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## **STRUCTURAL PLUMAGE COLORATION, MALE BODY SIZE, AND CONDITION IN THE BLUE-BLACK GRASSQUIT**

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# STRUCTURAL PLUMAGE COLORATION, MALE BODY SIZE, AND CONDITION IN THE BLUE-BLACK GRASSQUIT

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**Abstract.** In birds, the colors ultraviolet, blue, and green originate from feather microstructure rather than pigmentation. Structural plumage coloration may be maintained by sexual selection, yet there exists only limited evidence that structural colors can honestly signal individual quality. In this study, I found considerable individual variation in the blue-black to ultraviolet coloration of the wing coverts and rump of male Blue-black Grassquits (*Volatinia jacarina*), thereby revealing the potential for sexual selection on structural plumage coloration in this species. I used a principal components analysis (PCA) of four color characteristics to combine reflectance data into a single color score. Birds with high color scores have brighter, more intensely colored, and more saturated blue-black feathers. There was a significant positive relationship between color scores for both body regions and male condition. There was also a positive trend between the color score of the rump region and male body size. These results support recent findings that structural plumage coloration is condition-dependent, and this type of coloration may be an honest signal of male quality in the Blue-black Grassquit.

**Key words:** *Blue-black Grassquit, condition, honest advertisement, plumage, sexual selection, structural colors, Volatinia jacarina.*

## Coloración Estructural del Plumaje, Tamaño Corporal y Condición Física en Machos de *Volatinia jacarina*

**Resumen.** En las aves, los colores ultravioleta, azul y verde están dados por la microestructura de las plumas y no por la pigmentación. La coloración estructural del plumaje puede ser mantenida por selección sexual, aunque existe poca evidencia que indique que los colores estructurales son un indicador confiable de la calidad de un individuo. En este estudio encontré variación individual considerable en la coloración negro-azulada a ultravioleta de las cobertoras alares y la rabadilla de machos de *Volatinia jacarina*, revelando que la coloración estructural del plumaje en esta especie podría estar sujeta a selección sexual. Utilicé un análisis de componentes principales (PCA) de cuatro características de color para combinar datos de reflectancia en un solo valor de color. Las aves con altos valores de color tienen plumas más brillantes e intensamente coloreadas y más saturadas de color negro-azulado. Existió una relación positiva significativa entre los valores de color para ambas regiones del cuerpo y la condición física de los machos. También hubo una tendencia positiva entre el valor del color de la región de la rabadilla y el tamaño corporal de los machos. Estos resultados apoyan descubrimientos recientes que demuestran que la coloración estructural del plumaje depende de la condición física, y que este tipo de coloración puede ser una señal confiable de la calidad de los machos de *V. jacarina*.

## INTRODUCTION

Brilliant colors, particularly in birds, have long been considered a classic example of extreme trait expression driven by sexual selection (Darwin 1871). Considerable attention has been devoted to investigating how individual coloration functions as a signal influencing female mate choice and male-male competition (Andersson 1994). Although much of the research to date has focused on pigment-based colors, the sig-

naling potential of structural coloration has recently generated considerable interest.

Structural colors are ultraviolet, blue, and green colors, which originate from reflective feather microstructure rather than pigmentation. Structural colors superficially appear to lack the extensive variation in hue described in the carotenoid coloration of some species (Hill 1991, Hill and Montgomerie 1994) and the variation in patch size described in the melanin coloration of other species (Järvi and Bakken 1984, Møller 1987). However, this apparent lack of variation may be biased by the limitations of human vision. While humans have only three types of vi-

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sual cones, most birds have tetrachromatic vision, which includes sensitivity at shorter wavelengths (Cuthill et al. 2000). This sensitivity in the short wavelength region of the electromagnetic spectrum enables birds to detect ultraviolet wavelengths (300–400 nm) and allows for enhanced discrimination at all shorter wavelengths from ultraviolet to blue (Cuthill et al. 2000). Not surprisingly, the recent use of spectrometry as an objective measure of plumage coloration has revealed considerable individual variation in structural plumage coloration, particularly in the ultraviolet range (Andersson and Amundsen 1997, Bennett et al. 1997, Hunt et al. 1998, Keyser and Hill 1999). In fact, Keyser and Hill (1999) describe variation in the structural coloration of Blue Grosbeaks (*Guiraca caerulea*) comparable to the conspicuous variation of the carotenoid coloration in House Finches (*Carduelis mexicanus*; Hill 1991).

Variation in structural plumage characters appears to be maintained by sexual selection via female choice in several species, including Blue Tits (*Parus caeruleus*; Andersson et al. 1998, Hunt et al. 1998, Sheldon et al. 1999), captive and wild Bluethroats (*Luscinia svecica*; Andersson and Amundsen 1997, Johnsen et al. 1998), and European Starlings (*Sturnus vulgaris*; Bennett et al. 1997). However, the role of structural plumage coloration for intrasexual signaling remains largely unexplored, although some studies suggest that structural colors could serve as status signals in male-male competition (Keyser and Hill 2000).

Honest advertisement theory predicts that extreme expression of ornamental traits can evolve by sexual selection if variation in the trait accurately reflects the relative quality of individuals expressing the trait (Zahavi 1975, 1977, Kodric-Brown and Brown 1984). Since structural plumage coloration appears to be maintained by sexual selection in some species, we might predict that variation in structural coloration reflects individual quality. Indeed, recent studies provide support for the quality-indicating potential of structural colors. In Blue Grosbeaks, male “blueness” is partially dependent on nutritional condition, and the bluest males also exhibit several ecological indicators of superior quality and condition (Keyser and Hill 1999, 2000). Furthermore, in Blue Tits the saturation of the ultraviolet coloration of the crest can predict survival to the following breeding season (Sheldon

et al. 1999). Although accumulating evidence suggests that structural colors can be sexually selected traits, these recent studies documenting trends in two species are the first to describe a relationship between structural plumage coloration and indices of individual quality. Further investigation is required to determine whether the quality-indicating potential of structural colors is limited to a few species or is a more widely distributed phenomenon.

In this study, I assessed the extent of natural variation in the blue-black coloration of male Blue-black Grassquits (*Volatinia jacarina*) to determine whether this structural color could function as a sexually selected signal. Furthermore, I measured several indicators of current and past condition as well as body size in the Blue-black Grassquit to investigate the signal function of structural plumage coloration in this species.

## METHODS

### STUDY SPECIES

The Blue-black Grassquit is a small, Neotropical resident songbird favoring open habitats and ranging from Mexico to northern Chile and Argentina (Alderton 1963). In Mexico, males are in basic plumage from October to May and in alternate plumage from May to August (Howell and Webb 1995). Males in basic plumage are brown with patches of blue-black feathers on the head and upperparts, and their wings and tail are blue-black edged with brown. This species is conspicuously dichromatic even while in basic plumage, as females are an overall brown color with a streaked buff breast (Howell and Webb 1995).

During the course of this study, adult males were in basic plumage and were not undergoing molt. There are several reasons why male basic plumage may serve some signaling function. First, Blue-black Grassquits form large, mixed-sex flocks during the nonbreeding season (Howell and Webb 1995), providing females with ample opportunity to observe males in basic plumage. Second, in American Goldfinches (*Carduelis tristis*), basic plumage coloration is a significant predictor of alternate plumage coloration (McGraw and Hill 2001). Third, in some species, intraspecific interactions during the nonbreeding season can influence social and extra-pair partner choice during the breeding season

(Otter et al. 1998). Finally, male Blue-black Grassquits perform territorial and mate-attraction displays early in the breeding season while still in basic plumage (Alderton 1963, Ridgely and Tudor 1989), and some males breed before acquiring alternate plumage (Ridgely and Tudor 1989).

The field component of this study was undertaken in February of 2000 near the small community of Nuevo Becal (17°49'N, 89°09'W), in the Yucatán Peninsula, Mexico. The study site was a shifting-cultivation agricultural field where successional vegetation was 1.5–2 m tall; the field was surrounded by secondary tropical forest. Thirteen males were captured by daily passive mist netting between 06:00 and 11:30 CST. I did not measure captured juveniles and females; however, I could not distinguish between second-year males and older males in basic plumage. I marked each male on the rump with a dot of acrylic paint prior to release to avoid resampling the same individuals.

I recorded standard morphological measurements of captured birds. I also estimated the percentage of blue-black coverage (to the nearest 5%) on the crown, breast, mantle, rump, wing (including coverts) and tail of each male. This assessment has been found to be highly repeatable in a similar study (Keyser and Hill 1999). I used the mean percentage of all six body regions in statistical comparisons. Two of the males were released before this assessment was made.

I removed three to five wing covert and rump feathers from each bird for the spectral analysis of Blue-black Grassquit coloration (these body regions had the greatest percentage of blue-black coverage; 17% and 25% respectively). The feathers were removed from the center of these small patches to approximate the natural color patterns on these patches. I also removed the left outer rectrix of each male to assess daily growth rates (Michener and Michener 1938, Grubb 1989). One male was missing both outer tail feathers, so I did not assess feather growth rate for that individual.

#### SPECTRAL CHARACTERISTICS

To assess the spectral reflectance of the wing coverts and the rump, I taped individual feathers onto a nonreflective black velvet surface. I measured the feathers with an Ocean Optics S2000 spectrometer (Dunedin, Florida) combined with

a deuterium tungsten halogen light source (Analytical Instrument Systems, Inc., Flemington, New Jersey). The combined-spectrum light source provides illumination in both the ultraviolet region and the human visual spectrum (range 220–1000 nm). All measurements are expressed as the percent reflectance relative to the reflectance of a Spectralon® white standard, which reflects 97–99% of incident light. I measured feather reflectance with a fiber-optic probe that provides illumination from the light source and transfers reflected light to the spectrometer. The probe was held at a 90° angle, 3 mm from the feather surface, with a metal probe holder that excluded all external light from the measurement area. I took a Spectralon® reading before and after measuring each feather. I measured single feathers two to five times, placing the probe at an arbitrary location on the feather before each reading. I took dark and reference readings before measuring feathers from each individual. I calculated average percent reflectance curves, with readings at every 0.3 nm from 320 to 700 nm, for both the wing coverts and rump of every male. It should be noted that the percent reflectance curves obtained were relatively low because the transparency of the feathers did not allow them to fill the entire measurement field, letting the dark background show through. As such, the reflectance data reported here are likely underestimates of absolute percent reflectance values. Thus the magnitude of the percent reflectance data for Blue-black Grassquits is better suited for relative comparisons between individuals rather than interspecific comparisons.

The analyses of the spectral reflectance data were restricted to wavelengths between 320 and 700 nm, as evidence suggests there is a sharp decrease in lens transmission of the avian eye at 320 nm (Goldsmith 1990, Maier 1994), and 700 nm is likely the upper limit of the vertebrate visual spectrum (Lythgoe 1979, Jacobs 1981). To allow for simpler comparisons between color characteristics and indicators of male body size and condition, I summarized the reflectance data by computing values for brightness, intensity, hue, contrast, and chroma for both body regions (Endler 1990, Andersson 1999, Keyser and Hill 1999). Brightness ( $R_{320-700}$ ) is a measure of the total light reflected by the feather surface, and is calculated as the sum of percent reflectance values from 320 nm to 700 nm. The intensity of

TABLE 1. Eigenvectors for the first principal component (PC1) of a principal components analysis performed on four color characteristics for each of two body regions of the Blue-black Grassquit.

Variable	Wing coverts <i>n</i> = 13	Rump <i>n</i> = 12
Brightness	0.59	0.59
Intensity	0.61	0.61
Contrast	0.53	0.53
Peak $\lambda$	-0.05	-0.06
Eigenvalue	2.68	2.63
Variance explained (%)	67	66

the color is the maximum reflectance reached ( $R_{\max}$ ). The hue of the color is approximated as the wavelength of maximum reflectance ( $\lambda R_{\max}$ ). The contrast of the color, calculated as the difference between the maximum and minimum reflectance ( $R_{\max} - R_{\min}$ ), describes the spectral saturation of the color; more contrast indicates a richer color. Chroma, describing spectral purity, is the ratio of the total reflectance in the range of interest and the total reflectance of the entire spectrum (chroma;  $R_{\text{range}}/R_{320-700}$ ). For each bird, I calculated the UV chroma ( $R_{320-400}/R_{320-700}$ ) and the blue chroma ( $R_{400-500}/R_{320-700}$ ). The wavelength ranges were selected for the chroma computations by considering the intersection of lines describing the sensitivity of four cone types isolated in passerines (Bowmaker et al. 1997) and are meant to approximate the chroma of interest.

To summarize variation in spectral characteristics, I performed a principal components analysis (PCA) for each body region using the brightness, hue, intensity, and contrast variables calculated from the average reflectance curves. The first principal component (PC1) explained about two-thirds of the variation in structural plumage coloration for both the wing coverts and the rump (Table 1) and was the only principal component used in this study. The PC1 had strong positive loading from intensity, contrast, and brightness in both body regions, while wavelength at peak reflectance had a negligible negative influence on the PC1 (Table 1). Thus, birds with a high PC1 score were brighter, more intensely colored, showed greater spectral saturation, and tended to reflect maximally in the deep blue to ultraviolet range of the spectrum. I did not include the two calculated chroma values in the PCA as they decreased the amount of var-

iation in color that could be explained by PC1, thereby reducing its usefulness as a general color index. However, including both chroma values in the PCA did not change the significance of the main findings of this study.

#### MALE BODY SIZE AND CONDITION

I used wing chord length as the primary measure of body size in this study (Lemel and Wallin 1993, Keyser and Hill 2000). I also measured the tarsus length, tail length, and body mass of each male. As an index of current condition, I assessed the degree of fat stored in the furcula on a scale from 0 to 5 (Helms and Drury 1960). I also measured the width of alternating light and dark bands on the outer rectrices of the grassquits to assess feather growth rates (Michener and Michener 1938). Estimates of daily growth rates based on measurement of these growth bars have been shown to directly depend on nutritional condition in several passerines (Grubb 1989, 1991, Jenkins et al. 2001). Therefore, I used the daily growth rate of feathers as an indicator of nutritional condition of males during the previous molt period.

Growth bars were measured blind to identity of the bird from which the feather was collected. To measure the growth bars, I taped the outer rectrix of each male onto an index card. I then inserted an insect pin through the feather, piercing the index card underneath, to mark the proximal and distal ends of the feather and the center of every dark band I could clearly see. Since growth bars were more easily distinguishable near the distal end of the feather, I used a dissection microscope to measure the width of nine growth bars centered on a point two-thirds the length of the feather from the proximal end, and calculated a nine-day average daily growth rate (Grubb 1989).

#### STATISTICAL ANALYSES

I performed Shapiro-Wilk tests of normality on all of the variables calculated in this study to determine whether the distribution of each variable departed significantly from normality. When distributions were normal or when they could be normalized by standard transformations, I used parametric statistical tests. In some cases the data could not be normalized and I used nonparametric tests with those variables. All probabilities are two-tailed and values are reported as means  $\pm$  SE. I used a sequential

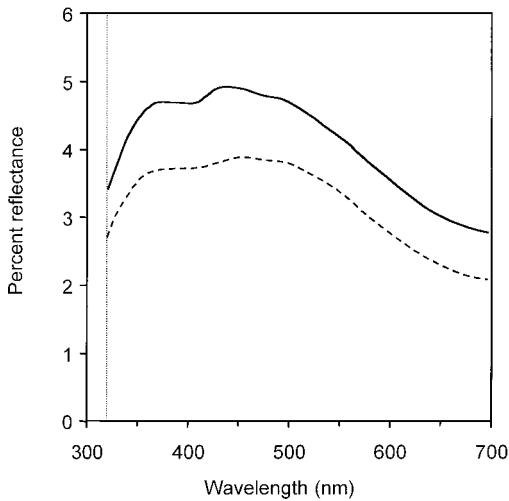


FIGURE 1. Average reflectance spectra of typical “blue” male Blue-black Grassquits (hue <math><600\text{ nm}</math>) for the wing coverts (solid line) and the rump (dashed line).

Bonferroni correction with a table-wide significance level of 10% each time I compared the six calculated plumage characteristics with either condition or body size (Chandler 1995); I only report results that remained significant after the Bonferroni correction was applied.

## RESULTS

Male Blue-black Grassquits reflected most strongly in the blue and ultraviolet regions of the spectrum for both the wing coverts and the rump (Fig. 1). The average reflectance curve for the rump region appeared lower than that of the wing coverts (Fig. 1); however there was no significant difference between the rump and wing coverts for any of the six spectral variables calculated (paired  $t$ -tests, all  $P > 0.3$ ) or the PC1 color scores (paired  $t$ -test,  $t_{11} = 0.6$ ,  $P > 0.6$ ). There was considerable variation between individuals in the size and shape of reflectance curves and spectral characteristics within each body region, with the brightest individuals having values more than twice as high as the duller individuals.

Despite individual variation in spectral characteristics, most males showed peak reflectance values in a relatively narrow range. For the wing coverts, 7 of 13 individuals reflected maximally in the ultraviolet range (320–400 nm), three in the blue range (400–500 nm), and three in the “brown” range (>600 nm). For the rump re-

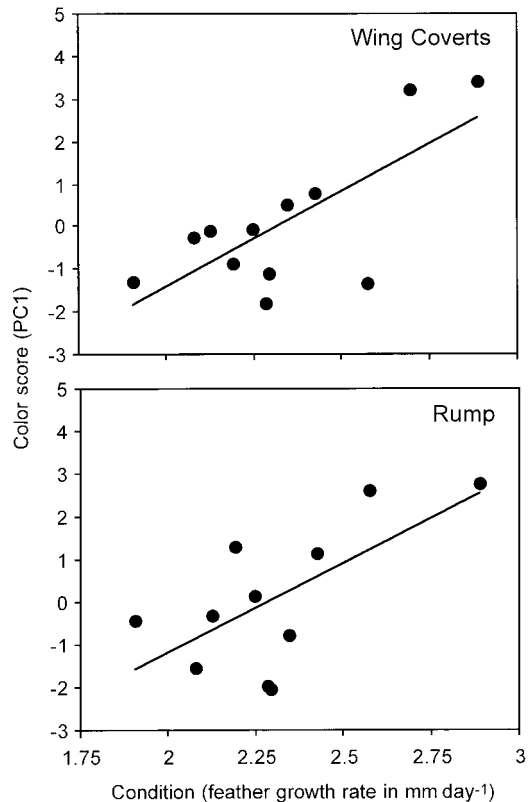


FIGURE 2. Relationship between plumage spectral characteristics and condition in Blue-black Grassquits. Trend lines indicate significant relationships. There is a significant positive relationship between color scores (PC1 of a PCA combining brightness, intensity, contrast, and hue) and male condition (feather growth rate) for both the wing coverts ( $r = 0.72$ ,  $n = 12$ ,  $P < 0.01$ ) and the rump ( $r = 0.65$ ,  $n = 11$ ,  $P = 0.03$ ).

gion, 9 of 12 individuals reflected maximally in the ultraviolet range, two in the blue range, and one in the brown range. Such variation in wavelength of maximum reflectance has also been described in Blue Grosbeaks (Keyser and Hill 1999). Exclusion of the “brown” ( $\lambda R_{\max} > 600$  nm) males did not change the significance of the main findings of this study, and therefore all birds were considered in the following analyses.

## CONDITION

Male condition, as measured by feather growth rate, was significantly positively related to the first principal component describing color for both body regions (Fig. 2). Thus males with high color scores were in better condition than males with low color scores. Analyzing the color char-

acteristics individually revealed that this pattern was principally driven by a significant positive relationship between condition and the brightness of wing coverts ( $r = 0.74$ ,  $n = 12$ ,  $P = 0.01$ ). None of the other individual color characteristics of the wing coverts or rump were significantly related to condition after sequential Bonferroni correction (Pearson or Spearman correlations,  $r$  or  $r_s = 0.06$ – $0.66$ , all  $P > 0.02$ ).

There was also a significant positive relationship between condition and the mean percentage of blue-black feathers over six body regions of male Blue-black Grassquits ( $r = 0.64$ ,  $n = 10$ ,  $P = 0.04$ ). There was no relationship between fat score and any of the spectral characteristics of the feathers of either body region or the average percentage of blue-black feathers on the birds (Spearman correlations,  $r_s = 0.08$ – $0.40$ , all  $P > 0.1$ ). Another measure of body condition, calculated as the residuals of body mass over tarsus length, was unrelated to any of the spectral characteristics of either body region or the percentage of blue-black coverage on the grassquits ( $r$  or  $r_s = 0.01$ – $0.42$ , all  $P > 0.1$ ).

#### BODY SIZE

Body size, as measured by wing chord (mm), was not related to the first principal component describing the color of the wing coverts (Fig. 3). There was, however, a nearly significant relationship between body size and the color score for the rump region (Fig. 3). No individual spectral characteristic was related to body size after sequential Bonferroni correction ( $r$  or  $r_s = 0.11$ – $0.61$ , all  $P > 0.02$ ). There was no relationship between body size and the mean percentage of blue-black feathers over six body regions on the males ( $r = 0.48$ ,  $n = 11$ ,  $P = 0.13$ ). Male body size was not related to male condition ( $r = 0.20$ ,  $n = 12$ ,  $P > 0.5$ ).

#### DISCUSSION

Detailed spectral measurements of the blue-black coloration of the wing coverts and rump of male Blue-black Grassquits revealed extensive individual variation in color, unveiling the potential for sexual selection on this trait. These findings support a growing body of literature suggesting that structural colors may be sexually selected; however mate choice studies are required to confirm that females of this little-studied passerine can and do select mates on the basis of plumage coloration. Interestingly, many of

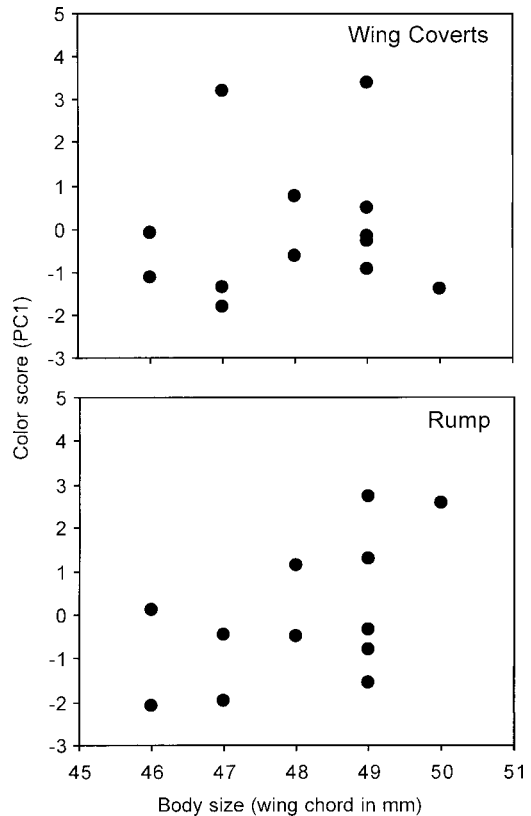


FIGURE 3. There is no relationship between body size (wing chord) and color scores (PC1) of the wing coverts of male Blue-black Grassquits ( $r = 0.08$ ,  $n = 13$ ,  $P = 0.78$ ). There is a nearly significant relationship between body size and spectral characteristics of the rump ( $r = 0.55$ ,  $n = 12$ ,  $P = 0.06$ ).

the birds reached maximum reflectance in the ultraviolet range, where most of the individual variation in color was concentrated.

Variation in color score was significantly positively related to the condition of the males, and explained a considerable proportion of the variation in male condition. This relationship suggests that structural coloration is condition-dependent in the Blue-black Grassquit, mirroring similar findings in the Blue Grosbeak (Keyser and Hill 1999). Removing brown males ( $\lambda R_{\max} > 600$  nm) from the analyses did not change the significance of the results; thus it is unlikely that the relationship between plumage coloration and condition is simply an artifact of age. These findings suggest that conspecifics could reliably assess male condition from overall variation in structural plumage coloration.



There was a positive trend between body size and the plumage color score of the rump, but not the wing coverts, in male Blue-black Grassquits. That is, the rump coloration of larger birds tended to be brighter and more intense with greater blue saturation, although these individual relationships were not significant after sequential Bonferroni correction. If body size is a measure of quality, the positive trend between body size and rump color characteristics suggests that condition-dependent structural coloration has the potential to reveal male quality in Blue-black Grassquits, although further study is required to confirm this.

Male rump coloration in particular may serve in intrasexual signaling. Many species of birds use patches of coloration as badges of social status, particularly during the nonbreeding season (Andersson 1994). These signals may be used as indicators of fighting ability, consequently reducing the need to resort to aggressive and often costly interactions (Rohwer and Ewald 1981). Birds are thought to have the most sophisticated color vision system among vertebrates (Cuthill et al. 2000). Thus, variation in structural coloration and percentage of blue-black coverage could serve as an indicator of male condition, body size, and perhaps social status in Blue-black Grassquits, thereby reducing the need for escalated contests over status or resources.

It may seem unusual that although both rump and wing color characteristics were significantly related to condition, only rump color characteristics appeared to be associated with body size. However, Keyser and Hill (2000) found that rump blueness was significantly related to body size, as well as male territory size, in male Blue Grosbeaks. Moreover, male Blue Grosbeaks display their rump patches almost exclusively during male-male interactions and typically have blue feathers on the rump even when they are mostly brown on other body regions (Keyser and Hill 2000). It appears that male Blue-black Grassquits, like Blue Grosbeaks (Keyser and Hill 2000), may prioritize the development of blue feathers on the rump region, as this was the body region with the greatest percentage of blue feathers. The rump of the Blue-black Grassquit is also apparent during its song display. Throughout the year, with increased frequency during the breeding season, males repeatedly fly up and down a short distance from perches in grassy fields while singing an explosive, buzzy

song (Weathers 1986, Ridgely and Tudor 1989). This conspicuous song and flight display appears to function in mate attraction and territory establishment (Alderton 1963, Almeida and Macedo 2001), and occurs while some males are in basic plumage (Alderton 1963, Ridgely and Tudor 1989). The rump is apparent throughout the entire display (Weathers 1986). My findings therefore suggest that Blue-black Grassquits use rump coloration as an intraspecific signal and may even use rump coloration as a status signal in male-male interactions.

Structural plumage coloration has been shown to be a sexually selected signal of quality, yet in contrast to pigment-based color signals (Olsen and Owens 1998), a mechanism whereby the honesty of structural color signals is maintained remains to be identified (Andersson 1999, Sheldon et al. 1999). Recent studies relating structural plumage characters to indicators of quality or viability, including this study, suggest that structural plumage coloration is not simply under runaway sexual selection (Fisher 1958). The handicap principle predicts that there must be a cost (handicap) associated with a signal for it to remain honest, so that only the fittest males can bear such costs (Zahavi 1975, 1977). One such cost may be increased predation pressure on brightly colored individuals by aerial predators (Slagsvold et al. 1995, but see Götmark 1994). A second potential cost is the cost of dominance itself; dominant males must fight to maintain their status (Ketterson 1979, Rohwer and Ewald 1981). If structural coloration is used as a male status signal, brighter males could suffer more frequent attacks, particularly from other dominant males (Mateos and Carranza 1997). There could also be a trade-off between the feather shape best amplifying the brightness of UV or blue coloration (Andersson 1999) and the feather shape most efficient for flight or thermoregulation. Alternatively, the costs associated with an honest signal may not directly affect survival, but could be related to costs of production and maintenance of the trait (Kodric-Brown and Brown 1984). Structural colors are produced by the constructive interference of coherently scattered light waves within the spongy medullary keratin matrix of feather barbs (Prum et al. 1998, 1999). The wavelength of the scattered light is dependent on the periodicity and spatial distribution of the scatterers (Prum et al. 1998, 1999). Thus, keratin deposition with the ideal period-

icity could conceivably be energetically costly, and birds in poor condition may not be able to devote as much energy to the task, such that production of the microstructure required could itself maintain the honesty of the signal. In contrast, it is perhaps unnecessary to incur costs in maintaining signal honesty; it has been suggested that structural coloration may amplify male quality (Fitzpatrick 1998). As with any amplifier, poor quality individuals who over-express the amplifying signal could incur high social costs (Hasson 1991, Fitzpatrick 1998). Alternatively, structural plumage coloration may be limited by parasite load (Hamilton and Zuk 1982). A number of these honesty-maintaining mechanisms of structural color signaling likely act in concert or vary between species. Empirical investigations of the honesty-maintaining mechanism of structural color signals are promising avenues for future research.

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