, 1986). Further, Nakagawa *et al.*'s (2007) meta-analysis found that the relationship between house sparrow chest patches and agonistic ability is robust across published studies, suggesting that these traits evolved to function as signals of agonistic ability.

Agonistic competition in winter flocks can be intense. Flock-mates regularly compete over priority access to food and shelter, so dominance relationships are important (Gosler, 1996; Schubert *et al.*, 2007). However, winter flock composition is highly variable (Clement *et al.*, 1993; Byers *et al.*, 1995). Even minor turnover in flock membership can mean an individual within a flock interacts with thousands of others during a winter. Signals of fighting ability allow rapid rival assessment of unfamiliar individuals without escalated contests (Senar & Camerino, 1998; Tibbetts & Lindsay, 2008; Tibbetts *et al.*, in press). Therefore, if patches function as signals of fighting ability, they may dramatically reduce the costs of conflict in large groups that have unstable membership (Senar & Camerino, 1998). The significant relationship between black colour patches and winter sociality indicates that benefits associated with signalling agonistic ability in winter flocks may be an important selective pressure favouring their evolution. Therefore, these plumage traits may have evolved via social selection (*sensu* West-Eberhard 1979).

Although this study indicates that the black colour patches evolved via social selection rather than mate competition, selective pressures are rarely discrete and often have substantial overlap. Traits that evolved in one context may be co-opted to function in other contexts. For example, if males with large plumage patches are more successful at acquiring resources during the nonbreeding season, females may come to prefer these males during the breeding season. However, aspects of quality may also tradeoff such that males that are successful in one context fall short in other contexts. In many taxa, males that succeed in aggressive competition are not preferred by females (Qvarnström & Forsgren, 1998). As a result, a signal that evolved to indicate competitive ability may not provide reliable information for potential mates. Without detailed behavioural research, it is difficult to assess the overlap between social and sexual selection in a particular system. However, our study suggests that black colour patches correspond more strongly with factors associated with signalling in a nonreproductive context rather than factors associated with mate competition, suggesting that they are likely to be signals that evolved for agonistic communication during the nonbreeding season.

This study focused on the evolution of black chest and throat patches in sparrows, a phenotype that is often referred to as the 'classic' badge-of-status. We focused on this phenotype because it occurs throughout sparrows, is easy to distinguish, and has produced extensive controversy (Senar, 2006). Behavioural analysis is necessary to definitively establish the function of plumage patches within a taxa, but previous work suggests that patches in many sparrows species may function as badges-of-status (Balph *et al.*, 1979; Watt, 1986; Maynard-Smith & Harper, 1988; Senar *et al.*, 1993; Senar, 2006; Nakagawa *et al.*, 2007). Although badges are common in the

sparrows, 'badge-of-status' is a general term that refers to conventional signals of agonistic ability rather than black plumage patches. Other types of plumage ornaments are thought to function as status badges, including the white forehead patches in collared flycatchers (Pärt & Qvarnstrom, 1997) the black and white cheek patches in chickadees (Mennill et al., 2003), and the yellow throat patch in rock sparrows (Griggio et al., 2007). Although there has been less research on badges in nonavian taxa, badges have also been found in other groups, including paper wasps (Tibbetts & Dale, 2004; Tibbetts & Lindsay, 2008) and lizards (Whiting et al., 2003; Stuart-Fox & Moussalli, 2008).

Across all taxa, status badges have a few consistent characteristics. Badges are conventional signals of agonistic ability which means they signal fighting ability but have no logical a priori connection with their bearer's fighting ability (Guilford & Dawkins, 1995; Searcy & Nowicki, 2005). For example, the colour of a karate belt conveys information about fighting ability, but there is no logical reason to assume that a person with a black belt will be a better fighter than a person with a yellow belt unless you know the convention. In comparison, antlers can be considered a nonconventional signal of fighting ability. There is no need for others to interpret this signal with respect to known conventions: larger antlers represent an individual's ability to win a fight (Barrette & Vandal, 1990). Badges are expected have low costs associated with ornament production. This may be one reason why avian badges are often black and/or white plumage patches; these pigments (or a lack of pigmentation) are thought to have lower production costs than other pigment types (McGraw et al., 2002; Roulin, 2004; Griffith et al., 2006). Finally, conventional signals are expected to reduce the costs of aggressive interactions between unfamiliar individuals. The results of the present study suggest that winter flocks are one context that may favour the evolution of conventional signals. Of course, the specific social circumstances that favour badge evolution may vary with taxa. For example, territorial competition may be the key selective force in lizards (Whiting et al., 2003).

Conclusions

The black chest and throat patches in New and Old World sparrows have been a source of controversy since they were first described in the 1970s. There have been persistent questions about their accuracy, their signal value, and the context in which they are used (Searcy & Nowicki, 2005; Senar, 2006). Our comparative analysis provides a new perspective on the evolution of these traits by testing the behaviours associated with their origin and maintenance of these traits. Although the selective pressures that produce phenotypes over evolutionary time may not always parallel the current function of these phenotypes, comparative analyses do

provide an important perspective on signal evolution (Doucet et al., 2007; Stuart-Fox & Moussalli, 2008). Our results suggest that black colour patches in the sparrow are unlikely to be soley involved in sexual selection. As such, they help clarify why previous research on black colour patches and sexual selection during the breeding season has been inconsistent. Instead, sociality in a nonbreeding context appears to be an important evolutionary force, as black colour patches have evolved multiple times in the sparrows, likely due to benefits associated with agonistic signalling during winter sociality. Therefore, future research focusing on black plumage patches during the nonbreeding season is likely to be most profitable.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 References for mating system and sociality data.

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