

Plumage brightness predicts male mating success in the lekking golden-collared manakin, *Manacus vitellinus*

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The evolution of colorful plumage has been dramatic in lekking species. Several studies show that the size of colorful traits influence female choice in leks; however, relatively little is known about the specific function of color, in particular its spectral properties, in lekking taxa. To determine the importance of color in a lekking species, we monitored the mating success of male golden-collared manakins, *Manacus vitellinus*, and related this to spectral measures of their colorful plumage, as well as other morphological and behavioral traits shown to be important in other lekking species. We found that lek centrality, male body size, and plumage brightness were associated with male mating success. Only plumage brightness, however, entered a multiple regression model, indicating that plumage is the overall best predictor of mating success. These results provide evidence that the spectral properties of colorful plumage predict male mating success in a lekking species and provide important insight into why many lekking birds are dichromatic and elaborate in coloration. *Key words*: leks, *Manacus*, manakins, plumage, sexual selection, visual signals. [*Behav Ecol* 17:41–47 (2006)]

There is overwhelming evidence that elaborate display traits are used in mate choice and aggressive interactions (reviewed in Andersson M, 1994; Bradbury and Vehrencamp, 1998). These traits include elongated tail feathers (e.g., Andersson, 1982; Petrie and Halliday, 1994; Pryke et al., 2001), complex songs (e.g., Baker et al., 1986; Catchpole, 1980; Searcy and Marler, 1981), and colorful patches (e.g., Baker MC and Baker AEM, 1990; Bennett et al., 1997; Boughman, 2001; Houde, 1987). In particular, conspicuous and colorful plumage of birds has received much attention, with many studies showing that the reduction or enlargement of these patches changes male attractiveness or ability to defend territories (e.g., Andersson and Amundsen, 1997; Bennett et al., 1997; Collias et al., 1979; Peek, 1972). Recent technical advances have allowed for objective quantification of variation among males in the specific spectral properties of their plumage and relating this variation to individual reproductive or mating success (e.g., Andersson et al., 1998; Doucet et al., 2004; Keyser and Hill, 2000; Safran and McGraw, 2004; Siefferman and Hill, 2003). These studies provide a more explicit understanding of the specific role of color in mate choice and male-male interactions, and how sexual selection drives the evolution of conspicuous coloration.

Work relating the spectral properties of male plumage with reproductive success, however, comes mostly from socially monogamous taxa (e.g., Doucet et al., 2004; Siefferman and Hill, 2003). In contrast, the specific role of color in nonresource-based polygynous mating systems, such as leks, is less understood. For instance, several studies in lekking taxa have shown that the size of colorful traits influences male mating success (e.g., Höglund et al., 1990; Petrie and Halliday, 1994) and that males of different mating strategies differ in overall coloration

(Lank et al., 1995). In terms of the spectral properties of color itself, Madden et al. (2004) failed to find a link between plumage color and male mating success in the spotted bowerbird, and Doucet and Montgomerie (2003) found that chroma was linked to parasite load, an index of male condition, in the satin bowerbird. With such limited information, more studies are needed to understand the role of color in leks, especially because more than 80% of lekking birds show extreme sexual dichromatism (see Johnsgard, 1994).

Several morphological and behavioral traits correlate with male mating success in leks, including lek centrality (e.g., Höglund and Lundberg, 1987; Hovi et al., 1994; Shorey, 2002), lek attendance (e.g., Hill W, 1991; Lanctot et al., 1998), display rate (e.g., Höglund and Lundberg, 1987), and body size (e.g., Shorey, 2002). In this study, we examined the importance of these behavioral and morphological traits, as well as plumage coloration, in predicting male mating success in the lekking golden-collared manakin, *Manacus vitellinus*. Because golden-collared manakins are sexually dichromatic, with males having bright golden collars and beards while females are olive throughout, we predict that the spectral properties of male color, such as brightness, hue, or chroma, should be under sexual selection and should influence male mating success.

METHODS

The study system

Golden-collared manakins inhabit the undergrowth of humid forests from western Panama through northern Colombia (Ridgley and Gwynne, 1989). Sexes are dichromatic, with males having golden collars and beards and black caps and back, while females are uniformly olive and drab (Ridgley and Gwynne, 1989). Some males are polygynous and congregate in arenas called leks to attract females (Chapman, 1935). Leks consist of three to eight males, with each male defending a separate and circular court (~1 m in diameter) on the ground (Chapman 1935). Each court is cleared of leaf and

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stick litter to expose the ground and encompasses at least two saplings restricted to its periphery. When a female enters the lek, court-owning males initiate rapid hops between the saplings and across the cleared court, accompanied by loud pops produced by their wings ("snap-grunt display," Chapman, 1935). During the snap-grunt display males expand their golden beards and collars (Chapman, 1935; Uy and Endler, 2004). A visiting female can simultaneously view several snap-grunt displays and may choose to join a single male on his court. Once on court, she may decide to mate with the male or leave and continue with the assessment of other potential mates (Chapman, 1935).

Monitoring mating behavior

We monitored four leks in the Republic of Panama, approximately 30 km east of Panama City: one lek in Soberania National Park (Pipeline Road) consisting of five active courts (lek 1), one lek in Gamboa Forest consisting of six active courts (lek 2), and two leks in the Canal Zone (Old Gamboa Road), one consisting of eight active courts (lek 3) and the other consisting of three active courts (lek 4). All leks were found in mature secondary forests adjacent to openings (e.g., creeks), which is the typical habitat for *Manacus* leks (Chapman, 1935; Ridgley and Gwynne, 1989; Uy and Endler, 2004).

Because each male defended a permanent court (Chapman, 1935; Uy and Endler, 2004), we monitored court-owning males with motion-sensor, video cameras (Samsung Hi8 SCL860). Each of the 22 courts had its own camera system mounted approximately 3 m from the court. Cameras began filming 6 s after the bird entered his court and continued filming for 30 s after the bird left his court (see Uy et al., 2000). The time and date were also recorded when the camera was activated. Cameras were active throughout the day, allowing for the continuous and simultaneous observations of mating activity at all courts not possible with standard behavioral observations from blinds. Males from each lek were monitored with video cameras as follows: lek 1, 9 March through 23 April 2004 (46 days); lek 2, 27 February through 23 April 2004 (57 days); lek 3, 27 March through 23 April 2004 (28 days); and lek 4, 15 March through 23 April 2004 (40 days). To ensure that all relevant behaviors were caught on camera and to verify court ownership of banded males, we conducted daily behavioral observations at each lek. Behavioral observations were 2 h in duration and conducted between 0600 and 0800 h or 1300 and 1500 h, which coincide with the peaks of mating and courtship activity in this species (Stein AC and Uy JAC, unpublished data). The behaviors that were caught on tape include (1) display, defined as a snap-grunt display without a female visible on the court (e.g., female is above the courts); (2) courtships, defined as a snap-grunt display with a female on the court excluding those that resulted in copulations; (3) lek attendance, defined as the number of activity bouts (e.g., courtships, displays, and court maintenance) a bird was caught on tape at his court; and (4) copulations.

When a female first enters a lek, she hops around the vegetation above the courts and males throughout the lek initiate snap-grunt displays. The female then decides on a specific male and joins him on his court for courtship, which involves the female following the male as he hops between the saplings on his court. She may then decide to mate or leave the court. An on-court courtship is thus different from displays with females above the court because an on-court courtship likely occurs only after a female has made a preliminary decision on a potential mate. Because most females were not banded, each courtship and copulation could not be assigned definitively to

a specific female. Therefore, courtship and copulation behaviors were scored as separate events only if at least 5 min of inactivity separated the events. For instance, copulations that took place with at least 5-min intervals were scored as different matings, while copulations that took place within a 5-min interval were considered to be with the same female and only counted once. We did this because in many lekking or polygynous taxa, marked females can return to the same male for consecutive matings (e.g., Petrie et al., 1992; Uy et al., 2001). Almost all time intervals between copulations, however, were several hours or days (e.g., only once did two matings occur within a 5-min time interval). Because all males were not monitored for the same number of days, we calculated mating success as the number of copulations a male received divided by the number of days that he was monitored with our motion-sensor camera. We calculated display and courtship rates as the number of displays and courtships divided by the number of days monitored. Likewise, we calculated lek attendance as the number of activity bouts divided by the number of days monitored.

The leks we monitored were at least several kilometers apart, and we did not observe territorial males move between them. Males in each lek are thus only competing with each other, and leks are independent. Therefore, to pool males from different leks for statistical tests, we standardized (mean = 0, variance = 1) all variables, including male mating success, by leks (e.g., Andersson, 1989; Gratson et al., 1991; Pryke et al., 2001). After traits and mating success were standardized, all variables were normally distributed.

Placement of court within a lek was determined by establishing a reference point in the lek and taking the distance and bearing from there to the center of each male's court. Courts were then plotted on an x - y graph, and the center of the lek was then determined as the median of the x and y coordinates of all males. The distance from this point and the male's court was then calculated (see Shorey, 2002). Males were ranked according to distance from lek center, starting with the male closest to the center.

Measuring male traits

All 22 court-owning males were caught with mist nets at or near the leks 1 week before monitoring and were fitted with a numbered aluminum leg band and a unique combination of color leg bands. At the time of capture we took standard morphological measurements of tarsus, wing, and tail lengths (mm), bill dimensions (mm), and body mass (g) (see Table 1). Because morphological traits are often correlated (e.g., Shorey, 2002), we performed a principal component analysis (PCA) to collapse these variables into fewer, orthogonal variables that serve as indices of body size.

We used an Ocean Optics USB2000 spectroradiometer and a Xenon flash light source (Ocean Optics PX-2) to obtain reflectance scans of the bird's plumage (see Uy and Endler, 2004). The tip of a micron fiber optic probe was housed in a hollow, black anodized aluminum sheath with an angled tip that contacted the bird's plumage. This technique ensured that (1) the Xenon flash was the only light source for our scans, (2) the distance between the probe and color patch was standardized at 1 cm, and (3) the angle of measure was standardized at 45° (this angle reduces specular glare, Endler, 1990). To allow for comparison across different measures, we used a spectrally flat 97% reflecting spectralon white standard (Labsphere, North Sutton, NH) and a dark current reading to standardize each scan. Scans were taken from an ~3-mm diameter circle at 0.40-nm intervals across 300–700 nm. Reflectance scans were taken at the time of capture. We focused on scanning the colorful golden patches because these patches

Table 1
Mean, standard deviation, and range for the unstandardized morphological and behavioral traits of the 22 golden-collared manakin males used in our study

| Male trait | Mean | SD | Range |
|-----------------------------|-------|-------|------------|
| Lek attendance | | | |
| (activity bouts on lek/day) | 4.63 | 2.99 | 0.92–11.36 |
| Display rate (displays/day) | 2.56 | 1.85 | 0.11–6.91 |
| Beard hue (UV) | 345.9 | 2.2 | 320–362 |
| Beard hue (MW/LW) | 519.1 | 4.8 | 506–524 |
| Beard chroma (UV) | 0.08 | 0.02 | 0.05–0.11 |
| Beard chroma (MW/LW) | 0.87 | 0.02 | 0.83–0.91 |
| Beard brightness | 106.2 | 14.53 | 80.3–139.7 |
| Collar hue (UV) | 343.7 | 12.1 | 320–364 |
| Collar hue (MW/LW) | 519.0 | 4.6 | 512–526 |
| Collar chroma (UV) | 0.09 | 0.03 | 0.03–0.13 |
| Collar chroma (MW/LW) | 0.85 | 0.04 | 0.75–0.92 |
| Collar brightness | 79.1 | 12.44 | 51.4–106.5 |
| Mass (g) | 18.7 | 0.8 | 17.5–20.0 |
| Tarsus (mm) | 21.4 | 0.5 | 20.4–22.3 |
| Beak depth (mm) | 3.75 | 0.16 | 3.30–4.10 |
| Beak width (mm) | 6.28 | 0.27 | 5.40–6.80 |
| Beak length (mm) | 8.43 | 0.50 | 7.50–9.10 |
| Wing length (mm) | 53.0 | 0.93 | 52–55 |
| Tail length (mm) | 33.5 | 0.65 | 32–35 |

MW, medium wavelength; LW, long wavelength; UV, ultraviolet.

are expanded and most visible to females during courtships (Uy and Endler, 2004) and are highly variable among males (Figure 1). Three consecutive measurements were taken for each of these color patches by lifting the probe and replacing it back onto the color patch. We averaged the three readings taken at each color patch to get a mean estimate for each male's beard and collar.

We quantified beard and collar color using standard descriptors of reflectance spectra: brightness, hue, and chroma (Endler, 1990). We calculated brightness or intensity of collar and beard by summing its reflectance from 300 to 700 nm, the approximate visible spectrum of most avian species (Hart, 2001). This measure assays the total intensity of light reaching the eye from the color patch. Because a spectrum consists of reflectance at each wavelength that is highly correlated, we used a PCA to collapse these reflectance variables into a few independent variables that summarize the shape of the spectrum (Cuthill et al., 1999; Endler, 1990). This is a standard

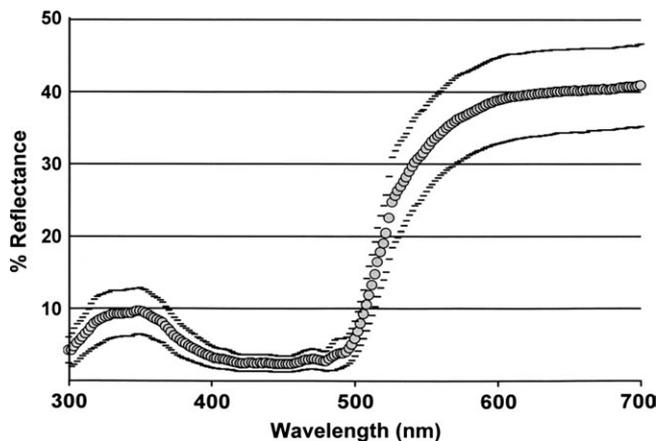


Figure 1
 The mean plumage reflectance spectra (± 1 SD) of golden collar ($n = 22$ court-owning males).

method to handle spectral data (e.g., Bennett et al., 1997; Endler and Théry, 1996; Hunt et al., 1998; Macedonia, 2001; Sheldon et al., 1999), especially well suited for spectra with multiple peaks (Cuthill et al., 1999). To do so, we first used brightness to standardize all reflectance scans before PCA. This provided us with principal components that explain the shape of the spectrum independent of its brightness. The resulting principal components (PC) values were thus indices of chroma and hue (Cuthill et al., 1999) with respect to the multiple peaks of golden-collared manakin plumage (Figure 1). We also calculated hue and chroma using another established method: (1) hue is a function of a spectrum's shape and is correlated with the wavelength of maximum slope (i.e., "cutoff wavelength") or peak and (2) chroma is a measure of the "saturation" of a color and is a function of how rapidly intensity changes around the cutoff wavelength (Endler, 1990; Siefferman and Hill, 2003). Spectra with two maximum slopes or peaks would have two values of hue and chroma (Endler, 1999). Because the golden plumage of golden-collared manakins has a minor peak in the ultraviolet (UV) and a larger plateau in the medium- to long-wavelength regions (Figure 1), we calculated hue and chroma for these two regions. We calculated UV chroma as the reflectance occurring between 300 and 400 nm (UV) divided by reflectance of the entire spectrum (see Doucet et al., 2004; Siitari and Huhta, 2002). We calculated yellow-red chroma as the total yellow-red reflectance (cutoff wavelength to 700 nm) divided by the reflectance of the entire spectrum (see Pryke et al., 2001). Because the PCA provides fewer, independent variables that represent chroma and hue, we used PCs in testing for correlates of male mating success (see below).

Statistical analyses

To determine how male traits relate to male mating success (i.e., copulation rate), we performed Pearson bivariate correlation analyses between male mating success and the following (standardized) traits: brightness and PCs (i.e., chroma and hue indices) of beard and collar, PCs for body size, lek attendance, display rate, and court centrality. Standard Bonferroni correction for this analysis sets the significant p -values to .004 (for 14 comparisons). We then subjected the traits that were strongly associated with male mating success to a stepwise, forward multiple linear regression to understand how each trait independently explained the variation in mating success among court-owning males (e.g., Pryke et al., 2001; Uy and Borgia, 2000). In addition, to determine which predictors would have entered the model if we had not measured male plumage, we performed a stepwise, forward multiple regression that included the same variables with the exception of the color values. Statistical analyses were performed using SPSS 11.5. All tests of significance are two tailed.

RESULTS

Male traits and mating success

Summary statistics of unstandardized male behavioral and morphological traits are presented in Table 1. PCA of male morphometrics extracted three principal components that together explained 62.4% of variation related to male size (PC1, 31.8%; PC2, 17%; PC3, 13.6%). Component loadings indicate the relationship between specific principal components and male morphology: PC1 was positively associated with body mass (0.54) and beak depth (0.52), length (0.99), and width (0.49); PC2 was positively associated with wing length (0.81); and PC3 was positively associated with tarsus (0.36) and tail (0.83) lengths.

Male golden plumage had a minor peak in the UV region and a larger plateau in the medium- to long-wavelength region (Figure 1). PCA of standardized collar spectra (i.e., controlled for brightness) extracted three principal components that together explained 97.15% of variation among males in hue and chroma (PC1, 42.92%; PC2, 42.04%; PC3, 12.19%). Likewise, PCA of standardized beard spectra extracted three principal components that together explained 94.91% of variation among males in hue and chroma (PC1, 62.28%; PC2, 24.03%; PC3, 8.60%). Component loadings from PCA of the standardized beard and collar spectra show that PC1 was positively associated with short wavelengths and negatively associated with long wavelengths, PC2 was positively associated with UV wavelengths, and PC3 was positively associated with medium wavelengths (Figure 2). These loadings indicate that PC1 was an index of orange-red (also blue) chroma and hue, PC2 was an index of UV chroma and hue, and PC3 was an index of yellow chroma and hue.

Courtship rate (i.e., displays that involved females on courts) and mating success are indices of male attractiveness (e.g., Andersson, 1992), and we found that the two variables were highly correlated ($r = .75$, $n = 22$, $p < .001$). Because mating success is a more direct measure of male attractiveness and male fitness, we restricted our analyses to using mating success as the dependent variable. We found a skewed distribution of male mating success in golden-collared manakin leks, with one or two males receiving most of the matings (Figure 3).

Collar brightness and lek centrality were associated strongly with male mating success; however, these relationships were not significant after Bonferonni correction (Table 2). Likewise, lek attendance, PC1 for collar color, and PC2 for body size were associated with male mating success (Table 2). Using the traits that were associated with male mating success (i.e., collar brightness, PC1 for collar color, lek centrality, lek attendance, and PC2 for body size) in a multiple regression model, we found that collar brightness was the only predictor of male mating success ($F_{1,20} = 6.21$, $r^2 = .246$, $p = .02$; Figure 4). Using the alternative measures of hue and chroma (summarized in Table 1) did not qualitatively change our results—collar brightness was still the only predictor that entered the multiple regression model. The multiple regression analysis that excluded the color values revealed that lek centrality was the only significant predictor of male mating success ($F_{1,20} = 6.13$, $r^2 = .235$, $p = .02$).

To directly explore how collar brightness was related to other behavioral and morphological traits, we looked at

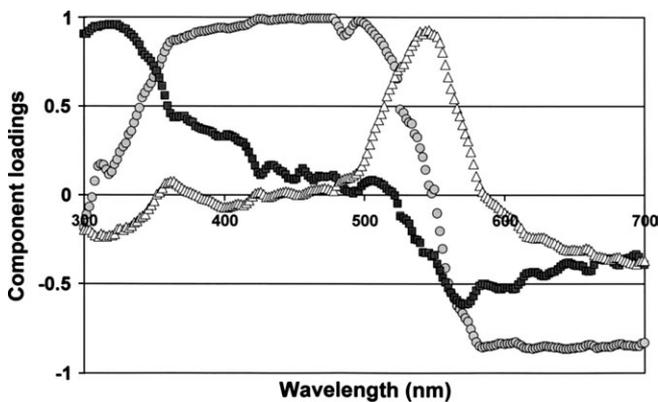


Figure 2 Component loadings from PCA of standardized male collar spectra: gray circles = PC1, dark gray squares = PC2, and white triangles = PC3. PCs for beard spectra have near-identical component loadings.

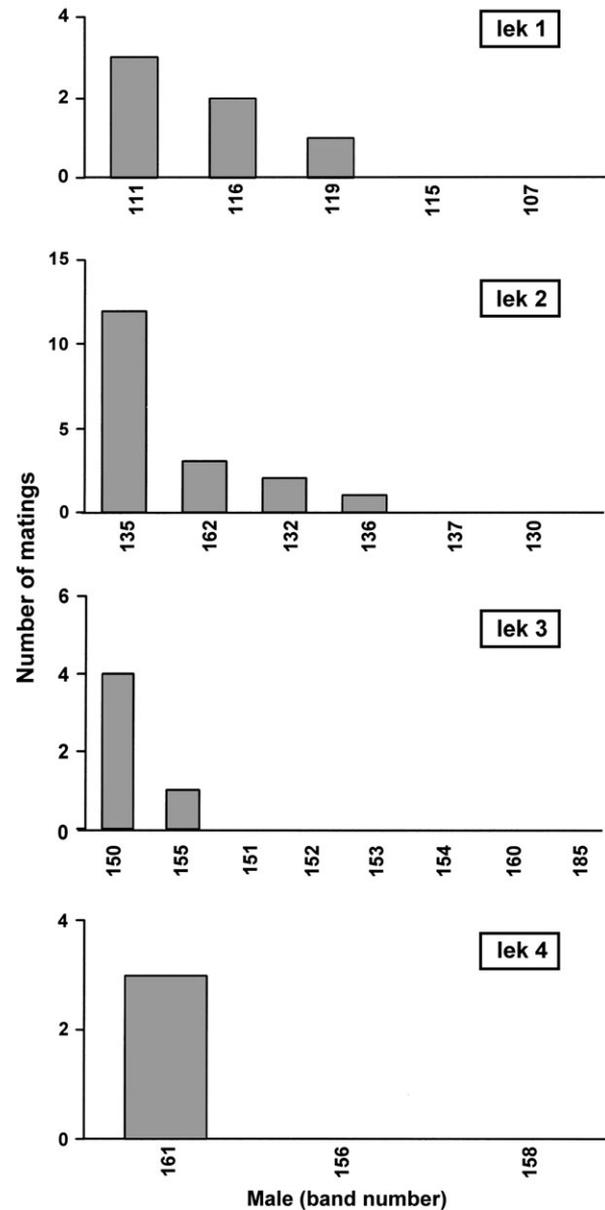


Figure 3 Distribution of male mating success for the four golden-collared manakin leks we monitored. Males are labeled by their uniquely numbered metal leg bands.

the relationship of collar brightness with PC1, PC2, and PC3 for collar and beard color, beard brightness, PC1, PC2 and PC3 for body size, court centrality, lek attendance, and display rate. PC1 for collar color ($r = .83$, $n = 22$, $p < .001$), PC1 for body size ($r = .54$, $n = 22$, $p = .01$), lek attendance ($r = .82$, $n = 22$, $p < .001$), and display rate ($r = .74$, $n = 22$, $p = .002$) significantly correlated with collar brightness. Court centrality ($r = -.34$, $n = 22$, $p = .13$) and PC2 for collar color ($r = .39$, $n = 22$, $p = .07$) showed a trend with collar brightness. None of the other traits showed a significant or strong association with collar brightness.

DISCUSSION

Bright plumage and leks

We found a strong correlation between collar brightness and male mating success in golden-collared manakins. In fact, it

Table 2
Bivariate Pearson correlations between standardized male traits and male mating success

| Male trait | <i>r</i> | <i>p</i> |
|-------------------|----------|----------|
| Lek centrality | -.484 | .022 |
| Lek attendance | .361 | .099 |
| Display rate | .194 | .388 |
| Beard brightness | .176 | .434 |
| Beard PC1 | .013 | .953 |
| Beard PC2 | -.018 | .936 |
| Beard PC3 | .270 | .224 |
| Collar brightness | .487 | .022 |
| Collar PC1 | .438 | .042 |
| Collar PC2 | .265 | .233 |
| Collar PC3 | .013 | .953 |
| Body size (PC1) | .302 | .172 |
| Body size (PC2) | -.411 | .058 |
| Body size (PC3) | .082 | .718 |

None of the correlations were significant after standard Bonferroni correction, which sets the significance level of $p = .004$ for 14 comparisons; $n = 22$ males.

was the only variable among several behavioral and morphological traits that factored in a multiple regression model that explained male mating success. Previous work on lekking or nonresource-based polygynous species indicate that the size of colorful traits influences mate choice (Höglund et al., 1990; Petrie and Halliday, 1994) and that the specific spectral property of male color is linked to an index of male condition (Doucet and Montgomerie, 2003). These studies show the importance of colorful traits in mate choice or male-male competition. Our results suggest that color itself is under sexual selection and provide a mechanism for the evolution of bright colors and dichromatism in lekking taxa.

Fiske et al. (1998) performed a meta-analysis of mating success on leks and found that lek centrality, lek attendance, display rate, and aggression rate were consistently the best predictors of male mating success. When we excluded plumage traits in our analyses, we found that lek centrality predicted male mating success. This is consistent with previous

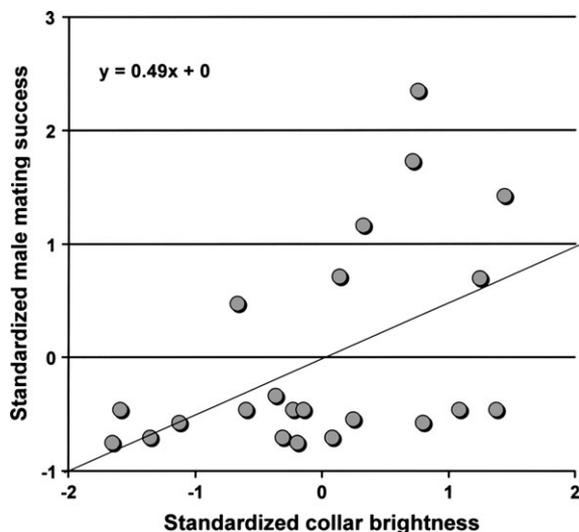


Figure 4
 Linear regression of standardized male mating success on standardized male collar brightness.

work on white-bearded manakins (*Manacus manacus*), a congener of our study species, which found an association between lek centrality and male mating success (Shorey, 2002). However, by including male coloration, the traits shown to be important in predicting mating success in previous studies were not factored into the model. Our results show that including male plumage in a multivariate analysis changes the relative importance of previously tested predictors of mating success. This calls for future research to include explicit measures of male color in the study of sexual selection in lekking species.

Bright plumage as an indicator of male condition

We found that collar brightness is correlated with body size, lek attendance, and display rate, which are traits that have been linked to male condition. For instance, Andersson S (1994) found that lek attendance and courtship displays in Jackson widowbirds were energetically costly, suggesting that only males in good condition can compete effectively in leks (see also Vehrencamp et al., 1989). Bright plumage in golden-collared manakins may thus signal male condition to visiting females or provide advantages to males in good condition during male-male interactions.

In several taxa, male condition is linked with the carotenoid content of male color, which in turn dictates chroma (Gray, 1996; Hill GE, 1991; Hill and Montgomerie, 1994; McGraw and Hill, 2000, 2001; Olson and Owens, 1998). In contrast, we found that plumage brightness, which was linked to several indices of male condition, was negatively correlated with male chroma in the long-wavelength region (i.e., positively correlated with PC1 of collar color). We do not have information on the biochemical basis of bright plumage in our study species; however, Hudon et al. (1989) found that red and yellow plumage of other manakin species have a carotenoid basis. If golden-collared manakin plumage is indeed carotenoid based, then our study seems contrary to previous work showing that chroma serves as an indicator of male condition (e.g., Hill GE, 1991). One possibility that may explain this seeming contradiction is that another component of golden plumage may be signaling male condition. Many birds with carotenoid-based plumage have a secondary peak in the UV region, which has a structural basis (Eaton and Lanyon, 2003). Shawkey and Hill (2005) found that the experimental removal of structural color from such carotenoid-based feathers resulted in these feathers appearing dull, indicating that structural tissue is critical in the expression of some carotenoid-based feathers. Golden-collared manakins have a similar secondary peak in the UV region, and we found that UV chroma/hue (i.e., PC2) of collar was positively related to collar brightness. This suggests the possibility that brightness signals male condition through structural colors and not the orange-red coloration. Several studies have shown that indeed structural colors can signal aspects of male quality, including viability (Sheldon et al., 1999), competitive ability (Siefferman and Hill, 2005), and parasite load (Doucet and Montgomerie, 2003). Our arguments are speculative and require biochemical and nanostructure studies for confirmation (Shawkey and Hill, 2005; Shawkey et al., 2003); however, they provide a possible explanation for why brightness and not red-orange chroma correlated with male mating success and the indices of male condition in our study.

We failed to find an association between collar and beard color properties within individuals. This is surprising considering that collar and beard feathers likely develop under similar mechanisms. Errors in our methodology may account for this disparity; however, we measured each patch three times to ensure a more accurate assay of patch color. In addition, we failed to find a correlation between beard and collar

brightness in the closely related orange-collared manakin, *Manacus aurantiacus* (Uy JAC, unpublished data). It is thus unlikely that measurement error alone can account for the observed discrepancy between male collar and beard spectral properties. Without knowledge of how beard and collar develop we cannot definitively explain our findings. One possibility is that differences in feather morphology between the collar and beard may result in differences in appearance despite a common developmental pathway. Beard feathers are long and thin and extend beyond the bill of males (Uy and Endler, 2004). Collar feathers, in contrast, are short and thick and are viewed against a male's back. This difference in general structure may account for the difference in brightness between collar and beard within each male. More work addressing the development, structure, and biochemical basis of male coloration is needed to obtain a better understanding of why beard and collar color is not correlated within a single individual.

Elaborate plumage and courtship displays

Bright and colorful signals in lekking species are assumed to be important in mate choice or male-male competition and, hence, are under intense sexual selection (e.g., Darwin, 1871; Endler and Théry, 1996; Heindl and Winkler, 2003; Uy and Endler, 2004). This assumption seems justified because most lekking birds are sexually dichromatic and accentuate their plumage during courtship displays to females (Johnsgard, 1994). For instance, golden-collared manakins expand their beards and collars during snap-grunt displays to females (Chapman, 1935). In addition, males clear display courts that augment the conspicuousness of their golden color patches by increasing the brightness and color contrasts of their plumage against the visual background (Uy and Endler, 2004). Similarly, several species of birds of paradise (Paradisaeidae), cock-of-the-rocks (Cotingidae), manakins (Pipridae), and hummingbirds (Trochilidae) expand or flare their colorful patches during courtship displays to females, with some species also building or clearing courts for displays (see Johnsgard, 1994). Because the bright plumage of golden-collared manakins correlated with male mating success, our results provide an underlying reason why males should expand these color patches to visiting females and clear display courts. Future work should focus on determining if females do pay direct attention to colorful plumage and how behavioral modifications explicitly enhance the attractiveness of bright and colorful signals.

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