

Achromatic plumage reflectance predicts reproductive success in male black-capped chickadees

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The size of achromatic (black, white, gray) plumage patches serves as a male status signal in many species of birds, but variation in the colors of these patches has received little attention. We assessed the relation between achromatic plumage reflectance, dominance rank, body condition, and reproductive success in male black-capped chickadees, *Poecile atricapillus*. We measured plumage reflectance for five body regions of 40 male chickadees in late winter and monitored these males throughout the following breeding season to determine whether they survived to breed, whether they successfully paired, whether their partner laid eggs, and both their apparent and realized reproductive success. As expected from past studies, a male's dominance rank significantly predicted whether his partner laid eggs. However, only achromatic plumage reflectance significantly predicted other measures of male reproductive performance. Among males who fledged at least one offspring, both the brightness of white plumage regions and the UV-chroma of melanin-based plumage regions were significant predictors of the proportion of within-pair young in their nests. When we consider all males we measured, assigning zero values to males who failed to sire any offspring, the UV-chroma of melanin-based plumage regions was a significant predictor of realized reproductive success. Bib size was also related to male realized reproductive success. Our findings suggest that individual variation in achromatic plumage may play an important role in sexual signaling in chickadees. *Key words*: achromatic reflectance, black-capped chickadee, dominance status, female choice, plumage color, *Poecile atricapillus*, reproductive success. [*Behav Ecol*]

In many species, females prefer males displaying the most elaborate ornaments (Andersson, 1994). According to indicator models, females prefer males with showy ornaments because such traits reveal various aspects of male quality (Grafen, 1990; Kodric-Brown and Brown 1984; Zahavi, 1975). Studies of plumage coloration in birds have supported indicator models in several species, finding that plumage color correlated with various aspects of male quality, including parasite load (e.g., Doucet and Montgomerie, 2003b), viability (e.g., Sheldon et al., 1999), territory quality (e.g., Keyser and Hill, 2000), and parental effort (e.g., Siefferman and Hill, 2003; Hill, 2002).

Achromatic plumage (white, gray, and black) has been well studied with respect to patch size (e.g., Järvi and Bakken, 1984; Møller, 1987; Pärt and Qvarnström, 1997; Thusius et al., 2001), particularly in the context of status signaling (reviewed in Senar, 1999). However, little attention has been devoted to understanding the signal function of variation among individuals in the color of achromatic plumage patches, despite experimental evidence that such variation may be important in mate assessment. Field observations and aviary-based mate choice experiments suggest that the plumage blackness of males may influence female choice in pied flycatchers (*Ficedula hypoleuca*; Sætre et al., 1994). In two other studies, females preferred males in full-spectrum light rather than UV-deficient viewing conditions (Bennett et al., 1996; Sitari et al., 2002), even though the plumage color most likely to be affected was (achromatic) white.

In this study, we sought to determine whether achromatic plumage reflectance could function as a signal of male quality in black-capped chickadees, *Poecile atricapillus*, a species whose plumage is comprised entirely of achromatic patches of white, gray, and black feathers. In our study population, individual variation in achromatic plumage reflectance accurately predicted the sex and dominance rank of these birds such that males had brighter white plumage patches and exhibited starker black-to-white plumage contrast than females, despite their sexually monochromatic appearance to humans (Mennill et al., 2003). In addition, males had significantly larger black bibs than did females, but there was no rank-based variation in the size of those bibs among males (Mennill et al., 2003). However, males of high and low dominance rank differed significantly in their black cap and grey mantle plumage coloration (Mennill et al., 2003).

Here we investigate whether achromatic plumage may serve as a signal of quality by examining the relation between achromatic plumage reflectance and reproductive success in male black-capped chickadees. Although they are socially monogamous, black-capped chickadees have a sexually promiscuous mating system whereby females obtain extrapair copulations from high-ranking neighbors (Mennill et al., 2004; Otter et al., 1998; Smith, 1988). In this study, we document how achromatic plumage reflectance, patch size, dominance rank, and body condition relate to various measures of male reproductive success.

METHODS

During January 2001, we captured black-capped chickadees at Queen's University Biological Station (44° 34' N, 76° 19' W; 40 km north of Kingston, Ontario, Canada) using Potter traps baited with sunflower seeds. We color-banded each bird and collected a small blood sample to determine its sex by

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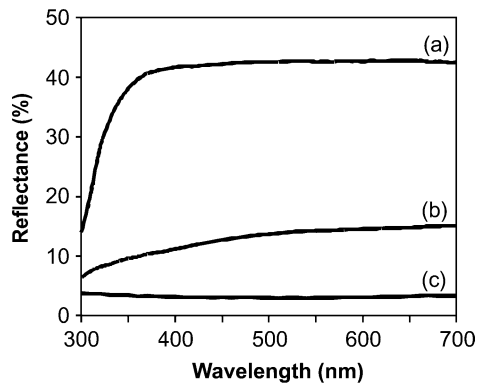


Figure 1
Representative plumage reflectance spectra for white (a), gray (b), and black (c) body regions in male black-capped chickadees. Shown here are average reflectance spectra ($n = 40$ males) for the white cheek patch, the gray mantle, and the black cap.

molecular analysis using sex-specific primers (Griffiths et al., 1998) and to perform paternity analyses (described below). We determined the age class (second-year versus after-second-year) of every individual by assessing the shape of its outer rectrices (Pyle, 1997; Smith, 1991). We calculated the absolute age of after-second-year birds from our long-term banding records.

Dominance rank assessment

We assessed male dominance hierarchies within winter flocks by tabulating pairwise interactions between color-banded birds at feeders. Between February and April, we observed 4000 pairwise dominance interactions between birds in 29 flocks ($n = 4\text{--}9$ birds/flock). 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). To obtain a continuous measure of rank for males in this population, we calculated a rank score as the number of interactions a male won divided by the total number of interactions he was involved in. This rank score was significantly correlated with the nominal rank scores (low, mid, high) used in other studies of this population (Spearman rank correlation, $r_s = .74$, $n = 40$, $p < .0001$; Otter et al., 1998).

Plumage measurements

From late February to early April, we recaptured 40 male chickadees and measured their plumage coloration using an Ocean Optics S2000 spectrometer and a PX-2 pulsed xenon lamp (Ocean Optics, Dunedin, Florida, USA)—see Mennill et al. (2003) for detailed methods of color measurements. Briefly, we measured plumage reflectance on five body regions of each individual: white cheek patch (behind the auriculars), white breast, black cap, black bib, and gray mantle (Figure 1). We obtained five readings from each region, moving the probe at least 5 mm before taking each reading. We used an average reflectance curve from the five readings for each region in the following analyses.

We measured the tarsus length and mass of each male and used the residuals from the regression of mass on tarsus (both log-transformed) as an index of body condition at the time of color quantification.

We restricted spectral analyses to wavelengths from 300–700 nm, a range generally corresponding to the chickadee visual spectrum (Chen and Goldsmith, 1986; Cuthill et al., 2000).

We summarized plumage reflectance data by calculating two color variables that seemed likely to vary among individuals in species with achromatic plumage: brightness and UV-chroma. We calculated brightness as the average percent reflectance in the 300–700 nm range and UV-chroma as the proportion of total reflectance occurring from 300–400 nm. We chose to focus on UV-chroma because, in other achromatically-colored species, UV reflectance has been shown to be important both in mate choice (Bennett et al., 1996; Siitari et al., 2002) and as a quality indicator (Siitari and Huhta, 2002). Also, in our data set, the coefficient of variation in UV-chroma was much greater than the coefficient of variation in blue, red, and green chroma for all five body regions measured (unpublished data). We averaged these color variables separately for white (cheek, breast) and melanin-based plumage regions (bib, cap, and mantle). We analyzed these two plumage types separately because white feathers contain no pigment and the shape of their reflectance spectra is largely determined by feather microstructure (Prum 1999), whereas black and gray feathers contain melanin, which largely determines the shape of their spectra.

There was no significant relation between date of capture and any of the color variables (all $r_s < .23$, $p > .15$). Thus, there was no indication that plumage wear unduly influenced the plumage color of these birds.

Patch size

We also measured the size of two black plumage patches in a subset ($n = 29$) of the males captured in this study. To do this, we photographed the melanin-colored bib and cap of each male by holding the bird against a ruled background at a standard distance from the camera lens, with the bill parallel to the body such that the base of the skull rested on the scapula (see Mennill et al., 2003; Otter and Ratcliffe, 1999). Approximately life-size photos were scanned at 8-bit grayscale on an HP Scanjet 7400c scanner. Bib and cap area were measured using a standardized thresholding procedure in ImageJ software (U.S. National Institutes of Health; <http://rsb.info.nih.gov/ij/>).

Assessing reproductive success

Throughout the study period, we closely monitored the 40 males for whom we had plumage reflectance information. We censused winter flocks every five to seven days between January and March and observed breeding pairs every two or three days from April to June. For all males that survived to the breeding season ($n = 38$), we noted whether they successfully paired, whether their partner laid eggs, and the number of offspring that fledged from their nests.

For paternity analyses, we collected a small blood sample from each nestling when it was approximately seven days old. We assigned paternity by polymerase chain reaction (PCR) amplification using radioactively-labeled primers for three highly variable microsatellite loci with combined exclusionary power of 0.995 (Mennill et al., 2004). We assessed band sharing on polyacrylamide gel autoradiographs. Offspring were considered to be extrapair if their microsatellite bands did not match those of their social father at two or more loci (no offspring mismatched their social mother). To assign extrapair paternity, we scored each individual's allele combinations relative to a standard run in 2–4 lanes on every gel. We compared the genotypes of extrapair offspring to those of all known males and re-ran gels with putative extrapair fathers next to extrapair offspring at all three loci to confirm assignments. For each extrapair offspring, only a single male was identified as the possible father.

Table 1

Nominal logistic regression predicting whether male black-capped chickadees' social mates laid eggs in relation to the male's dominance rank, age, body condition, and plumage color variables

Predictors	Partner laid eggs?	
	χ^2	<i>p</i>
Dominance rank	4.64	.02
Age	0.49	.22
Body condition	0.21	.66
White brightness	0.02	.13
White UV-chroma	3.29	.06
Melanin brightness	0.03	.87
Melanin UV-chroma	0.25	.61

Whole model $\chi^2 = 18.18$, $n = 34$, $p = .01$.

RESULTS

Dominance rank score was not significantly related to body condition ($r = .16$, $n = 40$, $p = .31$). Rank score was, however, related to the brightness of a male's white plumage regions ($r = .32$, $n = 40$, $p = .04$). No other plumage color variables were significantly associated with dominance rank (white UV-chroma, $r = -.10$, $n = 40$, $p = .55$; melanin brightness $r = .19$, $n = 40$, $p = .34$; melanin UV-chroma, $r = .02$, $n = 40$, $p = .19$), nor were any of the plumage color variables significantly related to body condition (white brightness, $r = -.003$, $n = 40$, $p = .83$; white UV-chroma, $r = -.01$, $n = 40$, $p = .95$; black brightness, $r = .11$, $n = 40$, $p = .50$; black UV-chroma, $r = -.01$, $n = 40$, $p = .96$).

The 2001 breeding season was unusual in that the density of chickadees in our study site was about twice the average from 1997 to 2002 (Mennill DJ, unpublished data). Although most of the birds in our study began excavating nest cavities, many pairs aborted their breeding attempts at various stages of the breeding cycle. Thus, of the 40 males we measured in winter, two died before they had the opportunity to breed, five failed to find a partner, and 10 had a partner who failed to lay eggs. Of the males who were alive at the beginning of the breeding season and successfully paired with a female, dominance rank was the best predictor of whether their partner eventually laid eggs (Table 1), although the UV-chroma of white plumage regions also approached significance.

Reproductive success and color

Of the 67 offspring that we monitored, 14 (21%) were identified as extrapair, and these were distributed among 50% of the broods. To determine the capacity of plumage color, dominance rank, and body condition to predict the reproductive success of male black-capped chickadees, we constructed stepwise multiple regression models using a backward elimination procedure. We included male dominance rank, body condition, and the four color variables as potential predictor variables and different measures of reproductive success as the dependent variable in each model. For males that successfully fledged at least one offspring ($n = 12$), none of these independent variables significantly predicted the number of young fledged from a male's brood (apparent reproductive success; all $p > .15$). However, when we accounted for extrapair fertilizations, both the brightness of a male's white plumage regions and the UV-chroma of his melanin-based plumage regions were significant positive predictors of the proportion of within-pair young in his nest (Table 2; Figure 2).

Table 2

Significant predictors of male reproductive success from multiple regression models constructed using a backward stepwise procedure

	R^2	β^a	df	<i>p</i>
Apparent reproductive success				
No significant predictors				
Proportion of within-pair young				
Whole model	.65		2, 9	.008
White brightness	.38	1.01	1, 10	.002
Melanin UV-chroma	.27	0.65	1, 10	.03
Overall realized reproductive success				
Melanin UV-chroma	.20		1, 38	.01

^a Standardized partial regression coefficients.

Each model was constructed using the four color variables (see Table 1), dominance rank, and body condition as potential predictor variables. Dependent variables (measures of male reproductive success) are shown in bold. Probability to leave the model was set at 0.05.

We also analyzed these same variables for all 40 males that we measured in winter, assigning zero fledglings to males who did not survive to breed, failed to attract a breeding partner, or whose partner failed to lay or hatch any eggs. In this analysis a male's overall realized reproductive success was significantly positively predicted by the UV-chroma of his melanin-based plumage regions (Table 2). Accordingly, males who fledged at least one offspring had greater UV-chroma in their melanin-based plumage regions than males who did not fledge any offspring (ANOVA, $F_{1,38} = 7.32$, $p = .01$; Figure 3).

Reproductive success and patch size

The sample of males for whom we had reproductive success, patch size, and plumage color data was too small to allow for a multivariate comparison of the relative importance of patch size and plumage color in predicting male reproductive success. However, univariate analyses suggest that male reproductive success may also be related to patch size. Bib area was not related to a male's apparent reproductive success ($r = .30$, $n = 10$, $p = .4$) nor to the proportion of within-pair young in his nest ($r = .57$, $n = 10$, $p = .09$). Bib area was, however, related to a male's realized reproductive success ($r = .77$, $n = 10$, $p = .008$). Cap area was not related to any measure of reproductive success (all $p > .6$).

DISCUSSION

Achromatic plumage reflectance predicts various components of reproductive success among male black-capped chickadees. In particular, males with brighter white plumage and greater UV-chroma in their melanin-based plumage sired a larger proportion of the offspring in their nests. Moreover, if we consider all males we measured, assigning zero reproductive success values to males who failed to sire any young, the UV-chroma of melanin-based plumage was a significant positive predictor of overall reproductive success. Thus, there was a clear association between the reflectance properties of achromatic plumage patches and male reproductive success. Our findings expand on those of Siitari and Huhta (2002), who showed that the UV-chroma of achromatic plumage in migratory male pied flycatchers was related to their arrival date on the breeding grounds, a correlate of reproductive success.

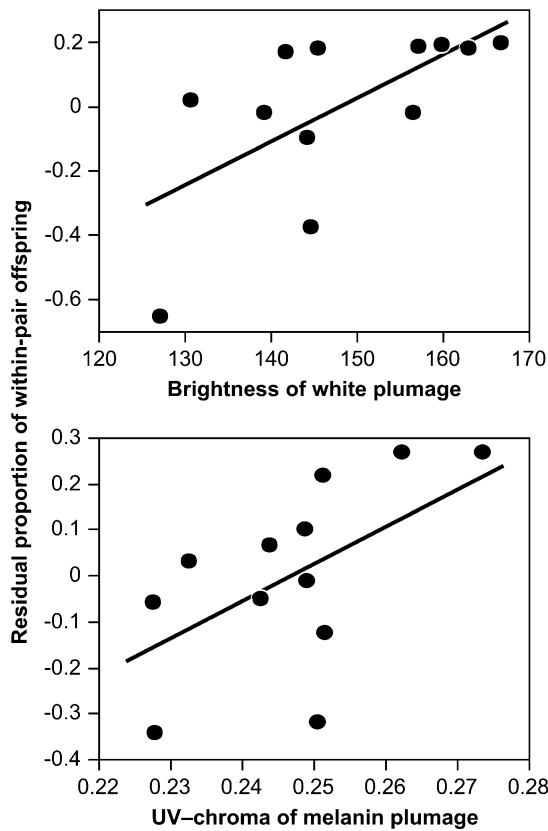


Figure 2
 Relationship between proportion of within-pair offspring and both the brightness of white plumage and the UV-chroma of melanin-based plumage among male black-capped chickadees who fledged at least one offspring ($n = 12$). Values for proportion of within-pair offspring were obtained from the fitted partial residuals of the multiple regression analysis shown in Table 2.

In many respects, the mating system of black-capped chickadees is well understood. We know, for example, that mating opportunities are influenced by male dominance in winter flock hierarchies: females paired to low-ranking males seek extrapair copulations from high-ranking neighbors (Mennill et al., 2004; Otter et al., 1998; Smith, 1988). Females paired to high-ranking males also lay larger clutches (Otter et al., 1999). Likewise, we show here that a male's dominance rank can predict whether or not he is likely to breed with a partner who successfully lays eggs. We also know that male song is closely associated with dominance status and reproductive success; high-ranking males have greater song output during the dawn chorus (Otter et al., 1997), and high-ranking males who hear an aggressive playback from simulated intruders are more likely to lose paternity in their nests than control males (Mennill et al., 2002). The patterns described in this and other recent studies (Mennill et al., 2003; Siitari and Huhta, 2002) suggest that achromatic plumage variation may be more important in female choice-driven sexual selection than previously thought. In fact, in our study population, plumage color appears to be a better predictor of reproductive success than dominance rank, age, and body condition. However, our investigation does not allow us to determine whether females use achromatic plumage variation as a signal of male quality. Moreover, several different mechanisms may be responsible for color variation among males (Mennill et al., 2003). Thus, controlled mate choice experiments and studies identifying the honesty-

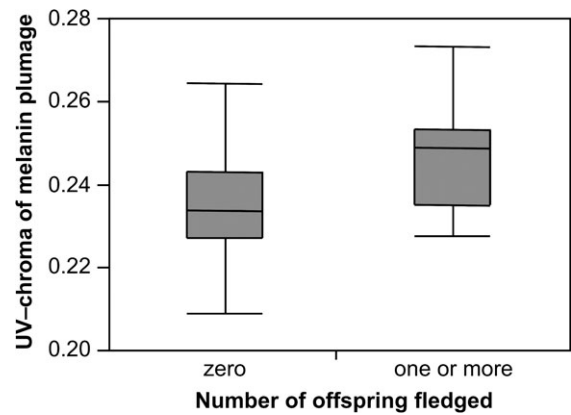


Figure 3
 Box plot showing the difference in UV-chroma of melanin-based plumage between males who failed to fledge any offspring and males who fledged at least one offspring ($n = 40$). Horizontal lines show 10th, 25th, 50th, 75th, and 90th percentiles.

maintaining mechanism of achromatic plumage reflectance will make an important contribution to our understanding of this often-overlooked plumage ornament.

We also show that the size of a male's black bib, a sexually dimorphic trait (Mennill et al., 2003; Otter and Ratcliffe, 1999), is positively related to his realized reproductive success. Our findings therefore suggest that both patch size and achromatic plumage reflectance may influence female mate choice in black-capped chickadees. In fact, these plumage traits may be good candidates for a multiple signal system, as plumage color and patch size might signal different aspects of male quality (e.g., Badyaev et al., 2001; Doucet and Montgomerie, 2003a) or might be used independently in female mate choice versus male-male competition (e.g., Pryke et al., 2001). Future studies should consider the interacting effects of these two signals; experimental manipulations of patch size and color would be particularly revealing.

Our findings may have important implications for studies of sexual signaling in birds. Achromatic plumage reflectance is widespread (Mennill et al., 2003), yet comparative studies of sexual ornamentation either categorize only the patch size of achromatic plumage regions or exclude some types of achromatic variation altogether (e.g., white or gray plumage patches; Gray, 1996). Moreover, few intraspecific studies have considered a female mate choice function of achromatic plumage patches (e.g., Møller, 1988; Sætre et al., 1994; Thusius et al., 2001), and fewer still have investigated variation in reflectance within these patches (Mennill et al., 2003; Siitari and Huhta, 2002). Our findings, along with other recent studies (Andersson et al., 1998; Cuthill et al., 1999; Hunt et al., 1998), also suggest that using apparent plumage dichromatism as a proxy for intensity of sexual selection (e.g., Barraclough et al., 1995) may be misleading, particularly in species where the mating system provides opportunity for sexual selection.

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