Within-Male Melanin-Based Plumage and Bill Elaboration in Male House Sparrows

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If there is a cost to producing a dark color patch, the size of a patch may not correspond with its pigment concentration. The plumage of male house sparrows represents a case of dark, melanin-based ornamentation, but also a case of neglecting the composite nature of dark signals in birds. Here, I investigated what kind of associations exist between the brightness, chroma, and hue of dark integumentary patches and the size of a secondary sexual trait, the bib, in male house sparrows. I found that males with a larger bib also had a darker bib and bill, and a more saturated bib, bill, epaulets, head crown, and breast than small-bibbed males. Male bib coloration in terms of brightness and chroma was more strongly related to bib size than the coloration of other integumentary patches. However, with respect to hue, only the hue of the bill and cheeks was related to bib size. My results indicate that size, brightness, and chroma of the bib, but also chroma of other deeply colored patches, convey redundant information about the signaler's quality in male house sparrows.

Key words: composite signals, melanin coloration, *Passer domesticus,* sexual ornaments

INTRODUCTION

The coloration of songbird plumage is mainly constituted of carotenoid and melanin pigments (Fox and Vevers, 1960; Brush, 1978), but also results from the structural organization of keratin, melanin, and air within feathers (Prum, 1999). The elaboration of plumage coloration can be related to nutritional condition (*e.g*. Hill, 1990; Keyser and Hill, 2000), parasite load (*e.g*. Lozano, 1994; Potti and Merino, 1996), or hormonal levels (Owens and Short, 1995; Buchanan *et al.*, 2003). While it is maintained that the expression of carotenoid-based coloration is condition-dependent, reflecting the degree of an individual's adaptation in a given environment (see Badyaev and Hill, 2003; Delhey *et al.*, 2003), variation in melanin-pigmented plumage seems under genetic rather than environmental control (Buckley, 1987; Roulin and Dijkstra, 2003, but see Griffith *et al.,* 1999; Griffith *et al.*, 2006).

Not only the suggested functional dichotomy but also different methodological approaches separate carotenoid- and melanin-based plumage systems. For example, the qualitative aspects of coloration are routinely examined for carotenoid-pigmented plumage (see Hill, 2003). In contrast, melanin-based ornamental traits are almost invariably examined only for their size (Jawor and Breitwisch, 2003). However, melanin-pigmented traits may vary in the proportion of melanized relative to non-melanized (*e.g*. buff feather tips) feather parts (Møller and Eritzøe, 1992), or the proportion of

eumelanin relative to phaeomelanin pigments stored in feathers (Roulin and Dijkstra, 2003). In addition, the appearance of melanized structures may be affected by the arrangement (Craig and Hartley, 1985) or concentration (Johnstone and Janiga, 1995; McGraw *et al.,* 2005) of melanin granules deposited in feathers, or by a variable contrast between melanized and adjacent non-melanized plumage patches (Menill *et al.,* 2003). Finally, the spectral expression of multi-layered color patches usually is under multiple control mechanisms (Grether *et al.,* 2004). Therefore, the question of whether the production of a composite melanin-based signal involves some physiological cost is far from being satisfactorily resolved without application of a multi-component signal approach.

The signaling function of the melanin-pigmented bib in male house sparrows, *Passer domesticus*, has received considerable attention among behavioral ecologists, particularly because bib size was found to be involved both in intra- as well as inter-sexual selection (*e.g*. Møller, 1987; Václav and Hoi, 2002) and because bib production was directly linked with testosterone plasma levels (see Buchanan *et al.,* 2003). Surprisingly, except for two studies that examined some components of the bib in male house sparrows by means of digital photography (McGraw *et al.,* 2002; Badyaev and Young, 2004), there have been few attempts to examine the relationships among the spectral and spatial components of a composite melanin-based signal in the house sparrow or other birds. This step is, however, crucial to understanding the selection pressures acting on the elaboration of melanin-pigmented sexual traits (Jawor and Breitwisch, 2003).

Here I examine whether there is a link between the size and pigmentation of the melanin-based bib and whether the

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color elaboration of the bib is associated with the coloration of other dark integumentary patches that are displayed in a sexual context by male house sparrows. If both the size and coloration of the bib are important for sexual signaling, with the two components signaling different information, and if there is a cost involved in producing large and deeply melanin-pigmented color patches, similar to that found for carotenoid-based plumage systems (Hill, 1993; Badyaev *et al.,* 2001), I predict that there should be a negative or no relationship between bib size and bib pigmentation. Alternatively, if bib size and pigmentation indicate overall signaler quality (*i.e.* if they are redundant signals; Møller and Pomiankowski, 1993), the size and pigmentation of the bib should be positively related.

METHODS

Spectral reflectance measurements were taken on twelve adult (more than one year old) male house sparrows during the beginning of December 2003. These sparrows were randomly chosen from a stock of birds kept in the aviaries of the Konrad Lorenz Institute, Vienna. Since house sparrows molt in autumn, the measurement time at the beginning of winter was chosen in order to obtain plumage reflectances that would not be extensively confounded by the effects of general plumage wear and soiling and/or by the effect of differential preening to the bib and other body patches. All males involved in this study showed good health, completed molt, and no sign of albinism. The total bib area (including the bib area con-
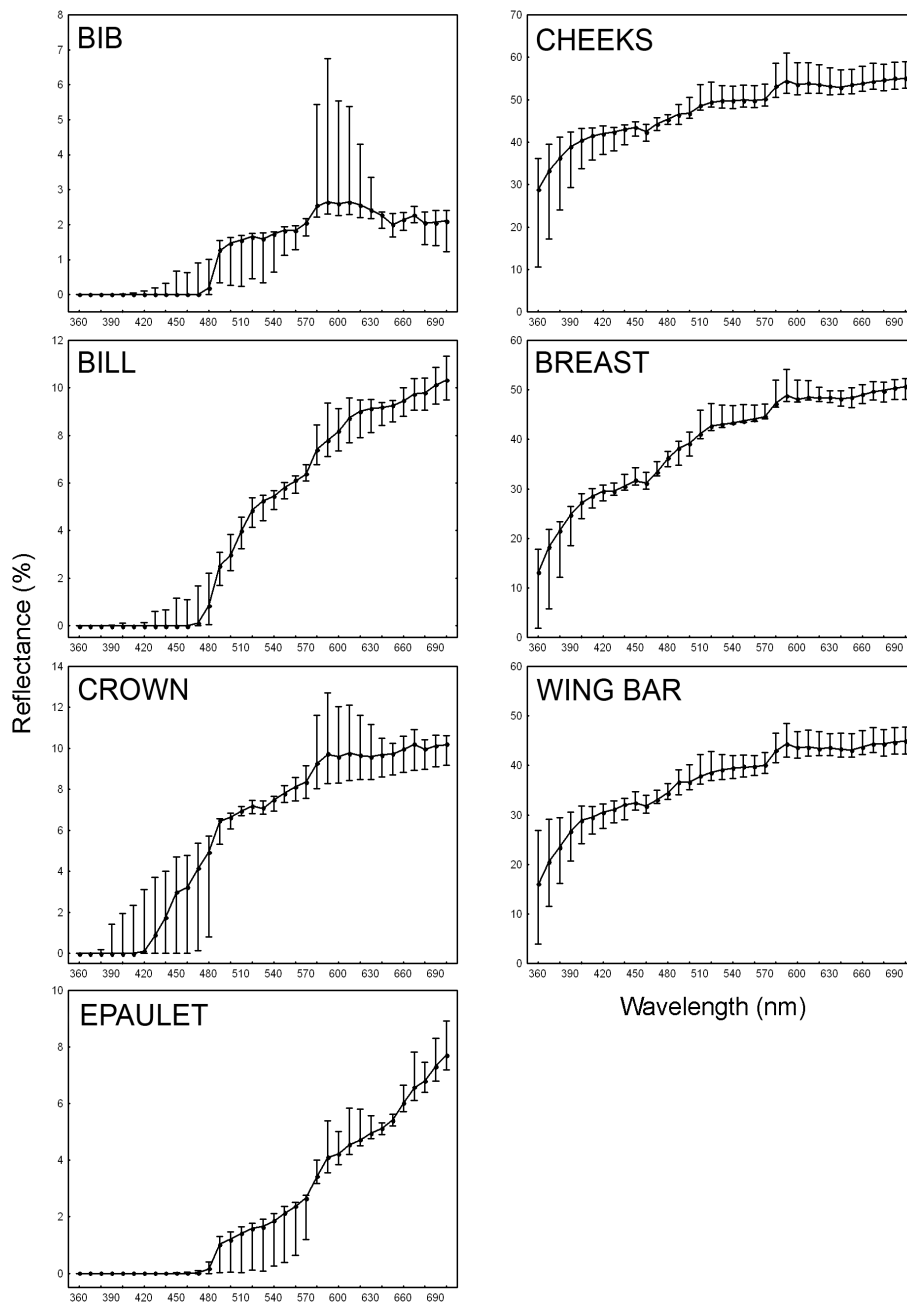

Fig. 1. Spectral reflectances of seven body regions in male house sparrows (*n*=12). The reflectances are medians and error bars indicate quartile range.

cealed by pale feather tips) and the unconcealed bib area were calculated with Adobe® Photoshop® from digital images of the ventral body side of birds. Images were taken with a 1.5-megapixel Sony DCR-TRV30 digital camera, using the camera's flash and with the camera positioned at a standard distance from the subjects. The percentage of the unconcealed bib area was calculated as (unconcealed/total bib area) × 100.

The plumage reflectance was measured with a USB2000 portable spectrophotometer (Ocean Optics) sensitive to wavelengths between 350 and 700 nm, using as the light source a DH-2000 deuterium-halogen lamp (Top Sensor Systems). For each individual, I collected approximately five reflectance measurements in different spots of each of the following body regions: 1) bib (the unconcealed, melanin-pigmented feathers on the chin and throat), 2) bill (the lateral sides of mandibles), 3) reddish wing epaulets (greater upper wing coverts), 4) grey crown, 5) breast (the pale area around the inferior part of the bib), 6) pale cheeks, and 7) pale wing bars (median upper wing coverts; see Fig. 1). In total, I recorded 413 reflectance spectra. The reflectance measurements were expressed relative to a Spectralon white standard. The spectrophotometer was calibrated to a black-and-white standard after every five measurements. There was high repeatability among measurements of the same patch in terms of brightness, chroma, and hue ($r_l > 0.78$, $9.58 < F < 283.5$, $P < 0.001$, df=11,47). Therefore, five reflectances for each patch were averaged for each individual. The spectral data for each reading were grouped into 10-nm bins, finally yielding 35 data points for every spectral reading. To avoid artificial peaks in the spectrum that could have arisen due to a lower integration time set for the spectrophotometer, grouping was achieved by calculating medians.

In order to evaluate the relationships between the color aspects of different integumentary patches and the size of the bib, I used segment classification analysis (SCA) (see Endler, 1990), in which the spectrum was divided into four segments: 350–440 nm, 440–530 nm, 530–610 nm, and 610–700 nm. Note that the crucial point of SCA is the principle of color opponency rather than the exact length of color segments (see Endler, 1990; Macedonia, 2001). Moreover, the segmentation that I used in this study roughly corresponds to the sensitivity ranges of the four photoreceptors described for UV-sensitive bird species (see Vorobyev et al., 1998).

A size index was calculated with principal component analysis (PCA) based on the values of tarsus length, wing length, and body mass. Factor loadings were calculated with the Varimax normalized factor-rotation method. Factor loadings for all variables exceeded a value of 0.7. All variables examined in this study showed normal distributions and were thus not transformed before calculations of correlations coefficients. I examined the character of associations between melanized patches within individuals, where coherence in associations is expected. Moreover, if more individual tests fall below α, it is less likely that they are all spurious (Moran, 2003). Therefore, in this study I did not decrease with any adjustments the type-I error due to multiple statistical testing.

RESULTS

The size index of male house sparrows correlated non-significantly with bib area (r_s=0.11, P=0.74, n=12). Nevertheless, I assessed the relationships between bib area and the color aspects of bib patch and six other patches using residuals of bib size after controlling for body size. Although male house sparrows show dark and pale body coloration, the reflectance curves even for apparently black patches such as the bib patch are not flat and display a considerable degree of variation, especially at long wavelengths (Fig. 1). Therefore, in addition to brightness, I also examined the chroma and hue of melanized integumentary patches. I found that the chroma of melanized, but also non-melanized, patches was negatively related to their brightness (dark patches: $-0.98 < r < -0.66$, $0.001 < P < 0.02$; pale patches: $-0.75 < r_s < -0.55$, $0.01 < P < 0.06$).

Bib brightness, but also the brightness of the bill, decreased significantly with both increasing total and apparent bib area (Table 1). The chroma of the bib, bill, epaulet, head crown, and breast were positively associated with total bib area, but only bib chroma was significantly linked also with apparent bib area (Table 1). Total bib size correlated negatively with the hue of wing epaulets and positively with the hue of pale cheeks (Table 1).

I detected positive relationships between the brightness/chroma of the bib and the brightness/chroma of other dark patches (Table 2), meaning that males with a darker and more saturated bib also showed darker and more saturated

Table 1. Pearson linear correlations between the brightness, chroma, and hue of seven different color patches and two spatial components of the bib patch. Correlation coefficients (P values) are shown in the table. Significant values are shown in bold letters.

			Color patch				
	Bib	Bill	Epaulet	Crown	Cheek	Breast	Wing-bar
Brightness							
Total Bib Area	**−0.76**	**−0.65**	−0.53	−0.55	−0.35	−0.33	−0.13
	(0.005)	(0.023)	(0.074)	(0.061)	(0.26)	(0.29)	(0.70)
Apparent Bib Area	**−0.59**	**−0.58**	−0.31	−0.32	−0.24	−0.06	0.21
	(0.044)	(0.050)	(0.32)	(0.31)	(0.46)	(0.86)	(0.51)
Chroma							
Total Bib Area	**0.78**	**0.7**	**0.73**	**0.64**	0.5	**0.67**	0.34
	(0.003)	(0.012)	(0.007)	(0.024)	(0.098)	(0.016)	(0.28)
Apparent Bib Area	**0.65**	0.5	0.56	0.43	0.53	0.55	0.31
	(0.023)	(0.097)	(0.059)	(0.16)	(0.076)	(0.064)	(0.32)
Hue							
Total Bib Area	0.44	0.2	**−0.74**	−0.19	**0.62**	0.51	0.53
	(0.16)	(0.54)	(0.006)	(0.56)	(0.032)	(0.087)	(0.079)
Apparent Bib Area	0.43	0.16	**−0.67**	−0.15	0.37	0.19	0.19
	(0.17)	(0.61)	(0.018)	(0.65)	(0.24)	(0.56)	(0.56)

Table 2. Pearson linear correlations between the brightness, chroma, and hue of seven different color patches and the brightness, chroma, and hue of the bib. Correlation coefficients (P values) are shown in the table. Significant values are shown in bold letters.

	Bib brightness	Bib chroma	Bib hue
Brightness			
Bill	**0.72 (0.008)**	-	-
Epaulet	**0.78 (0.003)**	-	-
Crown	**0.85 (0.001)**	-	-
Cheek	0.46 (0.13)	-	-
Breast	0.30 (0.35)	-	-
Wing-bar	0.01 (0.99)	-	-
Chroma			
Bill	-	**0.88 (0.001)**	-
Epaulet	-	**0.96 (0.001)**	-
Crown	-	**0.93 (0.001)**	-
Cheek	-	**0.69 (0.013)**	-
Breast	-	**0.65 (0.021)**	-
Wing-bar	-	0.55 (0.067)	-
Hue			
Bill	-	-	**0.58 (0.05)**
Epaulet	-	-	−0.30 (0.35)
Crown	-	-	0.36 (0.25)
Cheek	-	-	0.25 (0.44)
Breast	-	-	0.28 (0.37)
Wing-bar	-	-	0.28 (0.38)

dark patches in the rest of their body. There was no significant relationship between bib brightness and the brightness of pale plumage patches (Table 2), but bib chroma was positively related to the chroma of breast and cheeks (Table 2). Finally, only the hue of the bill was significantly related to bib hue (Table 2).

DISCUSSION

I found a significant negative association between bib area and bib brightness as well as a positive relationship between bib area and bib saturation in male house sparrows. Because the melanin concentration in dark feathers is strongly related to their brightness and saturation (McGraw *et al.,* 2005), it is reasonable to assume that house sparrows with larger bibs have their bib feathers more melanized than small-bibbed males.

Melanin polymers absorb light throughout the whole visible spectrum of birds, yet their peak absorbance occurs at UV and short wavelengths (*e.g.* Riley, 1997). In fact, Py *et al.* (2006) detected a genetic component to UV reflectance in melanin-based plumage of the barn owl, *Tyto alba*. I found that feathers in males with darker bibs were more saturated than those in males showing less dark bibs. This is in agreement with McGraw *et al.* (2005), who in addition demonstrated that feathers containing more melanin pigments are more saturated. Therefore, this work adds to the results of McGraw *et al.* (2005), suggesting that even melanin-based patches are not strictly achromatic and that ignoring their chromatic component is therefore unjustified.

Unlike songbirds with carotenoid-based ornamentation (Hill, 1993), male house sparrows do not seem to increase the expression of their throat patch by concentrating melanin pigments in a smaller area or by reducing the pigment concentration in other melanized plumage patches. Also, because I collected body reflectance data during winter, when pale bib-feather tips are largely unworn and still conceal a large part of the melanized bib feathers, this study indicates that males neither grow larger nor more intensely colored bibs by melanizing a smaller part of the bib feathers. Thus, male house sparrows do not appear to signal different information via the size, brightness, and chroma of their bib, supporting the idea that the expression of melanin-based plumage signals is under shared, genetic regulation (Buckley, 1987; Roulin and Dijkstra, 2003; Badyaev and Young, 2004). Nonetheless, studies using wild birds, food-limitation experiments with captive birds, and larger sample sizes are needed to confirm this result.

In addition to showing that spatial and spectral components of the bib are positively inter-correlated, I found that the brightness and mainly the chroma of the bib highly correlate with the respective color attributes of other dark color patches. Because it has not been investigated for house sparrows whether sexual selection acts on melanized patches other than the bib, it is not possible to ascertain whether the positive relationships between the coloration of the melanized patches examined and bib size arise from their shared genetic and/or condition dependence. Nevertheless, a stronger relationship between bib size and two color aspects of the bib as compared to the coloration of other dark patches indicates that bib coloration most reliably amplifies the spatial component of the bib patch in male house sparrows.

I found that bill brightness and chroma show just slightly less strong, but still highly significant, links with bib size. In contrast to plumage coloration, the expression of bill coloration varies considerably with time and has been shown to depend strongly on testosterone plasma titers in male house sparrows (*e.g.*, Witschi, 1961). Thus, my study indirectly suggests that males growing larger bibs maintain higher testosterone levels also during winter season. Taking into account the direct link between testosterone and bib size (Evans *et al.,* 2000) and the metabolic costs of high testosterone levels in house sparrows (Buchanan *et al.,* 2001), I suggest that it could be rewarding to consider bill coloration when examining the effects of condition on the expression of melanin traits.

During their displays, male house sparrows display not only their bib, but also cheeks, breast, wing panels, and tail. In fact, it appears that the display behavior of male house sparrows serves to advertise a dark bib against contrastingly pale cheeks and breast, as well as white wing-bars against dark epaulets (see Summers-Smith, 1963). I detected significant relationships between bib hue and the hue of rusty epaulets and pale cheeks, as well as a tendency for a relationship between bib hue and pale wing bars. Because bib hue seems to be disassociated from other components of the bib patch (but see Badyaev and Young, 2004), it is possible that the hue of the bib, epaulets, and some pale patches may signal different information than bib size. As eumelanin and phaeomelanin have been proposed to signal different information (Roulin *et al.,* 2000, 2001), I suggest that it would be rewarding to find out what specific melanins constitute the epaulets and other patches in male house sparrows.

As far as I am aware, this is the first work examining associations between the spatial and spectral components of a melanin-based signal while considering the spectral elaboration of other melanized patches. I suggest that the investigation of intra-individual relationships among multiple color patches can bring more insight into the cost of production and the evolution of animal coloration (see Cotton *et al.,* 2004). Also, experiments are necessary to reveal which color cues are crucial for bird perception of deeply colored surfaces.

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