



FEATURE ARTICLES

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SEXUAL DICHROMATISM, DIMORPHISM, AND CONDITION-DEPENDENT COLORATION IN BLUE-TAILED BEE-EATERS

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Abstract. The Blue-tailed Bee-eater (*Merops philippinus*) is a cooperatively breeding and socially monogamous member of the Coraciiformes that displays conspicuous coloration and elongated central rectrices (“streamers”). Humans cannot distinguish males from females; both sexes are brightly colored with a chestnut throat patch, a yellow chin, and green body coloration fading into a turquoise-blue rump and tail. We quantified coloration with ultraviolet- (UV) visible spectrometry and measured morphology to determine the extent of sexual dichromatism and dimorphism. Males displayed more exaggerated coloration, longer tail streamers, and were larger than females. Multiple plumage ornaments (measures of plumage coloration and streamer length) were positively correlated in both sexes. Males in better body condition expressed darker chestnut throats and more chromatic green body plumage. Females in better body condition, however, exhibited more chromatic blue rumps and yellow chins. This study represents the first objective description of plumage ornamentation in the order Coraciiformes.

Key words: *bee-eaters, condition-dependent traits, Coraciiformes, dichromatism, dimorphism, Merops philippinus, plumage coloration.*

Dicromatismo y Dimorfismo Sexual y Coloración Dependiente de la Condición en *Merops philippinus*

Resumen. *Merops philippinus* es un Coraciiforme que presenta cría cooperativa y monogamia social, coloración ostentosa y rectrices centrales alargadas. Los humanos no pueden distinguir los machos de las hembras; ambos sexos presentan colores brillantes con un parche gular castaño, una barbilla amarilla y una coloración verde del cuerpo que se desvanece a una rabadilla y cola de color azul turquesa. Cuantificamos la coloración con espectrometría visible-ultravioleta (UV) y medimos la morfología para determinar la magnitud del dicromatismo y el dimorfismo sexual. Los machos presentaron una coloración más exagerada y rectrices centrales más largas y fueron más grandes que las hembras. Varios ornamentos del plumaje (medidas de la coloración del plumaje y de la longitud de las rectrices centrales) estuvieron correlacionados positivamente en ambos sexos. Los machos en mejor condición corporal presentaron gargantas castañas más oscuras y plumaje corporal más verde. Sin embargo, las hembras en mejor condición corporal exhibieron rabadillas cromáticas más azules y barbillas amarillas. Este estudio representa la primera descripción objetiva de las ornamentaciones del plumaje en el orden de los Coraciiformes.

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INTRODUCTION

Males and females of many species differ in their morphological and ornamental traits. Although there are many examples of extreme sexual dimorphism in birds, the differences between the sexes are often subtle (Barraclough and Harvey 1995). However, three lines of evidence suggest that historical definitions of sexual dichromatism in birds may be overly conservative. First, birds are likely capable of differentiating colors within human color space that humans cannot discriminate (Vorobyev and Osorio 1998, Vorobyev et al. 1998). Second, most birds can see ultraviolet (UV) or near-UV light (Cuthill et al. 2000, Ödeen and Håstad 2003). Third, UV-reflecting plumages are common in birds (Eaton and Lanyon 2003). Indeed, the sexes of many species that appear sexually monochromatic to humans are easily distinguished using models of avian color perception in combination with reflectance spectrometry (Eaton 2005).

We studied body size and ornamental plumage coloration of Blue-tailed Bee-eaters (*Merops philippinus*). The Blue-tailed Bee-eater (Coraciiformes: Meropidae) is a migratory species that ranges from New Guinea to southern China. Birds nest both in colonies and in dispersed nests, excavating burrows in dry, sandy soils (Fry et al. 1992, Yuan et al. 2006). This species is socially monogamous and sometimes breeds cooperatively (Burt 2002, Coulter 2003). Males and females are not readily distinguished by humans; both are brightly colored with a chestnut throat, yellow chin, and green body coloration fading into a teal-blue rump and tail, and two elongated central rectrices ("streamers"). Although the color discrimination ability of Blue-tailed Bee-eaters is unknown, data from other coraciiforms suggests that the cone corresponding to short wavelength light is more sensitive to violet (403–426 nm) than ultraviolet wavelengths (355–380 nm; Ödeen and Håstad 2003).

Here, we describe the plumage coloration of Blue-tailed Bee-eaters and determine whether the sexes are dichromatic and dimorphic. We investigate relationships among multiple ornamental plumage traits and test whether ornamentation is correlated with body condition. Although many species have been examined for dimorphism, the majority of studies have

addressed temperate passerines. In general, species from the tropics and from Asia have been less well studied. This study represents both the first description of plumage coloration using reflectance spectrometry and the first investigation of condition-dependent plumage in Coraciiformes.

METHODS

FIELD METHODS

We collected data from May to June 2004 at a study site located on the eastern shore of Kinmen Island (also known as Quemoy), situated in the Taiwan Strait about 5 km east of China's eastern shore (approximately 118°24'E, 24°27'N).

We monitored burrows using a digital video camera mounted on a 2 m stick. If a bird was detected in the burrow, we placed a hoop net over the entrance and captured the bird as it emerged from the burrow. We recorded the following measurements for each bird: length of tarsus, wing chord, tail length, middle tail feather ("streamer") length, bill length (length of exposed bill culmen), and mass. We collected eight feathers from each of four body regions: rump (blue), back (green), throat (chestnut), and chin (yellow). To determine sex, we collected blood samples from each individual via brachial venipuncture. Approximately 100 µl of whole blood was stored in 250 µl of lysis buffer (Seutin et al. 1991). Blood was stored at ambient temperature at the study site and later at -20°C in the laboratory. We calculated an index of body condition using the residuals of a mass to body size regression (principal components analysis of tarsus, wing, tail, and bill; Jakob et al. 1996). Each bird was fitted with an aluminum numbered band issued by the Wild Bird Federation of Taiwan and, using paint pens, we marked birds with a unique combination of three colors.

GENETIC SEXING METHODS

Whole genomic DNA was extracted from each blood sample using phenol-chloroform-isoamyl alcohol-based extractions and then stored in tris EDTA buffer at -20°C. Genetic sexing was performed using polymerase chain reaction (PCR) amplification of an intron in the sex-linked chromobox-helicase-DNA-binding gene (CHD). The W and Z avian sex chromosomes

differ in intron length and can be used as markers for sex determination (Griffith et al. 1998) with primers P2 and P8. We viewed PCR products with electrophoresis using 1.8% agarose gels and recorded images using a gel documentation system. Sex was determined by number of bands: females exhibited two bands (W and Z chromosomes) and males exhibited one band (homozygous ZZ; Griffith et al. 1998).

SPECTROMETRY

Methods are described in detail by Siefferman and Hill (2003). Briefly, we measured plumage reflectance of plucked feathers using an Ocean Optics (Dunedin, Florida) S2000 spectrometer (range 250–880 nm). We used a bifurcated fiber-optic measuring probe (Ocean Optics) which provided illumination from a lamp (light source had both UV [deuterium] and visible [tungsten-halogen] bulbs) and transferred light reflected from the feather sample back to the spectrometer. The bulbs illuminated a 1 mm diameter area of the feather and the probe was held at a 90° angle to the feather surface. Ambient light was excluded by a block sheath that held the probe tip at a fixed distance (1 mm) from the feather surface. All reflectance data were generated relative to a white standard (WS-1; Ocean Optics). We taped feathers to matte black paper in an overlapping fashion to approximate placement on the bird's body. We took five spectral readings from each of the four plumage regions of every individual captured (chin, throat, back, and rump). We moved the probe at least 1 mm before taking a new reading. All recordings were taken under controlled laboratory conditions. White measurements were taken between each sample. The five spectrometer measurements from the same body region were strongly correlated (all $r > 0.95$, all $P < 0.01$).

Spectral measurements were expressed as percent reflectance of light per wavelength. We summarized reflectance data by calculating standard descriptors of avian reflectance spectra for each body region (Montgomerie 2006). Because simple measurements of spectral location and shape are correlated with human-perceived hue, chroma, and brightness (Endler 1990), we refer to the following spectral measurements as color. For blue, green, and yellow plumage regions, we calculated chroma

and hue. For the chestnut region, we calculated chroma and overall reflectance. We calculated chroma, a measure of spectral purity, differently for each body region because of the inherent reflectance properties of the colors. For the green, blue, and chestnut feathers, chroma was calculated as the proportion of the total reflectance (R300–700) that was in the green, blue, or red part of the spectrum (green: R512–575, blue: R400–512, red: R575–700) and expressed as a percentage. For blue, green, and chestnut coloration, the more ornamented birds should have higher chroma scores. To estimate chroma for the yellow region we calculated blue chroma, because this part of the spectrum corresponds to the region of greatest carotenoid absorption (McGraw et al. 2001, McDougall and Montgomerie 2003). Thus, yellow plumage with low chroma should have more carotenoid pigments and be more ornamented. Hue is the principal color reflected by the feather and is calculated as the wavelength of maximum slope for blue, green, and yellow plumage. Because hue of chestnut coloration (calculated as the wavelength of maximum slope) was invariant among birds, we do not report chestnut hue. Overall brightness, however, is a good predictor of the amount of melanin deposited in chestnut feathers (McGraw et al. 2003) and was calculated as mean total reflectance (R300–700). Birds with lower overall brightness should have more melanin pigments and thus be considered more ornamented.

STATISTICAL ANALYSES

Sample sizes vary because the streamer feathers of a few individuals were obviously broken (and thus were excluded from analyses) and we occasionally failed to collect data from all color patches. We tested for normality using Shapiro-Wilk tests; data conformed to normality. We used Pearson correlations to investigate relationships between multiple measures of plumage coloration. We used Student's *t*-tests and backwards logistic regression to determine whether males and females differed in plumage coloration and morphology. We also used backwards stepwise regression to determine whether ornamental traits predicted body condition and whether plumage measures predicted streamer length of males and females. We used SPSS version 11.5 (SPSS, Inc., Chicago, Illi-

TABLE 1. Comparisons of morphology and coloration of female and male Blue-tailed Bee-eaters. Values are means \pm SD (sample size).

Trait	Female mean \pm SD	Male mean \pm SD	<i>t</i>	<i>P</i>
Head (mm)	62.0 \pm 2.5 (53)	65.3 \pm 2.6 (51)	6.6	< 0.001
Bill (mm)	38.1 \pm 2.4 (52)	40.9 \pm 2.4 (51)	6.0	< 0.001
Tarsus (mm)	11.6 \pm 0.6 (53)	11.6 \pm 0.4 (51)	0.1	0.92
Tail (mm)	86.8 \pm 2.3 (53)	86.9 \pm 2.5 (50)	0.2	0.83
Streamer (mm)	124.4 \pm 6.9 (53)	137.0 \pm 7.5 (45)	5.7	< 0.001
Wing (mm)	131.2 \pm 3.3 (53)	135.2 \pm 3.1 (51)	6.5	< 0.001
Mass (g)	40.9 \pm 4.2 (53)	40.7 \pm 1.7 (50)	-0.3	0.77
Blue chroma (%)	31.9 \pm 0.0 (50)	33.2 \pm 0.0 (45)	2.7	< 0.01
Blue hue (nm)	538.6 \pm 10.0 (50)	533.8 \pm 9.7 (45)	-2.4	0.02
Yellow chroma (%)	15.9 \pm 0.0 (46)	13.8 \pm 0.0 (47)	-4.0	< 0.001
Yellow hue (nm)	580.5 \pm 8.9 (46)	581.6 \pm 7.4 (47)	0.6	0.55
Green chroma (%)	27.9 \pm 0.0 (50)	28.5 \pm 0.0 (46)	1.2	0.24
Green hue (nm)	575.7 \pm 7.0 (50)	577.0 \pm 9.4 (46)	0.8	0.44
Chestnut brightness (%)	12.1 \pm 1.6 (49)	11.7 \pm 3.2 (47)	0.7	0.47
Chestnut chroma (%)	62.6 \pm 0.0 (49)	63.3 \pm 0.1 (47)	0.7	0.51

nois) for all analyses and all statistical tests were two-tailed. We accepted statistical significance at $\alpha = 0.05$.

RESULTS

SEXUAL DIMORPHISM

Male and female Blue-tailed Bee-eaters were sexually dimorphic in body size ($R^2 = 0.65$, $-2 \log \text{likelihood} = 70.4$, $\chi^2 = 66.6$, $P < 0.001$; Table 1, 2) and our model categorized 90% of individuals correctly by sex. Males were larger overall than females. We also found that bee-eaters were sexually dichromatic ($R^2 = 0.38$, $-2 \log \text{likelihood} = 94.5$, $\chi^2 = 30.3$, $P < 0.001$; Table 1, 2) and our model categorized 72% of

TABLE 2. Summary of morphological and plumage color traits that were included in the final backwards logistic regression models used to predict sex of Blue-tailed Bee-eaters.

Model	Predictor	Wald	<i>P</i>
Morphological traits	Head (mm)	4.4	0.04
	Tail (mm)	8.2	< 0.01
	Wing (mm)	10.5	< 0.001
	Streamer (mm)	11.3	< 0.001
Color traits	Blue chroma (%)	5.7	0.02
	Yellow chroma (%)	10.5	< 0.001
	Green chroma (%)	3.5	0.06
	Green hue (nm)	7.4	< 0.01
All traits	Head (mm)	4.6	0.03
	Tail (mm)	6.1	0.01
	Wing (mm)	9.3	< 0.01
	Streamer (mm)	11.6	< 0.001
	Chestnut chroma (%)	5.2	0.02

individuals correctly by sex. Males exhibited more chromatic blue, green, and chestnut coloration, and less chromatic yellow coloration, than females. Further, males exhibited green and yellow hues that were characterized by longer wavelengths, blue hues with shorter wavelengths, and darker (less bright) chestnut coloration (Fig. 1). In all color patches, males expressed what we predicted would be the more ornamental color. If we included both morphometrics and coloration in the model (Table 2), 91% of males and females were correctly sexed ($R^2 = 0.70$, $-2 \log \text{likelihood} = 54.8$, $\chi^2 = 64.3$, $P < 0.001$).

RELATIONSHIPS AMONG PLUMAGE TRAITS

We found interdependency among many of the measures of plumage coloration in both sexes (Table 3). Males that displayed highly chromatic chestnut plumage also exhibited highly chromatic green plumage. In addition, males that expressed yellow plumage with hues shifted toward longer wavelengths also displayed green and blue plumage with hues shifted toward longer wavelengths. Females that displayed yellow plumage with greater chroma also displayed darker chestnut color. Likewise, females that exhibited highly chromatic green plumage displayed highly chromatic blue plumage.

To determine whether plumage coloration predicted streamer length of males and females, we constructed backwards stepwise multiple regression models. In these models, we included

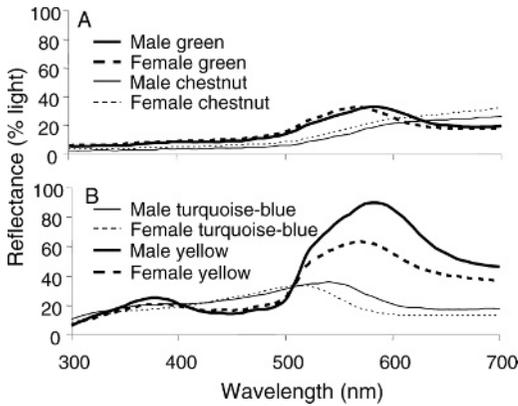


FIGURE 1. Reflectance spectra of plumage of typical male and female Blue-tailed Bee-eaters. A) Chestnut throat plumage and green body plumage. B) Turquoise-blue rump plumage and yellow chin plumage.

blue, green, yellow, and chestnut color scores as potential predictor variables. For males, all four plumage colors predicted streamer length. Males with darker and highly chromatic chestnut coloration, and with highly chromatic green, blue, and yellow coloration, exhibited longer tail streamers ($R^2 = 0.41$, $F_{5,37} = 5.4$, $P = 0.001$). For female bee-eaters, individuals exhibiting highly chromatic yellow plumage tended to have longer tail streamers ($R^2 = 0.07$, $F_{1,43} = 3.4$, $P = 0.07$).

PLUMAGE TRAITS AND BODY CONDITION

To determine whether plumage ornaments were associated with body condition of male and female Blue-tailed Bee-eaters, we constructed

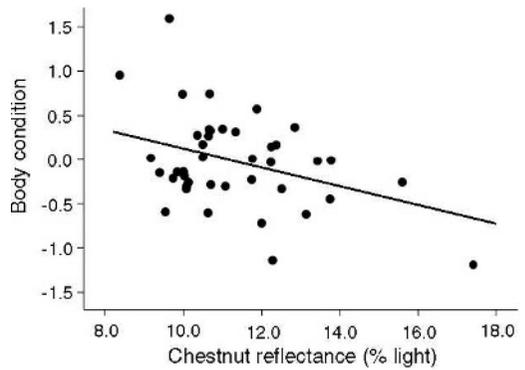


FIGURE 2. Male Blue-tailed Bee-eaters in better body condition display darker chestnut throat patches.

backwards stepwise multiple regression models. In these models, we included blue, green, yellow, and chestnut color scores and streamer length as potential predictor variables. For males, chestnut and green coloration was correlated with body condition. Males with darker chestnut coloration (Fig. 2) and more chromatic green coloration were in better body condition ($R^2 = 0.26$, $F_{2,38} = 6.7$, $P = 0.003$). Female bee-eaters with highly chromatic blue and yellow coloration were in better body condition ($R^2 = 0.13$, $F_{2,42} = 3.2$, $P = 0.04$).

DISCUSSION

Our results show that Blue-tailed Bee-eaters are sexually dichromatic and dimorphic. Male bee-eaters are larger overall and exhibit more exaggerated plumage than females, with more

TABLE 3. Results from a two-tailed Pearson correlation matrix among multiple color patches of male and female Blue-tailed Bee-eaters. Values are correlation coefficients with samples sizes in parentheses. One asterisk denotes $P \leq 0.05$, and two asterisks denote $P \leq 0.01$.

Sex	Plumage	Yellow chroma	Yellow hue	Green chroma	Green hue	Chestnut chroma	Chestnut brightness
Male	Blue chroma	0.02 (45)	-0.32* (45)	0.33* (45)	-0.29* (45)	0.32* (45)	0.11 (45)
Male	Blue hue	0.14 (45)	0.36* (45)	-0.33* (45)	0.41** (45)	0.46 (45)	-0.02 (45)
Male	Yellow chroma		-0.17 (47)	-0.05 (46)	-0.17 (46)	0.04 (47)	-0.06 (47)
Male	Yellow hue			-0.31* (46)	0.38** (46)	-0.11 (47)	0.04 (47)
Male	Green chroma				0.28 (46)	0.39** (46)	0.09 (46)
Male	Green hue					-0.15 (46)	-0.20 (46)
Female	Blue chroma	0.03 (46)	-0.12 (46)	0.54** (50)	-0.40** (50)	-0.09 (49)	0.13 (49)
Female	Blue hue	-0.18 (46)	0.24 (46)	-0.51** (50)	0.44** (50)	0.15 (49)	-0.20 (49)
Female	Yellow chroma		-0.33* (46)	-0.01 (46)	-0.08 (46)	-0.19 (45)	0.40** (45)
Female	Yellow hue			-0.31* (46)	-0.10 (46)	-0.11 (45)	0.17 (45)
Female	Green chroma				-0.71** (50)	0.10 (49)	-0.18 (49)
Female	Green hue					0.15 (49)	0.03 (49)

highly chromatic blue, yellow, green, and chestnut coloration and longer tail streamers.

Plumage color is most commonly derived from one, or a combination of three, mechanisms: carotenoid pigments, melanin pigments, or feather microstructure (Hill and McGraw 2006). Although we did not conduct biochemical pigment analyses, the reflectance curves suggest that the chestnut coloration of the throat feathers is created by a combination of eumelanin and pheomelanin pigments deposited in feathers (McGraw et al. 2004). The reflectance spectra of the yellow chin feathers exhibit the characteristics of the carotenoid canary xanthophylls (McGraw et al. 2001). The noniridescent blue and green plumage is most likely derived, at least partially, from coherent reflectance of light from nanostructural elements within the medullary layer of feather barbs (Prum 2006). Green coloration is thought to result from both carotenoid pigmentation and coherent reflection of light from underlying nanostructural elements (Prum 2006). The reflectance spectra of the green and the turquoise-blue feathers suggest that such colors might be derived from a combination of tissue nanostructure overlaid by carotenoid pigments. Future research will address extraction and quantification of pigments in the plumage of Blue-tailed Bee-eaters.

Within individuals, we found covariance between color regions. Not surprisingly, green coloration was highly correlated with both blue and yellow coloration in both sexes. These relationships are expected if coherently organized nanostructural elements influence the expression of green and blue plumage, and if blue, green, and yellow coloration is derived, in part, from carotenoid pigments. We also found some covariance between ornamental traits with different mechanistic bases. In females, expression of melanin (chestnut) and carotenoid (yellow) coloration was positively correlated. Males with redder melanin (chestnut) coloration exhibited more chromatic blue and green coloration. Moreover, birds with more exaggerated plumage coloration exhibited longer streamers.

Males in good condition exhibited darker chestnut and more chromatic green coloration, whereas females in better condition displayed more highly chromatic blue and yellow coloration. These data are consistent with weak

negative correlations between ectoparasite loads and color brightness in Blue-tailed Bee-eaters (Coulter 2003). The relationships between plumage color and body condition in bee-eaters are consistent with evidence for condition-dependent expression of carotenoid, melanin, and structural coloration in other species. Carotenoid coloration is affected by access to pigments (Hill 1992), exposure to parasites (Brawner et al. 2000, Hill et al. 2004), and food restriction (Hill 2000). Melanin coloration is influenced by social environment prior to molt (McGraw et al. 2003) and access to scarce amino acids (Poston et al. 2005) or rare minerals (McGraw 2003). Structural coloration is affected by exposure to parasites (Hill et al. 2005) and food restriction (McGraw et al. 2002, Siefferman and Hill 2005). To date, no research has investigated the condition dependence of plumage color derived from a combination of nanostructural and carotenoid pigments.

In summary, Blue-tailed Bee-eaters were sexually dichromatic and dimorphic and plumage coloration was correlated with body condition in both sexes. Although we detected sexual dichromatism and condition-dependent coloration using a spectrometer, we do not know that bee-eaters perceive this variation in coloration. However, these relationships suggest that important information is contained in plumage color and future research should investigate whether these traits are used in conspecific signaling.

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