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ORIGINAL ARTICLE

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Achromatic color variation in black-capped chickadees, *Poecile atricapilla*: black and white signals of sex and rank

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Abstract Sexual dichromatism and phenotypic variation in elaborate male traits are common products of sexual selection. The spectral properties of carotenoid and structurally-based plumage colors and the patch sizes of melanin-based plumage colors have received considerable attention as sexual signals in birds. However, the importance of variation in achromatic plumage colors (white, gray and black) remains virtually unexplored, despite their widespread occurrence. We investigated a potential signal function of the achromatic black and white plumage of black-capped chickadees (*Poecile atricapilla*). We captured and color-banded 178 free-living chickadees and assessed winter flock dominance hierarchies by tabulating pairwise interactions at feeders. We recaptured 73 of these birds and measured plumage coloration for six body regions using a reflectance spectrometer and the area of melanin-based plumage patches from standardized photographs. We found extensive individual variation in chickadee plumage traits and considerable sexual dichromatism. Male black-capped chickadees have significantly brighter white plumage than females, larger black patches, and greater plumage contrast between adjacent white and black plumage regions. We also found rank differences in the plumage reflectance of males; high-ranking males, who are preferred by females as both social and extra-pair partners, exhibit significantly darker black plumage and grow their feathers more rapidly than low-ranking males. This variation among individuals reveals a potential signal function for achromatic plumage coloration in birds.

Keywords Achromatic colors · Black-capped chickadee · Sexual dichromatism · Sexual selection · Social rank

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Introduction

Sexual selection often produces dramatic differences between the sexes and usually results in substantial phenotypic variation within one sex (Darwin 1871). In many animals, intrasexual competition over access to mates and resources drives the development of elaborate male traits that are used to attract females, compete with other males, or both (Andersson 1994). One obvious consequence of sexually selected male ornamentation is the divergence of male and female appearance, where the elaboration of female traits is suppressed by the naturally-selected benefit of crypsis. Individual variation in male phenotypes, on the other hand, can result from female choice and/or male-male competition (Andersson 1994). Sexually selected phenotypic variation manifests itself particularly creatively in bird plumage, where pronounced sexual dichromatism and showy male phenotypes are common.

The limitations of human vision, relative to avian color vision (Cuthill et al. 2000), make intraspecific variation in plumage coloration difficult for us to detect visually. For example, in the blue tit (*Parus caeruleus*), a species thought to have limited sexual dichromatism, reflectance spectrometry revealed that males and females exhibit substantial differences in plumage color, particularly in the ultraviolet (UV) range (300–400 nm; Andersson et al. 1998; Hunt et al. 1998), which encompasses wavelengths visible to most birds but invisible to humans (Cuthill et al. 2000). Thus, studies of visual signaling must consider the sensory capabilities of the intended signal receivers and use objective, rather than human-based, assessments of the traits under investigation. Blue tits are not likely to be the only species in which sexual dichromatism has been overlooked. Indeed, sexual dichromatism and male elaboration are expected whenever sexual selection is an important selective force (Møller and Birkhead 1994; Owens and Hartley 1998).

Beyond the role of plumage variation in sex differentiation, the elaboration of male phenotypes can result from female choice; female house finches (*Carpodacus mexicanus*), for example, prefer the reddest males as partners (e.g. Hill 1991, 2002), while female common yellowthroats (*Geothlypis frichas*) prefer males with the largest facial masks (Thusius et al. 2001). Alternatively, status signaling systems may be responsible for individual variation in male plumage patterns; in great tits (*Parus major*), the width of the black breast stripe is used as a status signal of male dominance (Järvi and Bakken 1984; Lemel and Wallin 1993). Some elaborate male traits may be both competitive male status symbols and the objects of female assessment during mate choice; for example, the size of melanin-based plumage badges of house sparrows (*Passer domesticus*; e.g., Møller 1987; Griffith et al. 1999b) and structural white plumage patches of collared flycatchers (*Ficedula albicollis*; e.g., Pärt and Qvarnström 1997) can both reflect male social status and predict female mating preferences. Despite interest in the signal function of achromatic plumage patches (see above-mentioned studies and Siitari et al. 2002), the variation in reflectance within these patches has been largely overlooked.

In this study, we investigate the signal function of variation in achromatic plumage color in the black-capped chickadee (*Poecile atricapilla*), paying particular attention to variation related to sex and social status. While sex, status, and quality signals have received considerable attention with respect to bright pigment-based colors (Andersson 1994) and, to a lesser extent, structural blue/UV colors (e.g., Hunt et al. 1998; Keyser and Hill 2000; Doucet and Montgomerie 2003), very little is known about the signal function of variation in achromatic plumage color. Many species exhibit achromatic plumage coloration, consisting of pigment-free white plumage and/or various degrees of melanized plumage (Fox 1976; Prum 1999). Given the composite nature of plumage traits (e.g., Badyaev et al. 2001) and the widespread occurrence of achromatic plumage colors, achromatic color variation may serve an important signal function.

Black-capped chickadees are non-migratory songbirds that appear sexually monochromatic to human observers (Smith 1993; Owens and Hartley 1998); both sexes display bright white cheek patches, a black cap, and a black bib. Dominance hierarchies in winter flocks structure the chickadee social system, where high-ranking males obtain preferential access to food resources during winter (Ficken et al. 1990) and become the target of female mate choice during the breeding season. High-ranking males are preferred as both social (Ramsay et al. 2000) and extra-pair copulation partners (Otter et al. 1998) and the consequent skew in male reproductive success suggests that chickadees are likely candidates for revealing sexually selected plumage variation (Møller and Birkhead 1994; Owens and Hartley 1998). Here, we use reflectance spectrometry to explore the potential for plumage variation in black-capped chickadees to reveal cryptic sex differences, social rank differences, or both.

Methods

In January 2001, we captured 178 black-capped chickadees at Queen's University Biological Station, Ontario, Canada (44°34'N, 76°19'W) using Potter traps baited with sunflower seeds. We color-banded all individuals, measured wing chord, tail, tarsus, and mass for each bird, and assessed each individual's age based on the shape of the outer retrices (second year SY versus after second year ASY; Pyle et al. 1987). We collected a small blood sample from each bird and determined sex by molecular analysis using sex-specific primers (Griffiths et al. 1998).

We assessed flock dominance hierarchies by tabulating pairwise interactions between color-banded birds at winter feeders. We inferred dominance when an individual (1) supplanted or chased an opponent, (2) resisted a supplanting attack by an opponent, (3) elicited a submissive posture in an opponent, or (4) fed while an opponent waited to approach a feeder (Ficken et al. 1990; Otter et al. 1998). Between February and April, we observed 4,000 pairwise dominance interactions between birds in 29 flocks (n=4–9 birds/flock). We used MatMan software (Noldus Information Technology) to reorder dominance interaction matrices to fit a linear hierarchy for each flock. We identified "high-ranking males" as the topmost male in flocks containing two or three males or the topmost two males in flocks containing four or five males. We identified "low-ranking males" as the bottom ranking male in flocks containing two or three males or the bottom two males in flocks containing four or five males. Five "mid-ranking males" (the middle ranking male in flocks containing three or five males) are included in sex comparisons but not rank comparisons. We restricted our analysis of dominance rank to males because female chickadees do not interact with each other as frequently as do males.

Plumage measurements

Chickadees molt in late summer into plumage that is borne throughout the following winter and breeding season (Smith 1993). Between February and April, we recaptured 33 female and 40 male chickadees and objectively assessed their plumage coloration using an Ocean Optics S2000 spectrometer and a PX-2 pulsed xenon lamp (Ocean Optics, Dunedin, Fla., USA). We used a bifurcated fiber-optic measurement probe, which provided illumination from the lamp and transferred light reflected from a ca. 3-mm^2 area of plumage back to the spectrometer. We maintained the probe at a fixed distance from and perpendicular to the feather surface with a rubber sheath that also excluded external light from the measurement area. Data were collected with Spectraware software on a Macintosh laptop computer.

We expressed all reflectance measurements as the proportion of the total reflectance from a Spectralon white standard measured before and after each bird. We measured plumage reflectance on six body regions of each individual: black cap, black nape, black bib, grey mantle, white cheek patch (behind the auriculars), and white breast. We obtained five readings for each region, moving the probe by at least 3 mm before taking each new reading. We used an average reflectance curve from the five readings for each region in the following analyses.

We restricted spectral analyses to wavelengths between 300 and 700 nm, a range likely corresponding to the chickadee visual spectrum (Chen and Goldsmith 1986; Cuthill et al. 2000). To summarize overall variation in plumage reflectance among individuals, we performed principal components analysis (PCA on correlation matrices with no factor rotation) on data calculated from average reflectance curves (Endler 1990; Hunt et al. 1998). For each reflectance curve we calculated mean reflectance values for each 10-nm interval across the avian visual spectrum, resulting in 40 mean reflectance values between 300 and 700 nm. We performed a separate PCA for each body region, using the 40 mean reflectance values as variables and the 73 chickadees as observations. For these analyses, the first principal component (PC1) explained a high proportion of the variation in total reflectance, ranging between 86.1% and 93.8% for the six body regions. The second and third principal components (PC2, PC3) explained between 1.0% and 9.2% of the variation in reflectance, and cumulatively the first three principal components explained between 96.1% and 99.6% of the variation among birds within body regions.

To facilitate the interpretation of the principal component scores, we calculated color characteristics relevant to achromatic colors and compared these to our PC scores. We calculated brightness as the average percent reflectance from 300 nm to 700 nm. We also calculated UV chroma (the proportion of total reflectance occurring between 300 and 400 nm) because variation in the shape of white and black reflectance curves was likely to occur where these curves were changing most rapidly, that is, in the UV region (Fig. 1). As expected (Endler 1990), PC1 was highly correlated with brightness for all body regions (all $r>0.999$, all $P<0.0001$, $n=73$). The remaining two principal components were associated with the shape of the reflectance curves, and hence represent variation in hue and chroma (Endler 1990; Hunt et al. 1998). PC2 showed high positive loadings from wavelengths below 400 nm and was positively correlated with UV chroma for all body regions (all $r>0.81$, all $P<0.0001$, $n=73$). Hence, birds with high PC2 scores had proportionately greater reflectance in the UV range. PC3 showed high positive loadings from very short wavelengths (less than 350 nm) and very long wavelengths (greater than 600 nm) and moderate negative loadings from intermediate wavelengths. Hence, birds with high PC3 scores reflected proportionately more at either end of the avian visual spectrum.

Patch size

To assess variation in patch size, we photographed the melanin-colored bib of 53 chickadees ($n=29$ males, 24 females) and black cap of 52 chickadees ($n=29$ males, 23 females). Birds were held with the bill parallel to the body such that the base of the skull rested on the scapula (see Otter and Ratcliffe 1999) and photographed against a ruled background at a standard distance from the camera lens. Photos were scanned at high resolution in 8-bit greyscale on a HP Scanjet 7400c scanner. Bib and cap area were measured with ImageJ software (U.S. National Institutes of Health) using a standardized thresholding procedure (the area of interest was separated from background on equalized images using a threshold with a lower limit of 0 and an upper limit of 40).

Feather growth rates

We assessed feather growth rates by measuring the width of alternating dark and light bars on the left outer rectrix of 52 individuals ($n=29$ males, 23 females). Each pair of dark/light bars represents one day's growth (Michener and Michener 1938) and the width of these bars has been associated with nutritional condition (Grubb 1991; Jenkins et al. 2001). We measured the width of five pairs of bars on each side of the midpoint of the feather, from which we calculated a 10-day average daily growth rate for each individual (see Hill and Montgomerie 1994).

Statistical analyses

We used canonical discriminant analyses to test whether plumage color variation could separate males from females and high-ranking males from low-ranking males. In separate analyses, sex or rank were classification variables and the first three principal components for each of the six body regions were measurement variables. We report all variables that show a significant correlation with the first canonical discriminant function for each analysis (Table 1). Canonical discriminant analyses were conducted using SAS 8.0 and all other analyses were conducted using JMP 4.0. All values are reported as mean±SE and all reported probabilities are two-tailed.

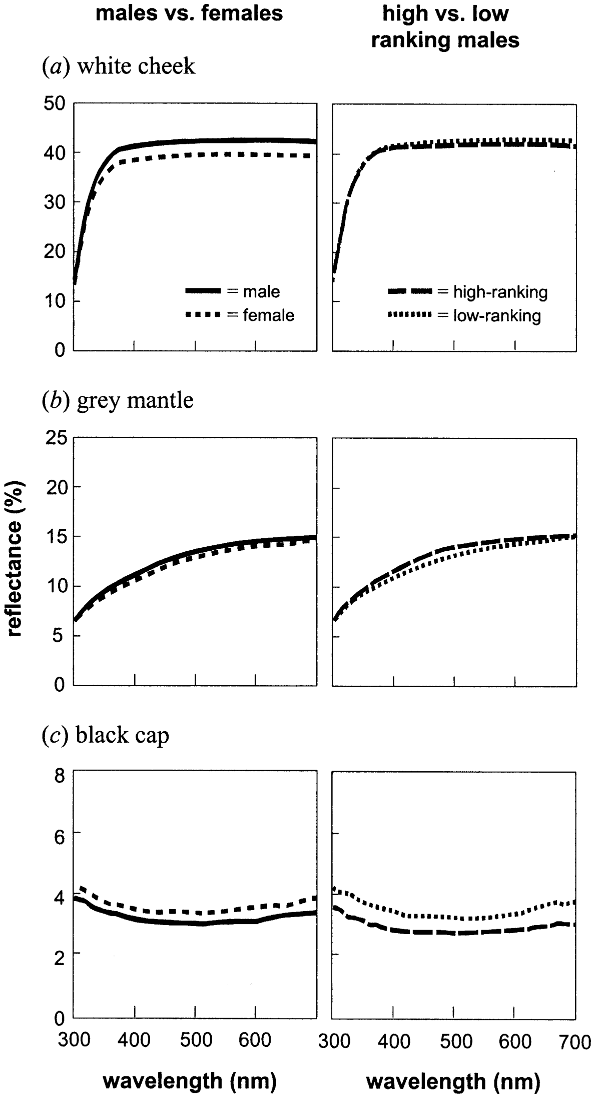

Fig. 1 Black-capped chickadee (*Poecile atricapilla*) plumage reflectance curves for three body regions, each representing a different plumage color. Plots at left show the average reflectance curves for males (*solid lines*; $n=40$) versus females (*dashed lines*; $n=33$). Plots at right show average reflectance curves for high-ranking males (*dashed lines*; $n=16$) versus low-ranking males (*dotted lines*; $n=19$). Curves were calculated from averages of reflectance curves. Note differences in reflectance scale for the different plumage regions

Table 1 Plumage features significantly contributing to discrimination of sex and rank differences in black-capped chickadee (*Poecile atricapilla*) coloration. Plumage variables with a significant correlation ($P<0.05$) with the first canonical discriminant functions are shown. Total canonical structure shows the total-sample correlations between the canonical variables and the PC scores. See Methods for interpretation of PC scores

Attribute	Measurement variable	*r*	*F*	*P*	Total canonical structure
Sex	Cheek brightness (PC1)	0.30	6.81[a]	0.01	0.47
	Mantle curve shape (PC3)	–0.26	5.30[a]	0.02	–0.42
Rank	Mantle curve shape (PC3)	–0.41	6.79[b]	0.01	–0.53
	Bib curve shape (PC3)	0.35	4.54[b]	0.04	0.45
	Black cap brightness (PC1)	–0.34	4.43[b]	0.04	–0.44

[a] *df*=1,71

[b] *df*=1,33

Results

Plumage reflectance

Plumage coloration in black-capped chickadees varied along a continuum from black to white (Fig. 1). White cheek and breast regions exhibited similar reflectance curves, although cheek reflectance was significantly brighter than breast reflectance (average percent reflectance: cheek=39.03±0.54%, breast=32.26±0.51%; ANOVA, $F_{1,71}=83.0$, $P<0.0001$). All black plumage regions showed very low reflectance with little variation across the chickadee's visual spectrum (Fig. 1c). There was variation in reflectance among the three black body regions (average percent reflectance: nape=3.11±0.07%, bib=3.32±0.10%, black cap=3.52±0.11%; $F_{1,71}=4.6$, $P=0.01$) where the nape was the darkest and the black cap was the lightest of the three black regions (Tukey-Kramer, $P<0.05$). Plumage reflectance was highly variable; coefficients of variation (CVs) for brightness scores of the six plumage regions (10.86–27.27%) were much higher than CVs for four morphological traits (body mass, tarsus length, wing chord, tail length; CVs: 3.52–6.86%).

Sexual dichromatism

The plumage of black-capped chickadees is sexually dichromatic. Canonical discriminant analysis significantly separated males from females (Fig. 2) and predicted sex with 79% accuracy (31 of 40 males and 27 of 33 females predicted correctly). Males had high canonical variate scores, with brighter cheeks (higher cheek PC1 scores), and mantles with proportionately greater reflectance at intermediate wavelengths (lower mantle PC3 scores) than females (Table 1). When bib area and cap area were included as measurement variables, discriminant analysis predicted sex with 90% accuracy (27 of 29 males and 20 of 23 females predicted correctly) with strong positive weighting from bib area in addition to the variables in Table 1.

One of the most striking plumage characteristics of chickadees is the strong contrast between adjacent light and dark plumage regions. To describe this trait directly, we calculated "achromatic contrast" as the difference between mean brightness values (% reflectance) for pairs of adjacent light and dark body regions. Males exhibited

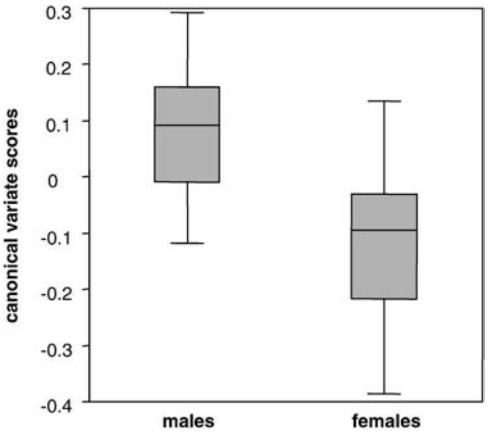

Fig. 2 Box plot of canonical variate scores for male (*n*=40) versus female (*n*=33) black-capped chickadees, demonstrating achromatic plumage color sexual dichromatism. The first three principal component scores of reflectance curves for each of six body regions were used in this canonical discriminant analysis. Box plots show horizontal lines for the 10th, 25th, 50th, 75th, and 90th percentiles

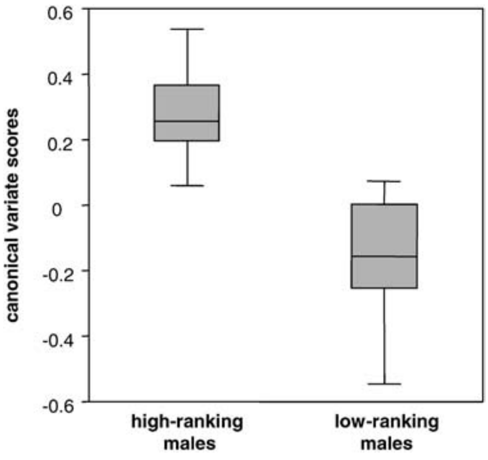

Fig. 3 Box plot of canonical variate scores for high-ranking (*n*=16) versus low-ranking (*n*=19) males, demonstrating the association between male rank and achromatic plumage color. The first three principal component scores of reflectance curves for each of six body regions were used in this canonical discriminant analysis. Box plots as in Fig. 2

significantly greater achromatic contrast than females for cheek-to-black cap (males: 36.9±0.7%; females: 33.8±0.8%; ANOVA, $F_{1,71}$=7.7, P=0.007), cheek-to-bib (males: 37.0±0.7%; females: 34.1±0.8%; $F_{1,71}$=7.2, P=0.009), and cheek-to-nape (males: 37.2±0.7%; females: 34.4±0.8%; $F_{1,71}$=6.9, P=0.01) comparisons. Males had slightly higher breast-to-bib achromatic (males: 29.6±0.7%; females: 28.2±0.8%; $F_{1,71}$=1.9, P=0.17) and mantle-to-nape achromatic contrast (males: 9.6±0.2%; females 9.0±0.2%; $F_{1,71}$=2.4, P=0.13) although these differences were not significant.

Rank-based plumage coloration

Male black-capped chickadee plumage coloration also varied with dominance rank. Canonical discriminant analysis separated high-ranking males from low-ranking males (Fig. 3) and predicted male rank with 94% accuracy (15 of 16 high-ranking males and 18 of 19 low-ranking males predicted correctly). High-ranking males had high canonical variate scores, with darker black caps (lower black cap PC1 scores), mantles with proportionately greater reflectance at intermediate wavelengths (lower mantle PC3 scores), and bibs with proportionately less reflectance at intermediate wavelengths (higher bib PC3 scores; Table 1). When bib area and cap area were added to the analysis as measurement variables, discriminant analysis predicted male rank with 100% accuracy.

Rank is related to age in black-capped chickadees, where older birds tend to be dominant to younger birds (Smith 1991). To compare the effects of male rank and male age on plumage color, we constructed backwards stepwise multiple regression models (probability to enter model=0.25, probability to leave model=0.10) with rank and age as predictor variables and the three plumage features which significantly discriminated between high and low-ranking males (Table 1) as measurement variables. Only rank was a significant predictor of male plumage color for all three body regions (mantle curve shape (PC3): age $F_{1,33}$=0.0, P=0.98, rank $F_{1,33}$=6.8, P=0.01; bib curve shape (PC3): age $F_{1,33}$=0.0, P=0.83, rank $F_{1,33}$=4.5, P=0.04; black cap brightness (PC1): age $F_{1,33}$=0.2, P=0.65, rank $F_{1,33}$=4.4, P=0.04).

Patch sizes

Males had significantly larger black bibs than females (males=3.70±0.08 cm^2, n=29, females=3.36±0.05 cm^2, n=24; ANOVA, $F_{1,51}$=12.3, P=0.0009). However, high-ranking males did not have larger bibs than low-ranking males (high-ranking males=3.66±0.09 cm^2, n=13, low-ranking males=3.71±0.08 cm^2, n=11; $F_{1,22}$=0.1, P=0.72). Black cap area was similar between males (4.32±0.07 cm^2) and females (4.08±0.39 cm^2; $F_{1,51}$=1.4, P=0.25) and between high-ranking males (4.39±0.08 cm^2) and low-ranking males (4.23±0.15 cm^2; $F_{1,22}$=1.0, P=0.34). As with brightness scores, CVs for bib area (10.83%) and cap area (9.05%) were higher than CVs for the four morphological traits we measured.

Tail feather growth rates

Males and females had nearly identical feather growth rates (males=2.31±0.08 mm/day, n=29, females=2.28±0.07 mm/day, n=23; ANOVA, $F_{1,52}$=0.1, P=0.78). High-ranking males (2.50±0.09 mm/day, n=12) had significantly faster feather growth rates than low-ranking males (2.08±0.11 mm/day, n=13; $F_{1,23}$=8.6, P=0.008).

Discussion

Reflectance spectrometry revealed significant variation in the black and white plumage of black-capped chickadees with respect to both sex and rank. Earlier studies have typically focused on badge size for both melanin-based black plumage patches (e.g., Møller 1987; Lemel and Wallin 1993; Thusius et al. 2001) and unpigmented white plumage patches (e.g., Pärt and Qvarnström 1997). Here, we demonstrate that variation in the brightness and shape of achromatic reflectance curves, as well as contrast in brightness between adjacent achromatic plumage regions, could serve as important plumage signals and reveal information about the signaler independent of patch size. Our findings suggest that variation in this type of plumage may be sufficient to reveal important sex and quality differences between individuals. A quick survey reveals that more than half of North American passerines have significant amounts of black and white plumage on the head and breast. Given the widespread occurrence of this type of plumage in birds, achromatic signaling deserves further attention.

Despite their sexually monochromatic appearance to humans (Smith 1993), black-capped chickadees show considerable sexual dichromatism. In general, males have brighter white and grey plumage regions, more striking contrast between adjacent light and dark plumage regions, and larger bibs than females. Across avian taxa, plumage dimorphism is associated with frequency of extra-pair fertilizations (Møller and Birkhead 1994; Owens and Hartley 1998). As such, it is fitting that our measurements unveil considerable sexual dichromatism in chickadee plumage, given the variance in male reproductive success resulting from female-initiated extra-pair copulations in this species (Otter et al. 1998; Mennill et al. 2002).

We also demonstrate an association between achromatic plumage color and male rank.

High-ranking males have darker black caps and exhibit differences in the shapes of their reflectance curves for different plumage regions. Rank-based differences in plumage coloration could arise through three non-exclusive mechanisms.

1. High-ranking males may be of better genetic quality and this could be revealed in their plumage (e.g.,

Norris 1993; Qvarnström 1999). An exclusively genetic explanation seems unlikely, however, because plumage patterns vary considerably across years in this species (Otter and Ratcliffe 1999) and male rank may change from one year to the next (Smith 1991).

2. Rank-based differences in plumage patterns could arise because high-ranking males, by definition, have preferential access to food throughout much of the year (Ficken et al. 1990). Evidence from some studies suggests that such environmental effects could influence the expression of melanin-based ornaments (Veiga and Puerta 1996; Griffith et al. 1999a; Fitze and Richner 2002). This explanation is indirectly supported by our data; high-ranking males had significantly faster feather growth rates than low-ranking males. Feather growth rates increase with nutritional condition (Grubb 1991; Jenkins et al. 2001) and have been used as indicators of quality in several species (e.g., Hill and Montgomerie 1994; Doucet 2002). Thus, high-ranking males have better access to resources that may play a role in both the synthesis and organization of melanin and the structural organization of feather keratin, which are responsible for black and white plumage coloration, respectively (Fox 1976).
3. Rank-based variation in plumage coloration may also be an indirect consequence of male rank. For example, the feathers of high-ranking may suffer less abrasion (Bonser 1995) or may accumulate less dirt than those of lower–ranking males, particularly if dominance status allows high-ranking males to devote more time to maintenance activities or avoid situations associated with feather wear. Thus, rank-based differences in plumage coloration could become accentuated over time, becoming most apparent during the breeding season (i.e. when we measured plumage).

Rank-based differences in male plumage coloration may serve two important functions: plumage may signal male quality during female mate choice or it may indicate status during male-male competition. Chickadee partnerships mostly form in autumn (September–November) when birds assemble in flocks (Smith 1991). At this time of year, females must make mate choice decisions in the absence of important cues of male quality, such as dawn chorus song rate (Otter et al. 1997) or male performance in song contests (Mennill et al. 2002) and must assess male quality based on other signals, such as male plumage. Moreover, an aviary-based mate choice experiment revealed that female black-capped chickadees exhibited consistent preferences for particular individuals, although no outstanding differences could be identified in preferred males (K. Otter, personal communication). This suggests that females may have been using some unmeasured signal of male quality, possibly plumage coloration. In an intrasexual context, rank-based differences in male plumage coloration may serve as an honest indicator of status, particularly when males first establish their relative positions in flock hierarchies. Such badges of status may reduce the need to resort to escalated and costly aggressive interactions (Senar 1999). For example, in the related great tit, the width of the breast stripe is a useful signal of status, although this is only true when males have no prior experience with each other (Lemel and Wallin 1993).

In animals with stable social groups, phenotypic variation may be important for individual recognition (Whitfield 1987; Dale et al. 2001). While sex and rank signals may be important during mate choice and group establishment, the importance of these signals may become subsidiary to individual recognition after groups consolidate. In social animals, individual recognition cues could facilitate maintenance of stable group hierarchies and reduce the need for aggressive encounters with known individuals of know fighting ability (Whitfield 1987). Individual recognition may also facilitate the defense of flock home ranges during the winter and territory defense against former group members during the subsequent breeding season. Black-capped chickadees show large inter-individual variation in plumage reflectance as revealed by the relatively large coefficients of variation for the plumage traits we measured compared to body size traits. Plumage features in black-capped chickadees may thus be ideally suited to facilitate individual recognition, in addition to, or in concert with, sex and rank differentiation. Given their highly stable winter flocks, black-capped chickadees may be an excellent species in which to study individual recognition in relation to plumage traits.

Birds are renowned for their sophisticated color vision (e.g., Cuthill et al. 2000; Hart 2001). Our study, however, reveals pronounced variation in the reflectance patterns and patch sizes of achromatic plumage regions. The perception of variation in achromatic colors may be detected by double cone receptors (e.g., Vorobyev et al. 1998; Hart 2001) that make up at least half of the photoreceptors in diurnal birds (Cuthill et al. 2000; Hart 2001). It should be noted, however, that while the sex- and rank-based differences reported here are detectable with the use of a spectrometer, experimental studies will be necessary to determine whether chickadees can detect these differences, and whether they actually use these differences as signals of sex, rank or individual identity.

Several studies have unsuccessfully attempted to use the size or shape of plumage patches to differentiate between sexes in black-capped chickadees (Mosher and Lane 1972; Gochfeld 1977; Otter and Ratcliffe 1999) and here we provide the first conclusive evidence that these birds are indeed sexually dichromatic. Interestingly, sex differentiation was influenced most by white plumage patches, while rank differentiation generally involved black plumage patches. This observation may hint at the mechanistic basis for sex and rank differentiation in black-capped chickadees; unpigmented white plumage traits may be more influenced by developmental or genetic factors (Prum 1999) while melanized black plumage traits may be more influenced by environmental and social factors (e.g. Griffiths et al. 1999a; McGraw et al. 2003).

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References

Andersson MB (1994) Sexual selection. Princeton University Press, Princeton, N.J.

Andersson S, Örnborg J, Andersson M (1998) Ultraviolet sexual dimorphism and assortative mating in blue tits. Proc R Soc Lond B 265:445–450

Badyaev AV, Hill GE, Dunn PO, Glenn JC (2001) Plumage color as a composite trait: developmental and functional integration of sexual ornamentation. Am Nat 158:221–235

Bonser RHC (1995) Melanin and the abrasion resistance of feathers. Condor 97:590–591

Chen DM, Goldsmith TH (1986) Four spectral classes of cone in the retinas of birds. Comp Physiol. A 159:473–479

Cuthill IC, Partridge JC, Bennett ATD, Church SC, Hart NS, Hunt S (2000) Ultraviolet vision in birds. Adv Study Behav 29:159–214

Dale J, Lank DB, Reeve HK (2001) Signaling individual identity versus quality: a model and case studies with Ruffs, Queleas, and House Finches. Am Nat 158:75–86

Darwin C (1871) The descent of man and selection in relation to sex. Murray, London

Doucet SM (2002) Structural plumage coloration, male body size, and condition in the blue-black grassquit. Condor 104:30–38

Doucet SM, Montgomerie R (2003) Multiple sexual ornaments in satin bowerbirds: UV plumage and bowers signal different aspects of male quality. Behav Ecol (in press)

Endler JA (1990) On the measurement and classification of colour in studies of animal colour patterns. Biol J Linn Soc 41:315–352

Ficken MS, Weise CM, Popp JW (1990) Dominance rank and resource access in winter flocks of Black-capped Chickadees. Wilson Bull 102:623–633

Fitze PS, Richner, H (2002) Differential effects of a parasite on ornamental structures based on melanins and carotenoids. Behav Ecol 3:401–407

Fox DL (1976) Animal biochromes and structural colours. Univiversity of California Press, Berkeley

Gochfeld M (1977) Plumage variation in Black-capped Chickadees: Is there sexual dimorphism? Bird-Banding 48:62–66

Griffiths R, Double MC, Orr K, Dawson RG (1998) A DNA test to sex most birds. Mol Ecol 7:1071–1075

Griffith SC, Owens IPF, Burke T (1999a) Environmental determination of a sexually selected trait. Nature 400:358–360

Griffith SC, Owens IPF, Burke T (1999b) Female choice and annual reproductive success favour less-ornamented male house sparrows. Proc R Soc Lond B 266:765–770

Grubb TC (1991) A deficient diet narrows growth bars on induced feathers. Auk 108:725–727

Hart NS (2001) The visual ecology of avian photoreceptors. Prog Retin Eye Res 20:675–703

Hill GE (1991) Plumage coloration is a sexually selected indicator of male quality. Nature 350:337–339

Hill GE (2002) A red bird in a brown bag: the function and evolution of colorful plumage in the house finch. Oxford University Press, New York

Hill GE, Montgomerie R (1994) Plumage colour signals nutritional condition in the house finch. Proc R Soc Lond B 258:47–52

Hunt S, Bennett ADT, Cuthill IC, Griffiths R (1998) Blue tits are ultraviolet tits. Proc R Soc Lond B 265:451–455

Järvi T, Bakken M (1984) The function of the variation in the breast stripe of the great tit (*Parus major*). Anim Behav 32:590–596

Jenkins KD, Hawley DM, Farabaugh CS, Cristol DA (2001) Ptilochronology reveals differences in condition of captive White-throated Sparrows. Condor 103:579–586

Keyser AJ, Hill GE (2000) Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. Behav Ecol 11:202–209.

Lemel J, Wallin K (1993) Status signaling, motivational condition and dominance: an experimental study in the great tit, *Parus major*. Anim Behav 45:549–558

McGraw KJ, Dale J, Mackillop EA (2003) Social environment during molt and the expression of melanin-based plumage pigmentation in male house sparrows (*Passer domesticus*). Behav Ecol Sociobiol 53:116-122

Mennill DJ, Ratcliffe LM, Boag PT (2002) Female eavesdropping on male song contests in songbirds. Science 296:873

Michener H, Michener JR (1938) Bars in flight feathers. Condor 40:149–160

Møller AP (1987) Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signaling. Anim Behav 35:1637–1644

Møller AP, Birkhead TR (1994) The evolution of plumage brightness in birds is related to extra-pair paternity. Evolution 48:1089–1100

Mosher JI, Lane S (1972) A method of determining the sex of captured Black-capped Chickadees. Bird-Banding 43:139–140

Norris K (1993). Heritable variation in a plumage indicator of viability in male great tits *Parus major*. Nature 362:537–539

Otter K, Ratcliffe L (1999) Relationship of bib size to age and sex in the black-capped chickadee. J Field Ornithol 70:567–577

Otter K, Chruszcz B, Ratcliffe L (1997) Honest advertisement and song output during the dawn chorus of black-capped chickadees. Behav Ecol 8:167–173

Otter K, Ratcliffe L, Michaud D, Boag PT (1998) Do female black-capped chickadees prefer high-ranking males as extra-pair partners? Behav Ecol Sociobiol 43:25–36

Owens IPF, Hartley IR (1998) Sexual dimorphism in birds: why are there so many different forms of dimorphism? Proc R Soc Lond B 265:397–407

Pärt T, Qvarnström A (1997) Badge size in collared flycatchers predicts outcome of male competition over territories. Anim Behav 54:893–899

Prum RO (1999) The anatomy and physics of avian structural colours. In: Adams N, Slotow R (eds) Proc Int Ornithol Congr 22:1633–1653

Pyle P, Howell SNG, Yunick RP, DeSante DF (1987) Identification guide to North American passerines. Slate Creek Press, Bolinas, Calif.

Qvarnström A (1999). Genotype-by-environment interactions in the determination of the size of a secondary sexual character in the collared flycatcher (*Ficedula albicollis*). Evolution 53:1564–1572

Ramsay SM, Otter KA, Mennill DJ, Ratcliffe LM, Boag PT (2000) Divorce and extrapair mating in female black-capped chickadees (*Parus atricapillus*): separate strategies with a common target. Behav Ecol Sociobiol 43:25–36

Senar JC (1999) Plumage coloration as a signal of social status. In: Adams N, Slotow R (eds) Proc Int Ornithol Congr 22:1669–1686

Siitari H, Honkavaara J, Huhta E, Viitala J (2002) Ultraviolet reflection and female mate choice in the pied flycatcher, *Ficedula hypoleuca*. Anim Behav 63:97–102

Smith SM (1991) The Black-capped Chickadee: Behavioral Ecology and Natural History. Cornell University Press, Ithaca, N.Y.

Smith SM (1993) Black-capped chickadee (*Parus atricapillus*). In: Poole A, Gill F (eds) The Birds of North America, no 39. The Birds of North America, Philadelphia

Thusius KJ, Peterson KA, Dunn PO, Whittingham LA (2001) Male mask size is correlated with mating success in the common yellowthroat. Anim Behav 62:435–446.

Veiga JP, Puerta M (1996) Nutritional constraints determine the expression of a sexual trait in the house sparrow, *Passer domesticus*. Proc R Soc Lond B 263:229–234.

Vorobyev M, Osorio D, Bennett ATD, Marshall NJ, Cuthill IC (1998) Tetrachromacy, oil droplets and bird plumage colours. J Comp Physiol A 183:621–633

Whitfield DP (1987) Plumage variability, status signaling and individual recognition in avian flocks. Trends Ecol Evol 2:13–18