The Evolution of Signal Design in Manakin Plumage Ornaments

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Online enhancement: table.

abstract: Animal signals are characterized by two design components: efficacy (detectability) and content (message being conveyed). Selection for efficient signal perception should favor the evolution of traits that exhibit an optimal balance between these two design components. We examined the evolution of signal design in the colorful plumage ornaments of manakins (Aves: Pipridae). We used a model of avian color space to quantify how differences in plumage coloration would be perceived by a typical passerine bird and examined patterns of coloration across 50 species of manakin. Using phylogenetically independent contrasts, we show that plumage contrast against the background increases with sexual dichromatism in males but not females, suggesting that sexual selection has favored the evolution of male plumage ornaments that enhance signal efficacy. Plumage contrast within individuals also increased with dichromatism in males but not females. Finally, plumage colors produced by different mechanisms, which may reveal different aspects of quality, resulted in different degrees of contrast against the background. Our findings suggest that selection for signal efficacy and content may sometimes be opposing, creating a trade-off between these two components of signal design. Manakins may mediate this trade-off by combining multiple plumage ornaments that differ in efficacy and content.

Keywords: manakins, signal efficacy, signal content, avian color space, vision, plumage.

Animal signals are characterized by two important design components: efficacy and content (Andersson 2000). Signal efficacy is a signal's detectability or conspicuousness and is therefore influenced by the structural design of the signal, the environment in which it is perceived, the perceptual abilities of the signal receiver, and receiver psychology (Hailman 1977; Endler 1990; Guilford and Dawkins 1993; Vorobyev et al. 1998; Théry 2006). Signal content, on the other hand, is the information or message conveyed by the signal. Research has generally focused on one or the other of these components of animal signals, creating an artificial boundary in studies of animal communication (but see Andersson 2000). Even subcomponents of signal efficacy are often studied in isolation because they require information from such disparate fields as behavioral and evolutionary ecology, sensory physiology, and neuropsychology. A more thorough understanding of animal communication, however, necessitates the integration of these different components of signal efficacy (Lythgoe 1979; Endler 1990; Bennett et al. 1994).

Many of the best-understood signals are the visual signals produced by the color and patterning of animals' fur, feathers, scales, or skin. These signals may be directed at individuals of other species (e.g., aposematic coloration) or conspecifics (e.g., signals of identity, dominance status, age, sex, or mate quality). Among intraspecific signals based on color or patterning, sexual ornaments have received the most research attention to date (Andersson 1994), and studies of sexual ornamentation have generally focused on the information content of these ornaments. In particular, research has focused on testing indicator models of sexual selection (Zahavi 1975; Kodric-Brown and Brown 1984; Grafen 1990) by investigating whether sexual ornaments can honestly reveal some aspect of individual quality or competitive ability. Although theory predicts that sexual selection will lead to the evolution of ornaments that exhibit an optimal balance between signal efficacy (detectability) and content (honesty; Schluter and Price 1993), studies of signal content rarely incorporate any aspect of signal efficacy.

Our goal in this study was to investigate the evolution of signal design for efficacy and content in the colorful plumage ornaments of birds. Neotropical manakins (Aves:

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Pipridae) are an ideal system for this investigation because their plumage varies from nearly sexually monochromatic in some species to highly sexually dichromatic in other species (Prum 1997; Snow 2004). Moreover, the males of many species of manakin are ornamented with multiple plumage patches of different colors, and these patches often result from distinct color production mechanisms. Most manakins follow a lek-based mating system in which assemblages of displaying males compete for copulations with females and females are solely responsible for parental care (Snow 2004). This mating system leads to extreme female choosiness, resulting in high variance in male mating success and, consequently, a high intensity of sexual selection (McDonald 1989; Shorey 2002). These features of manakin social organization and diversity in plumage ornamentation allowed us to test three hypotheses relating to signal design in manakin plumage ornaments.

We tested the hypothesis that sexual selection has favored the evolution of plumage ornaments that enhance signal efficacy by maximizing contrast against the background. Elaborate male ornaments are thought to have evolved by sexual selection through female mate choice and male-male competition (Andersson 1994). Selection should act to maximize the conspicuousness of these ornaments to facilitate assessment by conspecifics (Endler 1990; Schluter and Price 1993). One important measure of the conspicuousness of colorful ornaments is how much chromatic (color) and achromatic (brightness) contrast they create against the visual background (Endler 1978, 1990). We tested our first hypothesis by examining whether the degree of sexual dichromatism is associated with the degree of plumage contrast against the background across species of manakin. If sexual selection favors the evolution of plumage colors that enhance signal efficacy, we predict a positive relationship between the degree of sexual dichromatism and the degree of male plumage contrast against the background. It should be noted that increases in sexual dichromatism can result from sexual selection for increased plumage ornamentation in males or natural selection for decreased plumage ornamentation in females (Irwin 1994; Omland 1997; Burns 1998; Badyaev and Hill 2003). To determine whether evolutionary changes in dichromatism in manakins are associated with changes in male plumage, changes in female plumage, or changes in the plumage of both sexes, we examined the relationship between dichromatism and plumage contrast against the background in both males and females.

Conspicuousness can arise either through the contrast between an individual and the background or through contrast between different plumage patches within an individual (Endler 1990). We therefore also tested the hypothesis that sexual selection has favored the evolution of ornaments that enhance signal efficacy by maximizing plumage contrast between plumage patches within males. Higher within-male plumage contrast should facilitate assessment by conspecifics through increased conspicuousness at shorter viewing distances (Endler 1978; Endler and Théry 1996; Heindl and Winkler 2003*a*, 2003*b*; Uy and Endler 2004). We tested this hypothesis by examining the relationship between degree of sexual dichromatism and degree of within-male plumage contrast across species of manakins. If sexual selection favors high within-male plumage contrast, we predict a positive relationship between sexual dichromatism and degree of within-male plumage contrast.

If efficient signal transmission were the only important determinant of ornament elaboration, we might expect sexual ornaments to converge on one idealistic, conspicuous form, particularly for species living in similar environments and with similar visual systems (Heindl and Winkler 2003*b*). However, a number of other factors influence signal design in sexual ornaments, including variation in predation pressure (Endler 1980), sensory biases (Endler and Basolo 1998), receiver psychology (Guilford and Dawkins 1993; Bennett et al. 1994), phylogenetic constraints (Badyaev and Hill 2003), and, of course, the message being conveyed by the ornament (Hill 2006). Comparative studies of signal content pose some difficulties because accurate information on signal content requires comprehensive long-term population studies (e.g., Hill 2002). However, we can gain general insight into the content of plumage signals by examining variation in plumage colors produced by different mechanisms (Gray 1996; Fitzpatrick 1998; Owens and Hartley 1998; Badyaev and Hill 2000). There are two primary mechanisms of color production in birds: pigmentation and reflective feather microstructure (Fox and Vevers 1960). The two main pigment types in passerine bird feathers are carotenoids and melanins. Carotenoids are responsible for red, orange, and yellow feather coloration and must be obtained from the diet (Fox and Vevers 1960; McGraw 2006*a*). By contrast, melanin pigments can be synthesized de novo from amino acid precursors and are responsible for producing black and gray colors (eumelanins) and rusty brown colors (phaeomelanins; Fox and Vevers 1960; McGraw 2006*b*). Structural colors can also be subdivided into two categories. Noniridescent structural colors are produced by coherently scattered light within a matrix of keratin and air spaces in feather barbs and generally produce blue, violet, and ultraviolet colors (Prum et al. 1999, 2003; Shawkey et al. 2003; Doucet et al. 2004). Iridescent structural colors are produced by coherently scattered light from stacked arrays of melanin granules within feather barbules and can produce iridescent hues spanning the bird-visible spectrum (Brink and van der Berg 2004; Doucet et al. 2006; Prum 2006). Colors produced by different

mechanisms are known to reveal different aspects of male quality within species (McGraw and Hill 2000; McGraw et al. 2002; Jawor and Breitwisch 2004). However, because colors produced by different mechanisms are associated with particular hues (or dominant wavelengths), they will likely also differ in the amount of contrast they create against the visual background. Thus, colors produced by different mechanisms may differ not only in signal content but also in signal efficacy, resulting in a potential tradeoff between these two components of signal design (Schluter and Price 1993; Andersson 2000). We tested the hypothesis that colors produced by different mechanisms would result in different degrees of contrast against the background. Based on the assumption that the main visual background in the forested habitat of manakins is green vegetation (rich in middle wavelengths), we predicted that carotenoid colors, phaeomelanin colors, and structural blue colors would result in high chromatic contrast against the background because they exhibit high reflectance at either end of the visual spectrum of birds (Hart 2001). Conversely, we predicted that eumelanin and white structural colors would result in low chromatic but high achromatic contrast against the background because they exhibit uniformly low or high reflectance across much of the visual spectrum of birds, respectively.

We tested these three hypotheses by measuring the plumage coloration of museum specimens of 50 species of manakin. To assess differences in plumage color from the perspective of a typical passerine bird, we constructed a visual model to calculate differences in color as distances in avian perceptual color space (Vorobyev et al. 1998) based on published information for photoreceptor sensitivities, photoreceptor noise, and the transmission properties of avian ocular media (Maier 1992; Hart et al. 2000). To approximate the environment in which these plumage signals would be perceived (Endler 1990; Vorobyev et al. 1998), our model also incorporated data we collected on light environment and background reflectance in the tropical forest habitat of manakins.

Methods

In March 2003 and January 2004, we measured museum specimens from 50 available species of manakin at the Louisiana State University Museum of Natural Science and the American Museum of Natural History, respectively. With a few exceptions, we measured five males and five females of each species (table A1 in the online edition of the *American Naturalist*). We measured only specimens showing no obvious signs of molt and only male specimens that were in full adult (definitive) plumage. For each specimen measured, we recorded the genus, species, subspecies, location of capture, date of capture, and sex.

Spectral Reflectance of Specimens

We measured the spectral reflectance of all specimens using a USB2000 spectrometer (range 200–1,100 nm) and PX-2 pulsed xenon lamp (range 220–750 nm; Ocean Optics, Dunedin, FL). Light was delivered from the light source to the specimen and from the specimen to the spectrometer by a bifurcated fiber-optic cable mounted in a metal-encased probe (BIF200-UV-VIS, Ocean Optics). The probe was mounted in a matte black rubber holder that excluded external light and maintained the probe at a fixed 5 mm distance from and perpendicular to the measurement surface. All measurements were expressed as the proportion of reflectance relative to an Ocean Optics WS-1 white standard, which reflects 97%–98% of incident light. For each specimen, we measured at least five body regions, broadly defined as head (forecrown, crown, and nape), back (mantle and rump), front (throat, breast, and belly), tail, and wings. We took five measurements per region. When there were distinct plumage patches associated with these regions, we measured the center of the patch. Otherwise, we measured the center of the region. In some species, there was more than one distinct plumage patch within each region, so we measured these additional plumage patches.

As part of another study, we investigated the influence of sampling location and the age of museum specimens on plumage coloration in long-tailed manakins, *Chiroxiphia linearis*. We found significant effects of both location of capture and specimen age on plumage coloration (S. M. Doucet and G. E. Hill, unpublished data). Both effects were subtle, however, and are unlikely to affect the broad interspecific comparisons made in this study. To minimize these effects, we compared specimens collected in similar locations and at similar times within species whenever possible.

Avian Color Space Modeling

We used a model developed by Vorobyev and colleagues (Vorobyev and Osorio 1998; Vorobyev et al. 1998) to approximate how different patches of color would be perceived by a typical passerine bird. Our model takes into account avian photoreceptor sensitivities and transmission of ocular media (Hart et al. 2000), photoreceptor noise (Maier 1992; Vorobyev et al. 1998), and environment and visual background (Endler 1990; Vorobyev et al. 1998; Théry 2006). We describe below how these data were obtained and incorporated into our model.

Background and Irradiance Spectra

We collected background and irradiance measurements from March to July in 2003 and 2004 in Santa Rosa National Park, Guanacaste, Costa Rica. Manakins are forest-dwelling birds (Ridgely and Tudor 1994; Snow 2004), and the visual background against which plumage signals are perceived consists primarily of green vegetation (Vorobyev et al. 1998; Heindl and Winkler 2003*b*). Thus, we collected reflectance spectra from vegetation surrounding primary display perches at 14 leks of the long-tailed manakin located in evergreen bottomland moist tropical forest. Using the equipment and configuration described above for measuring museum specimens, we measured the reflectance of one green leaf from each of the four plants or saplings that were nearest to each display perch. We took five readings from each leaf and averaged these within leaves and across all leaves ($n = 56$) to obtain an average green-leaf background spectrum (fig. 1*A*). This spectrum closely resembles other published vegetation spectra (e.g., Vorobyev et al. 1998), as expected from the absorbance properties of chlorophyll.

Manakins occupy primarily lower and middle strata of the forest (Ridgely and Tudor 1994; Snow 2004). Although a variety of light environments may be available to forest-dwelling birds (Endler 1993), the most common light environment in the forest understory is forest shade (Endler 1993). Some species of manakin are known to seek out particular subsets of the light environment during courtship displays (Endler and Théry 1996; Heindl and Winkler 2003*a*, 2003*b*). However, for many species of manakin, basic life-history information is still lacking (Snow 2004), let alone specific details on the light environment used during display. We therefore chose to focus on the perception of manakin plumage ornaments in a forest-shade environment, as this light environment is common to all species of manakin. Because forest shade is common in the forest understory, some species will undoubtedly perform their courtship displays in this light environment. In

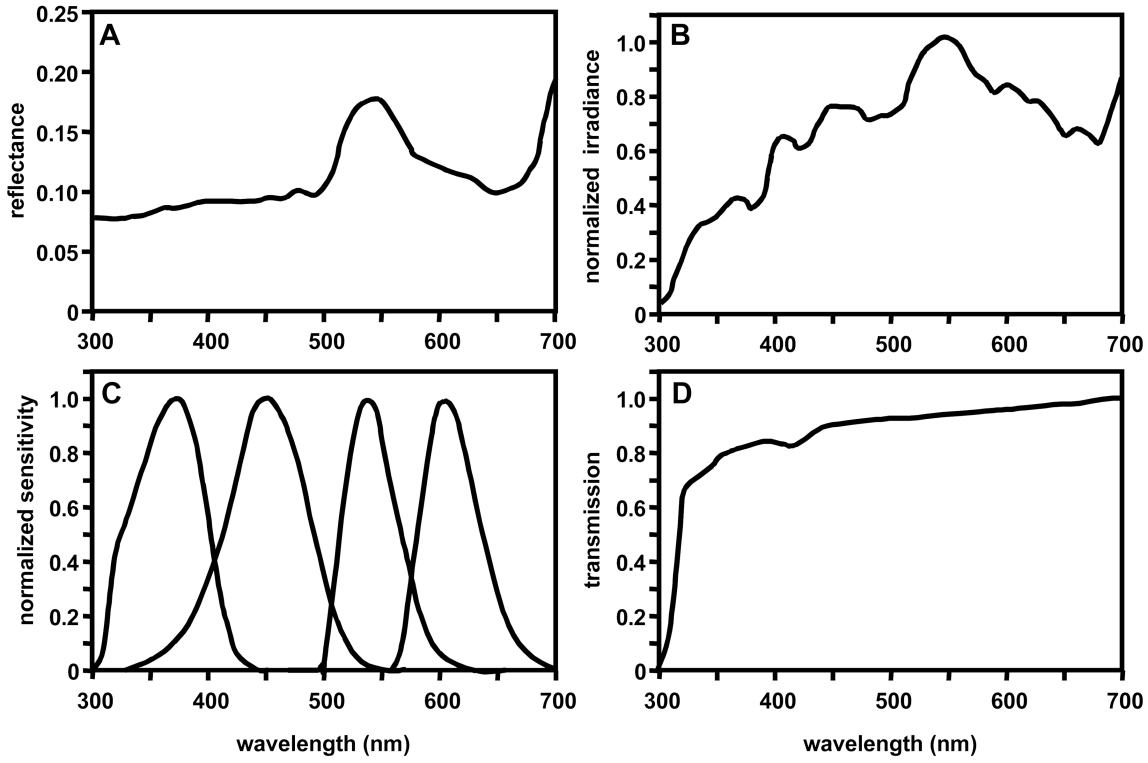

Figure 1: Data used in the formulation of avian color-space models. Calculations are based on models by Vorobyev et al. (1998). *A*, Average reflectance spectrum ($n = 56$) of green vegetation surrounding 14 *Chiroxiphia linearis* leks in bottomland evergreen forest in Costa Rica. *B*, Normalized forest-shade irradiance spectrum from an average of five spectra collected at each of 14 *C. linearis* leks in shady conditions. *C*, Normalized spectral sensitivities including the effects of oil droplets for the four cone types in *Parus caeruleus* (from left to right: ultraviolet sensitive, short-wavelength sensitive, medium-wavelength sensitive, long-wavelength sensitive). *D*, Transmission spectrum for the ocular media of *P. caeruleus*. Data for *C* and *D* from Hart et al. (2000).

many species of manakin, individual males tend to perform their displays in the same area (Théry 1992) and often on the same perch (McDonald 1989) or cleared display court (Uy and Endler 2004). This tendency to display at fixed locations probably imposes constraints on the availability of the less common subsets of the light environment, as the position of small gaps varies unpredictably over the course of the day (Heindl and Winkler 2003*a*). Indeed, many species studied to date display at least part of the time in forest shade (Endler and Théry 1996; Heindl and Winkler 2003*a*; S. M. Doucet, unpublished data). However, some species clearly prefer to display in different subsets of the forest light environment (Endler and Théry 1996). Thus, our analyses using a forest-shade light environment should be interpreted in the appropriate context: we are assessing manakin plumage conspicuousness in a light environment that is common to all manakins, where most species are likely to spend much of their time, but not necessarily the light environment in which they prefer to display.

We measured ambient light spectra using a cosine-corrected fiber-optic probe (P400-2-UV-VIS, Ocean Optics) with a 180° angle of acceptance and a measurement surface of 6 mm in diameter (CC-3-UV, Ocean Optics). At each measurement location, we calibrated the spectrometer with a calibration light source of known color temperature (LS-1-CAL, range 300–1,050 nm; Ocean Optics). We measured the ambient light at each of 14 long-tailed manakin leks. We took five readings per lek at the height of the display perch (range 26–92 cm from the ground) with the measurement surface oriented skyward and the probe held perpendicular to the ground. All spectra were taken in forest shade between 0540 and 1100 hours (CST). We transformed readings into units of photon flux as described by Endler (1990) and averaged these readings across leks to obtain an average forest-shade irradiance spectrum (fig. 1*B*). Forest-shade light is filtered through leaves in the canopy before reaching the understory, thereby developing a greenish appearance as revealed by the relatively higher irradiance at middle (green) wavelengths and relatively lower irradiance at long and short wavelengths (fig. 1*B*; Endler 1993; Heindl and Winkler 2003*a*).

Modeling Avian Color Space

The color of an object, such as a plumage patch, is determined by the relative proportions of different wavelengths of visible light that it reflects and will therefore be influenced by inherent properties of the plumage patch (e.g., pigments and microstructure) and the color of light illuminating the patch (Wyszecki and Stiles 1982). Once light reflected from an object reaches the eye, it must be transmitted through the ocular media (cornea, lens, aqueous and vitreous humor) and be coded into neural responses by photoreceptors. Light travels as photons that differ in energy, depending on wavelength, and the number of photons captured by a photoreceptor per unit time is termed "photoreceptor quantum catch." Photoreceptor quantum catch varies as a function of both the photons reaching the photoreceptor and the spectral sensitivity of that photoreceptor. Color vision requires at least two photoreceptors with different spectral sensitivities, the outputs of which can be compared simultaneously by the nervous system (Hart 2001). Single-cone photoreceptors are responsible for color discrimination in vertebrates, and most diurnal birds have four types (Hart 2001). These four photoreceptor types are characterized by the wavelengths to which they are most sensitive: long-wavelength sensitive (LWS), medium-wavelength sensitive (MWS), short-wavelength sensitive (SWS), and ultraviolet/violet sensitive (UVS/VS). The spectral sensitivity of LWS, MWS, and SWS photoreceptors is highly conserved across avian taxa, whereas the spectral sensitivity of UVS/VS photoreceptors falls into one of two categories, peaking near 370 nm (UVS) in most passerines or near 410 nm (VS) in most nonpasserines (Hart 2001).

The color of an object can be represented by a point in perceptual color space whose coordinate axes represent the quantum catches of cone photoreceptors (Goldsmith 1990). For birds, this perceptual space can be likened to a tetrahedron with one of the four photoreceptor types located at each of its vertices (Burkhardt 1989; Goldsmith 1990). Variation in how two different colors are perceived can be approximated by calculating Euclidean distances between two points in this tetrachromatic color space (Goldsmith 1990; Théry and Casas 2002; Heindl and Winkler 2003*b*; Uy and Endler 2004). However, distances between points in such a color space do not correspond directly to perceived differences in color because these distances must exceed a certain threshold to be distinguishable, and this threshold depends on noise that originates in photoreceptors and at further stages of neural processing (Vorobyev and Osorio 1998; Vorobyev et al. 1998). Vorobyev and colleagues have developed receptor-noise-limited color-space models that take into account visual sensitivities, transmission of the ocular media, light environment, visual background, and receptor noise, and these models agree well with behavioral data in a variety of taxa (Vorobyev and Osorio 1998; Vorobyev et al. 1998, 2001; Osorio and Vorobyev 2005).

We implemented an avian version of this color-space model to calculate how different colored plumage patches and differences between plumage patches and the background would be perceived by manakins. All equations follow Vorobyev et al. (1998). Spectral sensitivities have

not been measured in manakins. Thus, because most passerines have UVS cones (Cuthill et al. 2000; Hart 2001), we used spectral sensitivity data from the blue tit *Parus caeruleus*, a species with UVS cones (Hart et al. 2000; Hart 2001), to estimate photoreceptor quantum catches in manakins (fig. 1*C*). The spectral sensitivities used in our study include the effects of colored oil droplets, which narrow photoreceptor spectral sensitivities (Hart et al. 2000; Hart 2001) and thereby improve color discriminability (Vorobyev et al. 1998; Vorobyev 2003). Photoreceptor sensitivities are calculated based on best-fitted pigment templates (Govardovskii et al. 2000; Hart et al. 2000; Hart 2001).

We calculated photoreceptor quantum catches for all plumage patches of manakins (separated by sex and species). We calculated photoreceptor quantum catch (Q) as a proportion of total quantum catch for each of the four types of avian photoreceptors using the following equation:

$$Q_i = \frac{\int_\lambda R_i(\lambda)S(\lambda)I(\lambda)O(\lambda)d\lambda}{\int_\lambda R_i(\lambda)d\lambda}, \quad (1)$$

where λ represents wavelength, $R_i(\lambda)$ is the spectral sensitivity of receptor type i, $S(\lambda)$ is the reflectance of the color patch, $I(\lambda)$ is the irradiance of the illuminant (forest shade; fig. 1*B*), and $O(\lambda)$ is the transmission of the ocular media (fig. 1*D*). Data for spectral sensitivities, irradiance, and ocular transmission were normalized to 1, and all data spanned the range from 300 to 700 nm. Using equation (1), we calculated receptor quantum catches for each of the four avian single cone types (UVS, SWS, MWS, LWS). This equation assumes that birds are viewing the color patches in isolation, whereas in reality, bird color patches are viewed against a surrounding background (green vegetation in this case). Photoreceptors undergo physiological adaptation to pre-exposed or surrounding background stimuli, a process termed "chromatic adaptation" (Wyszecki and Stiles 1982). Chromatic adaptation has an important influence on the appearance of colored objects and must be taken into account when calculating photoreceptor quantum catches. We can account for chromatic adaptation by normalizing the photoreceptor quantum catches of plumage patches to the photoreceptor quantum catches of the adapting background using the von Kries scaling algorithm (Wyszecki and Stiles 1982):

$$q_i = k_i Q_i, \quad (2)$$

where the scaling factor, k_i, is defined as

$$k_i = \frac{1/\int_\lambda R_i(\lambda)S(\lambda)I(\lambda)O(\lambda)d\lambda}{\int_\lambda R_i(\lambda)d\lambda}, \quad (3)$$

where $S(\lambda)$ is the reflectance spectrum of the background (fig. 1*A*). The normalized quantum catches calculated from equation (2) represent responses to physical variation in color stimuli. According to Fechner's law, the perceived magnitude of a visual stimulus is proportional to the physical magnitude of that stimulus (Wyszecki and Stiles 1982). Thus, the receptor signal (f_i) is proportional to the normalized receptor quantum catch (q_i) and can be calculated as follows:

$$f_i = \ln(q_i). \quad (4)$$

Using equation (4), we calculated receptor signals for each of the four avian cone types. The perception of color is achieved by comparing receptor signals across different receptor types. Similarly, perceived differences in color between two objects can be determined by comparing differences in receptor signals across different receptor types. For each receptor type, the difference in receptor signals between two colored patches will equal Δf_i. For an avian tetrachromat, we can calculate the discriminability between two colored patches using the following equation:

$$\begin{aligned}\Delta S^2 = {} & [(\omega_1\omega_2)^2(\Delta f_4 - \Delta f_3)^2 + (\omega_1\omega_3)^2(\Delta f_4 - \Delta f_2)^2 \\ & + (\omega_1\omega_4)^2(\Delta f_3 - \Delta f_2)^2 + (\omega_2\omega_3)^2(\Delta f_4 - \Delta f_1)^2 \\ & + (\omega_2\omega_4)^2(\Delta f_3 - \Delta f_1)^2 + (\omega_3\omega_4)^2(\Delta f_2 - \Delta f_1)^2]/ \\ & [(\omega_1\omega_2\omega_3)^2 + (\omega_1\omega_2\omega_4)^2 + (\omega_1\omega_3\omega_4)^2 + (\omega_2\omega_3\omega_4)^2], \end{aligned} \quad (5)$$

where ΔS is the distance in tetrachromatic perceptual color space, Δf_i is the difference in receptor signals at each of the four avian receptor types (UVS, SWS, MWS, LWS), and ω_i is the noise-to-signal ratio (Weber fraction). Under bright viewing conditions, the Weber fraction can be modeled as follows:

$$\omega_i = \frac{\nu_i}{\sqrt{\eta_i}}, \quad (6)$$

where ν is the noise-to-signal ratio in a single photoreceptor of type i and η is a scaling factor that accounts for the relative number of photoreceptors of type i. We used data from the red-billed leiothrix *Leiothrix lutea* (Maier 1992) to estimate noise-to-signal ratios and data from the blue tit to estimate the relative abundance of receptor types (Hart et al. 2000). The distance in avian perceptual color space between any two colors can be measured with ΔS. Below, we describe how we used ΔS to compare differences in color between plumage patches within and across species as well as differences between plumage patches and

the background. Calculated values of ΔS only quantify differences in color and not differences in brightness, so we refer to distances in perceptual color space (ΔS) as "chromatic contrast."

Quantifying Chromatic Contrast and Dichromatism

We used the equations above to calculate the distance in perceptual color space (ΔS) between manakin plumage patches and the green vegetation background (chromatic contrast against the background). We calculated these distances for all plumage patches within each species and averaged across plumage patches to obtain species means, using separate analyses for males and females. Because data were normalized to the background, the normalized receptor quantum catch for the background was $(q_i) = 1$, and, consequently, $f_i = 0$. To obtain measures of sexual dichromatism in plumage, we calculated distances in perceptual color space (ΔS) between homologous plumage patches in males and females and averaged these within species to obtain mean chromatic dichromatism values for each species. To obtain measures of within-individual plumage contrast, we calculated distances in perceptual color space (ΔS) between all possible combinations of plumage patches in each species and then averaged these within species to obtain mean within-plumage chromatic contrast values for each species. We conducted these analyses separately for males and females.

Quantifying Achromatic Contrast

Because variation in brightness also influences the conspicuousness of signals, we calculated measures of brightness contrast (hereafter "achromatic contrast") to correspond to the measures of chromatic contrast we described above. In birds, double cones are thought to be used for achromatic signal detection (Cuthill et al. 2000; Hart 2001). We therefore calculated receptor signals for double cones (f_D) using the formulas described above and spectral sensitivity data from blue tit double cones (Hart et al. 2000). Because receptor noise (ω_D) is unknown for double cones and the background is the same for all comparisons, f_D was calculated directly from Q_D (expressed as a percentage rather than a proportion to facilitate interpretation of positive and negative values). Thus, the perceived brightness of a color patch can be estimated as f_D, and the perceived difference in brightness between any two patches (achromatic contrast) can be estimated as Δf_D. Because there is only one type of double cone, receptor noise would be the same for all comparisons and would only affect absolute and not relative differences in receptor signals (Stuart-Fox et al. 2003). Thus, Δf_D should serve as a good approximation of differences in perceived brightness. High achromatic contrast can result from the reflection of more light than the patch of comparison or less light than the patch of comparison, so we used absolute values in our analyses. We calculated a measure of achromatic contrast for each measure of chromatic contrast described above.

Sensitivity of the Model

The model we constructed in this study makes a number of assumptions. To determine the sensitivity of the model to these assumptions, we repeated many of our analyses using different variables. One of our main assumptions was that the short-wavelength photoreceptor of manakins was, like that of the blue tit (Hart et al. 2000), sensitive to near ultraviolet wavelengths. We repeated our analyses using spectral sensitivity data from the chicken *Gallus gallus*, which has VS cones instead of UVS cones (Govardovskii and Zueva 1977), and found that models using the different receptor types were qualitatively very similar. For example, mean plumage dichromatism scores obtained from UVS and VS visual systems were highly correlated ($r = 0.71$, $n = 49$, $P < .0001$). Another important assumption was that plumage patches were viewed in a forest-shade light environment, which is rich in middle wavelengths and poor in short wavelengths. We therefore repeated our analyses using a blue-sky light environment, which is rich in short wavelengths and poor in long wavelengths (Endler 1993). Changing the light environment would not affect the main conclusions of our study, as we obtained very similar measures of dichromatism and plumage contrast against the background with both light environments. For example, mean chromatic dichromatism scores were highly correlated between the two light environments ($r = 0.86$, $n = 49$, $P < .0001$), and mean values of chromatic and achromatic contrast against the background for the blue mantle of *C. linearis* (fig. 2*B*) changed from 13.41 and 0.86 in a forest-shade light environment to 12.77 and 0.85 in a blue-sky light environment, respectively. Estimates of receptor noise can also be problematic (Vorobyev et al. 1998), although our models were even less sensitive to variation in this parameter (S. M. Doucet, D. J. Mannill, and G. E. Hill, unpublished data). Thus, the models we constructed are relatively robust, and subtle variation in specific parameters will probably have little effect on the overall conclusions of this study. However, a more detailed investigation of the consequences of using different visual models is certainly warranted.

Comparative Analyses

For analyses involving comparisons of plumage contrast with discrete variables such as sex or body regions, we first

performed each analysis by including all 50 species that we measured. However, because closely related species tend to exhibit more similar patterns than expected by chance, we repeated each analysis using only one species per genus (chosen arbitrarily) as a means of controlling for phylogenetic nonindependence (Harvey and Pagel 1991; Hausmann et al. 2003). We also compared the intensity of sexual selection (estimated as the degree of sexual dichromatism) to variation in chromatic and achromatic contrast across manakins. To control for the effects of phylogeny in such analyses involving continuous variables, we used CAIC (ver. 2.0) to calculate independent contrasts for our comparisons (Felsenstein 1985; Purvis and Rambaut 1995). We used the phylogeny derived by Prum (1997) from cladistic analysis of syringeal morphology (Prum 1992) and variation in plumage character states. Our analyses were therefore restricted to the 37 species we measured that were included in Prum's (1997) phylogeny. In the absence of branch-length data, we assumed that branches were of equal length in our analyses. We regressed independent contrasts of chromatic and achromatic plumage contrast against the background and between body regions (dependent variables) onto independent contrasts of sexual dichromatism (independent variable) with regression lines forced through the origin.

Assessing Mechanism-Based Variation

To assess differences in chromatic and achromatic contrast resulting from different mechanisms of plumage color production, we classified each color patch for each species according to its probable production mechanism. We then compared mean values of contrast against the background for colors produced by different mechanisms. To classify color patches according to mechanism of production, we first visually assessed specimens and confirmed these assessments by examining reflectance spectra. Although caution is warranted in such assessments of color-production mechanisms, particularly in nonpasserines (McGraw et al. 2004), production mechanisms in passerine birds are relatively well characterized. Moreover, colors produced by

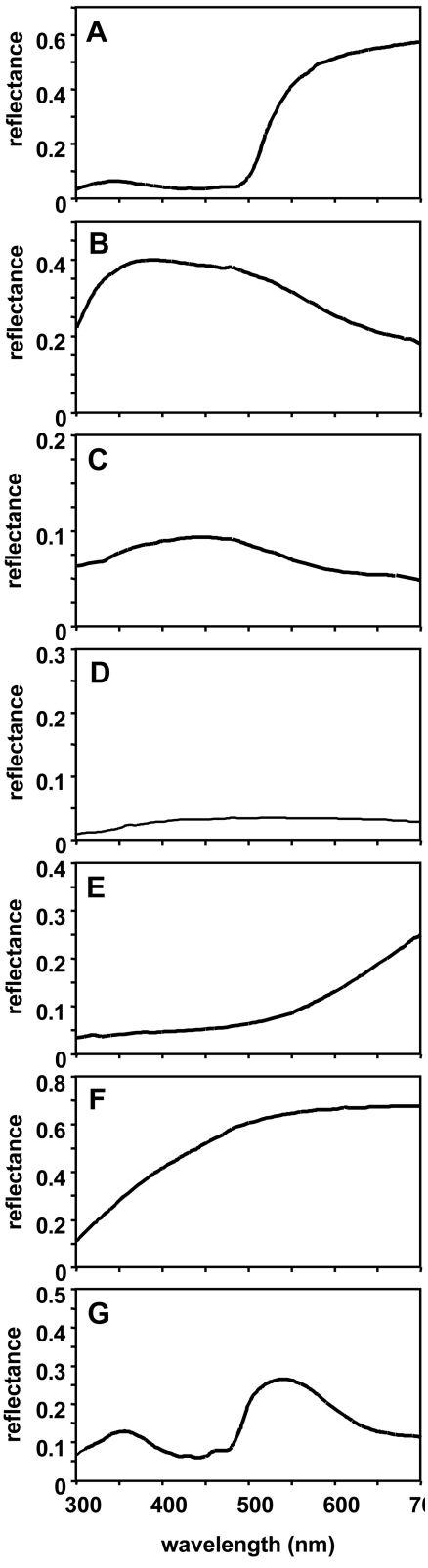

Figure 2: Representative reflectance spectra of plumage colors produced by different mechanisms. All spectra are an average of spectra from five males. *A*, Orange carotenoid crown reflectance of *Pipra erythrocephala*. *B*, Ultraviolet/blue noniridescent structural mantle reflectance of *Chiroxiphia linearis*. *C*, Blue black iridescent structural mantle reflectance of *Corapipo gutturalis*. *D*, Black eumelanin breast reflectance of *C. linearis*. *E*, Rufous brown phaeomelanin mantle reflectance of *Machaeropterus deliciosus*. *F*, Structural white throat reflectance of *C. gutturalis*. *G*, Green carotenoid/structural rump reflectance of *Lepidothrix iris*. Note that *Y*-axis scale changes to emphasize differences in the shape of reflectance spectra.

different mechanisms have distinctive reflectance spectra owing to the particular absorptive properties of different pigments or reflective properties of different nano-ordered tissues. We classified colors as carotenoid based when they were red, orange, or yellow and showed little reflectance at wavelengths below 500 nm and a steep increase in reflectance culminating in a plateau at longer wavelengths (fig. 2*A*). Carotenoid pigments have been isolated in *Pipra* (Hudon et al. 1989) and *Chiroxiphia* (S. M. Doucet and K. J. McGraw, unpublished data) manakins, and reflectance spectra of red, orange, and yellow plumage in other species closely resembled those of known carotenoid-based colors. We classified colors as noniridescent structural when feather barbs were blue or turquoise and showed a distinct peak in reflectance at wavelengths below 500 nm (fig. 2*B*). Color-producing nanostructures have been identified in both genera of manakins in which species have blue plumage patches, namely, *Lepidothrix* (Frank 1939; Théry 1990; Prum 2006) and *Chiroxiphia* (S. M. Doucet, unpublished data). We classified colors as iridescent structural when feather barbules were blue-black and changed in color with angle of observation and their reflectance spectra showed a distinct reflectance peak within the bird-visible range (fig. 2*C*). We classified colors as eumelanin-based when they were black and showed low, even reflectance across the spectrum (fig. 2*D*) and classified them as phaeomelanin-based when they were rufous brown and showed increasingly high reflectance at longer wavelengths (fig. 2*E*; McGraw 2006*b*). We classified colors as white structural when they were white and had reflectance spectra that showed a steep increase in reflectance at short wavelengths (300–350 nm) and high, even reflectance in the rest of the bird-visible spectrum (fig. 2*F*; Shawkey and Hill 2005). We classified colors as a mixture of carotenoid pigments and structural color when they were green or olive green and showed peaks in reflectance at UV and longer-wavelength portions of the spectrum and a notable decrease in reflectance at about 450 nm (fig 2*G*). Dyck (1978) described this combined mechanism of carotenoid pigmentation and reflective nanostructure in some passerine species with green coloration, including one *Manacus* manakin. We recognize that these categories are in some cases an oversimplification; however, they should represent the mechanism responsible for causing most of the variation in color between individuals.

Analyses

We used Shapiro-Wilk tests to test for normality in our variables and applied standard transformations to improve fit to normality when possible. When data could not be normalized by transformation we used nonparametric tests. Small variations in sample size occur because not all data were available for all species.

Results

Comparison of Male and Female Plumage Conspicuousness

Chromatic plumage contrast against the green vegetation background varied significantly by sex and body region in manakins (fig. 3*A*; two-way ANOVA, $F = 35.49$, df $= 9, 485$, $P < .0001$; sex: $F = 68.66$, $P < .0001$; region: $F = 37.32$, $P < .0001$). Males exhibited higher chromatic plumage contrast against the vegetation background than did females, and the head, front, and back exhibited higher chromatic contrast than the wings and tail (fig. 3*A*). There was also a significant interaction between sex and body region (sex × region: $F = 24.76$, $P < .0001$), as the degree of difference between males and females varied across body regions (fig. 3*A*). These sex and body-region differences in chromatic contrast against the background remained highly significant even when we included only one species per genus in our analyses (two-way ANOVA, $F = 16.83$, df $= 9, 170$, $P < .0001$; sex: $F = 31.92$, $P < .0001$; region: $F = 17.47$, $P < .0001$; sex × region: $F = 12.41$, $P < .0001$).

Achromatic plumage contrast against the green vegetation background also varied significantly by sex and body region in manakins (fig. 3*B*; two-way ANOVA, $F = 22.28$, df $= 9, 485$, $P < .0001$; sex: $F = 180.7$, $P < .0001$; region: $F = 4.27$, $P = .002$). Males exhibited much higher achromatic plumage contrast against the vegetation background than did females, and, as with chromatic contrast, the head, front, and back exhibited higher achromatic contrast than the wings and tail (fig. 3*B*). There was no significant interaction between sex and body region (sex × region: $F = 0.66$, $P = .61$), as the degree of difference between males and females did not vary across body regions (fig. 3*B*). Sex differences in achromatic contrast against the background remained highly significant even when we included only one species per genus in our analyses (two-way ANOVA, $F = 7.65$, df $= 9, 170$, $P < .0001$; sex: $F = 64.64$, $P < .0001$). However, variation in achromatic plumage contrast across different body regions disappeared when only one species per genus was included in the analysis (region: $F = 0.59$, $P = .66$).

Males exhibited much higher within-individual plumage contrast than did females, both in terms of chromatic contrast between patches (fig. 3*C*; paired *t*-test: $t = -7.67$, $n = 49$, $P < .0001$) and achromatic contrast between patches (fig. 3*D*; paired *t*-test: $t = -8.05$, $n = 49$, $P < .0001$). These differences remained highly significant when only one species per genus was included in the analyses

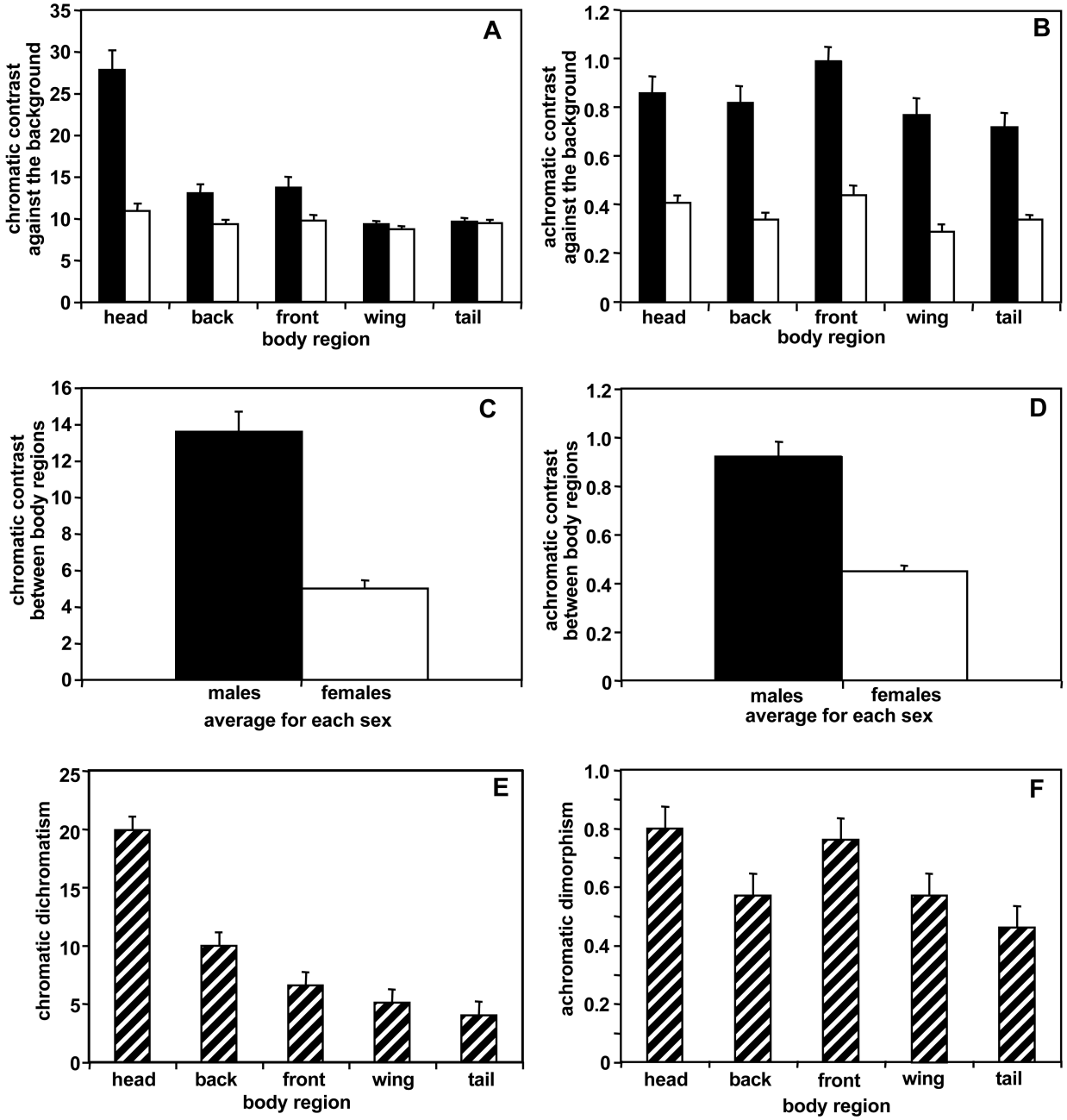

Figure 3: *A–D*, Mean values of chromatic (*A*) and achromatic (*B*) contrast against the green vegetation background and chromatic (*C*) and achromatic (*D*) contrast between body regions for male (*black bars*) and female (*white bars*) manakins in a forest-shade light environment. *E*, *F*, Mean values of chromatic (*E*) and achromatic (*F*) dichromatism in a forest-shade light environment for different body regions (distance between males and females in perceptual color space). Vertical bars show standard errors.

(chromatic contrast between patches, paired *t*-test: $t = -4.84$, $n = 18$, $P = .0002$; achromatic contrast between patches, paired *t*-test: $t = -4.73$, $n = 18$, $P = .0002$).

The magnitude of the difference between male and female plumage coloration (i.e., degree of sexual dichromatism) was not evenly distributed across body regions (fig. 3*E*; ANOVA, $F = 29.54$, df $= 4, 240$, $P < .0001$). The degree of sexual dichromatism in head plumage was significantly higher than in all other body regions, and the degree of dichromatism in back plumage was significantly

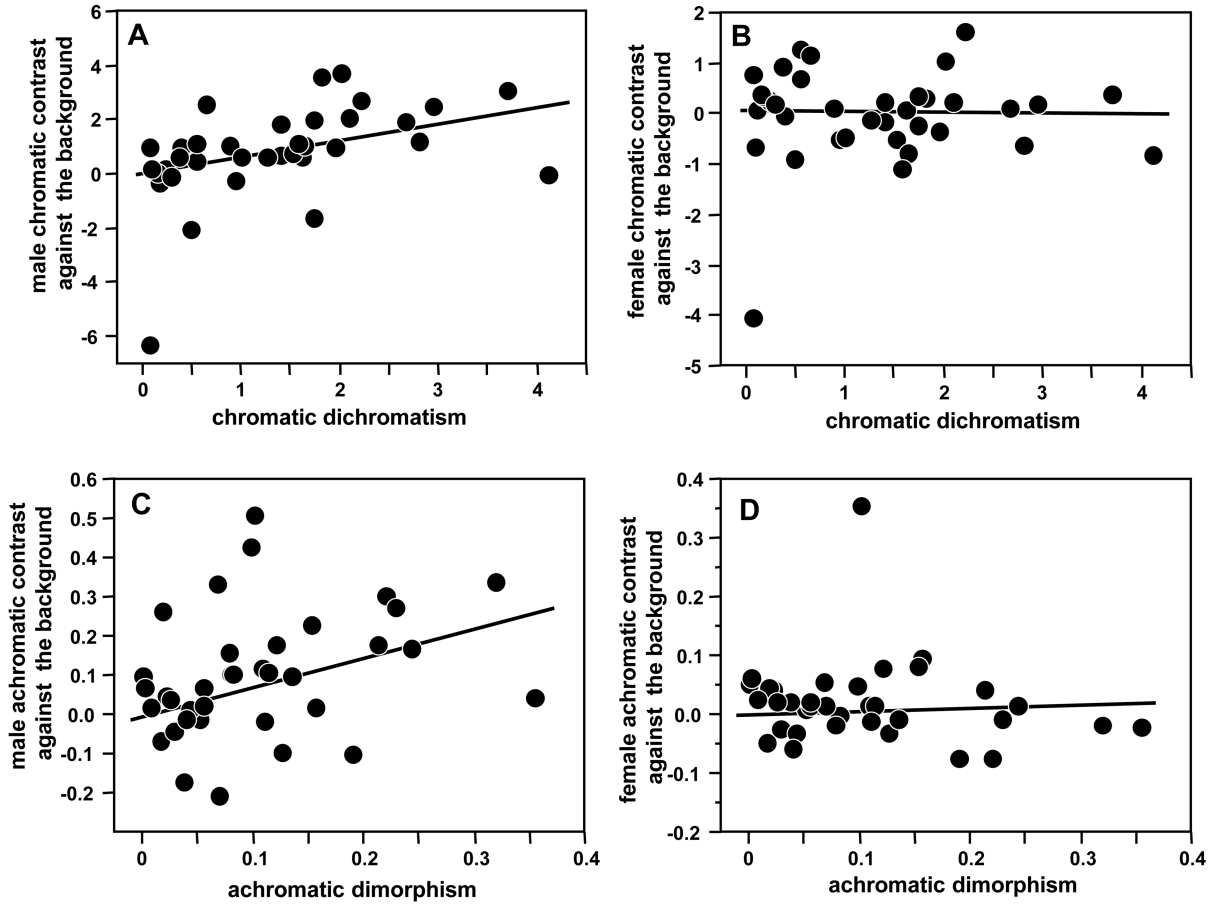

Figure 4: Relationship between chromatic contrast against the green vegetation background and chromatic sexual dichromatism for male (*A*) and female (*B*) manakins in a forest-shade light environment and relationship between achromatic contrast against the green vegetation background and achromatic sexual dimorphism for male (*C*) and female (*D*) manakins in a forest-shade light environment. All data are independent contrasts controlling for the effects of phylogeny with regression lines forced through the origin.

higher than dichromatism in wing and tail plumage (Tukey-Kramer tests, $P < .05$). This difference in degree of sexual dichromatism between body regions remained highly significant when only one species per genus was included in the analyses (ANOVA, $F = 12.14$, df $= 4, 85$, $P < .0001$). There were similar, albeit less pronounced, differences in achromatic sexual dimorphism across body regions (fig. 3*F*; ANOVA, $F = 3.52$, df $= 4, 240$, $P = .008$). The degree of achromatic sexual dimorphism was significantly higher for the head and front than for the tail (Tukey-Kramer test, $P < .05$). Variation in the degree of achromatic sexual dimorphism between body regions was no longer significant when only one species per genus was included in the analyses (ANOVA, $F = 1.87$, df $= 4, 85$, $P = .12$).

Sexual Dichromatism and Background Plumage Contrast

In analyses using phylogenetically independent contrasts of 36 species of manakin, there was a significant positive relationship between sexual dichromatism and mean chromatic contrast against the background in males (fig. 4*A*; $r = 0.57$, $F = 17.26$, df $= 1, 35$, $P = .0002$) but not females (fig. 4*B*; $r = 0.00$, $F = 0.00$, df $= 1, 35$, $P = .96$). When we considered each body region separately, we found a significant positive relationship between degree of sexual dichromatism and chromatic contrast against the background in male plumage for the head ($r = 0.86$, $F = 100.12$, df $= 1, 35$, $P < .0001$), front ($r = 0.75$, $F = 43.95$, df $= 1, 35$, $P < .0001$), back ($r = 0.66$, $F = 27.75$, df $= 1, 35$, $P < .0001$), and wings ($r = 0.54$, $F = 14.63$, df $= 1, 35$, $P = .0005$), but not the tail ($r = 0.22$,

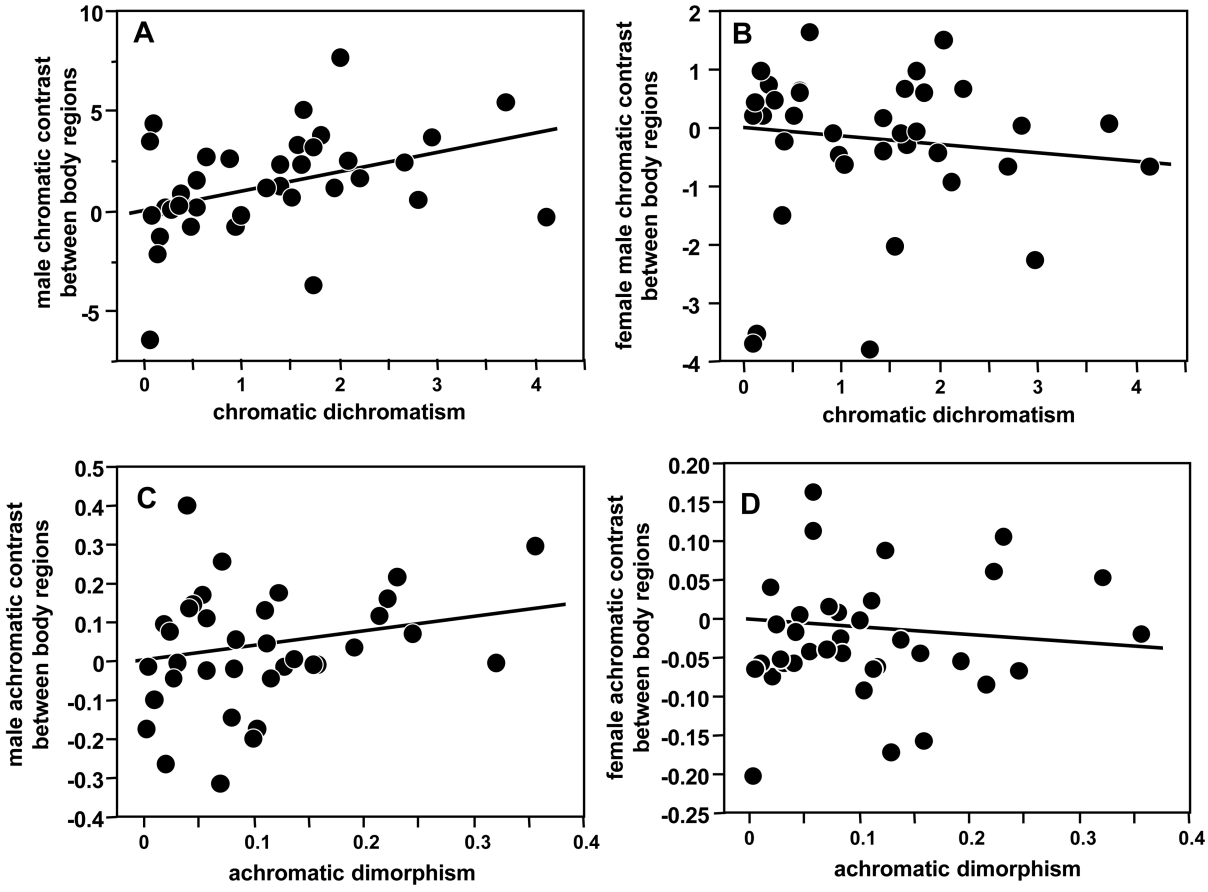

Figure 5: Relationship between chromatic contrast between body regions and chromatic sexual dichromatism for male (*A*) and female (*B*) manakins in a forest-shade light environment and relationship between achromatic contrast between body regions and achromatic sexual dimorphism for male (*C*) and female (*D*) manakins in a forest-shade light environment. All data are independent contrasts controlling for the effects of phylogeny with regression lines forced through the origin.

$F = 1.67$, df $= 1, 35$, $P = .20$). Among females, there was no significant relationship between the degree of sexual dichromatism and chromatic contrast against the background for any body region (all $P > .14$).

Similarly, analyses using phylogenetically independent contrasts revealed a significant positive relationship between overall degree of achromatic sexual dimorphism and achromatic contrast against the background in males (fig. 4*C*; $r = 0.57$, $F = 17.13$, df $= 1, 35$, $P = .0002$) but not in females (fig. 4*D*; $r = 0.10$, $F = 0.42$, df $= 1, 35$, $P = .23$). When we considered each body region separately, there was a significant positive relationship between achromatic dichromatism and achromatic contrast against the background in male plumage for the head ($r = 0.78$, $F = 53.81$, df $= 1, 35$, $P < .0001$), back ($r = 0.86$, $F = 99.83$, df $= 1, 35$, $P < .0001$), front ($r = 0.73$, $F = 41.68$, df $= 1, 35$, $P < .0001$), wing ($r = 0.68$, $F = 30.87$, df $= 1, 35$, $P < .0001$), and tail ($r = 0.73$, $F = 40.34$, df $= 1, 35$, $P < .0001$). Among females, only the relationship between achromatic sexual dimorphism and achromatic contrast against the background for the back approached significance ($r = 0.30$, $F = 3.30$, df $= 1, 35$, $P = .08$, all other $P > .1$).

Sexual Dichromatism and Within-Plumage Contrast

In analyses using phylogenetically independent contrasts, there was a significant positive relationship between chromatic sexual dichromatism and mean chromatic contrast between body regions in males (fig. 5*A*; $r = 0.57$, $F = 16.29$, df $= 1, 35$, $P = .0003$) but not in females (fig. 5*B*; $r = -0.17$, $F = 1.14$, df $= 1, 35$, $P = .29$). Similarly, there was a significant positive relationship between achromatic sexual dimorphism and mean achromatic contrast between body regions in males (fig. 5*C*; $r = 0.33$, $F =$

Table 1: Comparison of chromatic contrast against the green vegetation background in a forest-shade light environment for plumage colors produced by different mechanisms across different body regions of male manakins

Region	CAR	EUMEL	PHAEOMEL	STRUCT	IRID	WHITE	CAR/STRUCT	*F*	df	*P*
Head	38.9 (28)	8.2 (4)	19.7 (2)	17.0 (3)	11.3 (4)	7.6 (4)	9.9 (5)	24.15	6,43	<.0001
Back	35.2 (3)	9.2 (17)	23.5 (3)	16.1 (8)	12.3 (4)	7.5 (3)	11.6 (20)	22.84	6,51	<.0001
Front	21.3 (18)	8.7 (19)	17.6 (7)			7.2 (7)	17.6 (7)	9.41	4,50	<.0001
Wing	9.82 (2)	9.3 (22)	10.9 (7)		12.9 (2)	7.1 (5)	8.5 (12)	3.69	4,30	.007
Tail		8.9 (26)	11.1 (16)				8.75 (5)	4.81	2,44	.01

Note: CAR = carotenoid, EUMEL = eumelanin, PHAEOMEL = phaeomelanin, STRUCT = noniridescent structural, IRID = iridescent structural, WHITE = white structural, CAR/STRUCT = combination of carotenoids and microstructure. Test statistics are from ANOVAs. We only included mechanisms in statistical comparisons when they were expressed by males of at least two different species. Values in parentheses indicate number of species expressing each mechanism for that body region.

4.52, df = 1,35, $P = .04$) but not in females (fig. 5*D*; $r = -0.17$, df = 1,35, $P = .29$).

Plumage Contrast and Mechanisms of Production

Among male manakins, there were significant differences in the degree of chromatic plumage contrast against the background for colors produced by different mechanisms for all body regions (table 1). In general, carotenoid colors resulted in the highest values of chromatic contrast against the background, followed by phaeomelanin colors and noniridescent blue structural colors. Eumelanin colors and white structural colors resulted in the lowest values of chromatic contrast against the background (table 1). The degree of chromatic contrast against the background exhibited by colors produced by particular mechanisms was conserved across body regions (table 1). Indeed, when plumage patches are grouped by mechanism of color production within species, there are significant differences in the chromatic contrast of male plumage colors produced by different mechanisms (fig. 6*A*; ANOVA, $F = 42.47$, df = 6,128, $P < .0001$), with carotenoid colors exhibiting significantly more contrast than all other color mechanisms and structural colors exhibiting significantly more contrast than white structural colors (Tukey-Kramer test, $P < .05$). These differences remained highly significant even when only one species per genus was included in the analysis (ANOVA, $F = 10.07$, df = 6,39, $P < .0001$).

Similarly, among male manakins, there were significant differences in the degree of achromatic contrast against the background for colors produced by different mechanisms for all body regions (table 2). In general, white structural colors, noniridescent blue structural colors, and eumelanin colors resulted in the highest values of achromatic contrast against the background (table 2). Phaeomelanin colors and colors produced by a mixture of carotenoid pigments and feather microstructure resulted in the lowest values of achromatic contrast (table 2). The degree of achromatic contrast against the background exhibited by colors produced by particular mechanisms was conserved across body regions (table 2). Indeed, when plumage patches are grouped by mechanism of color production within species, there are significant differences in achromatic plumage contrast against the background for colors produced by different mechanisms (fig. 6*B*; ANOVA, $F = 30.81$, df = 6,128, $P < .0001$), with white structural colors exhibiting significantly more achromatic contrast than all other color mechanisms, followed closely

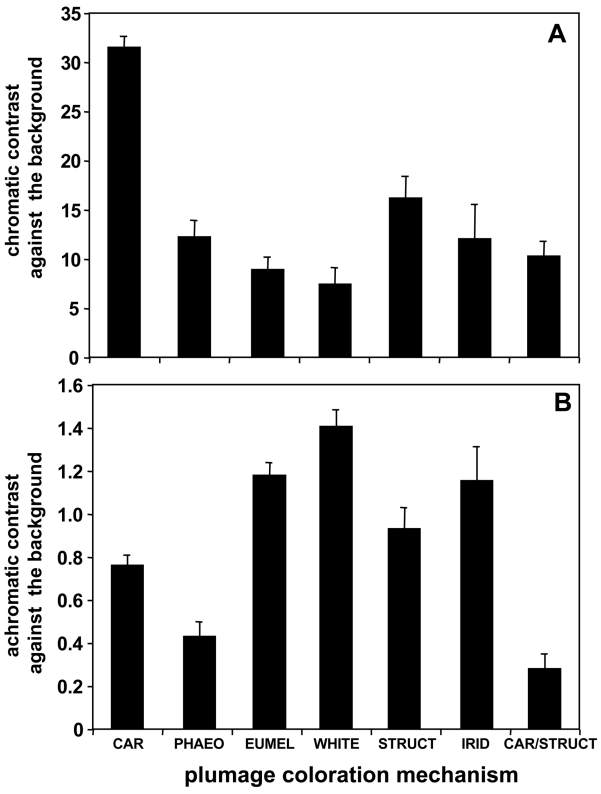

Figure 6: Comparisons of variation in chromatic (*A*) and achromatic (*B*) contrast against the green vegetation background in a forest-shade light environment for colors produced by different mechanisms. See table 1 for mechanism abbreviations. Vertical bars show standard errors.

Table 2: Comparison of achromatic contrast against the green vegetation background in a forest-shade light environment for plumage colors produced by different mechanisms across different body regions of male manakins

Region	CAR	EUMEL	PHAEOMEL	STRUCT	IRID	WHITE	CAR/STRUCT	*F*	df	*P*
Head	.68 (28)	.95 (4)	.43 (2)	1.40 (3)	1.21 (4)	1.83 (4)	.54 (5)	8.56	6, 43	<.0001
Back	.51 (3)	1.2 (17)	.23 (3)	.82 (8)	1.19 (4)	1.41 (3)	.45 (9)	16.13	6, 51	<.0001
Front	.96 (18)	1.24 (19)	.80 (7)			1.45 (7)	.09 (4)	17.46	4, 50	<.0001
Wing	1.14 (2)	1.08 (22)	.32 (7)		.74 (2)	1.24 (5)	.20 (12)	15.90	5, 44	<.0001
Tail		1.06 (26)	.34 (16)				.15 (5)	59.36	2, 44	<.0001

Note: CAR = carotenoids, EUMEL = eumelanin, PHAEOMEL = phaeomelanin, STRUCT = noniridescent structural, IRID = iridescent structural, WHITE = white structural, CAR/STRUCT = combination of carotenoids and microstructure. Test statistics are from ANOVAs. We only included mechanisms in statistical comparisons when they were expressed by males of at least two different species. Values in parentheses indicate number of species expressing that particular mechanism.

by eumelanin colors, iridescent structural colors, and noniridescent structural colors (Tukey-Kramer test, $P < .05$). Carotenoid colors exhibited significantly more achromatic contrast against the background than phaeomelanin colors and colors produced by a mixture of carotenoids and microstructure, which exhibited the least amount of achromatic contrast against the background (Tukey-Kramer test, $P < .05$). These differences remained highly significant even when only one species per genus was included in our analyses (ANOVA, $F = 14.09$, df $= 6, 39$, $P < .0001$).

Discussion

By integrating data from avian visual sensitivities, ocular transmission, reflectance of the visual background, and irradiance of the light environment, we constructed an avian perceptual color-space model that allowed us to assess the conspicuousness of plumage ornaments from the perspective of a typical passerine bird. Using this model, we assessed how the plumage coloration of 50 species of manakin would be perceived in a tropical forest habitat. When compared with the olive green plumage of most females, the plumage of male manakins exhibited significantly higher levels of chromatic (color) and achromatic (brightness) contrast against the green vegetation background typical in the forested habitat of manakins. Analyses using phylogenetically independent contrasts revealed that sexual dichromatism was positively associated with the degree of chromatic and achromatic plumage contrast against the background in males. Our findings therefore support the predictions of our first hypothesis. If degree of sexual dichromatism serves as an indirect measure of the intensity of sexual selection (e.g., Owens and Hartley 1998; Badyaev and Hill 2003), our findings suggest that sexual selection has favored the evolution of conspicuous plumage ornaments that enhance signal efficacy in male manakins by creating high visual contrast against the background.

Evolution of Dichromatism

Evolutionary changes in sexual dichromatism can be attributed to interspecific changes in male plumage, changes in female plumage, or changes in both sexes (Badyaev and Hill 2003). We can determine whether changes in dichromatism resulted primarily from changes in male plumage or from changes in both sexes by examining patterns of interspecific variation in female plumage. A positive association between female plumage contrast against the background and sexual dichromatism could result from the genetically correlated evolution of male and female traits (e.g., Lande 1987), as strong selection for these traits in males combined with weaker selection against them in females could lead to the expression of ornamental coloration in females. By contrast, a negative association between female plumage contrast against the background and sexual dichromatism would suggest that dimorphism evolved in part from natural selection for cryptic female plumage. Such a pattern might be expected because females are solely responsible for parental care in manakins, and they should therefore experience strong natural selection for crypsis (Martin and Badyaev 1996). However, we found no relationship between female plumage contrast against the background and sexual dimorphism in manakins. Our findings do not imply that females are not experiencing selection for cryptic plumage. Rather, our findings suggest that increased sexual dichromatism in manakins resulted primarily from selection on male plumage, causing male plumage to diverge away from background coloration and thereby increase in conspicuousness.

Variation in Dichromatism across Body Regions

When we considered each body region separately, there was a positive association between chromatic sexual dichromatism and male plumage contrast against the background for all body regions except the tail. Similarly, there was a strong positive relationship between achromatic sex-

ual dimorphism and male plumage contrast against the background for all body regions. Interspecific variation in dichromatism across body regions has been documented in other species of birds (e.g., Badyaev 1997) and can be explained, in this case, by considering patterns of plumage ornamentation in manakins. Most colorful plumage patches are found on the crowns, rumps, throats, and occasionally the wings of male manakins (Prum 1997), which probably explains why these body regions exhibited more chromatic sexual dichromatism and showed an association between dichromatism and chromatic contrast against the background in males. By contrast, the tails of most male manakins are black or brownish in coloration, resulting in low chromatic contrast against the background and low chromatic sexual dimorphism. These patterns of coloration may also explain the even distribution of achromatic sexual dimorphism across body regions and the consistently positive associations between achromatic dimorphism and contrast against the background for all body regions in males. Colorful plumage patches on the crowns, rumps, throats, and wings of male manakins result in high achromatic dimorphism and contrast against the background by being brighter than the same plumage patches in females and brighter than the background, whereas the dark tails of males result in high achromatic contrast by being darker than these patches in females and darker than the background.

Selection for Signal Efficacy

Taken together, our findings suggest that sexual selection for signal efficacy has had a strong influence on the signal design of manakin sexual ornaments. Our perceptual models were based on a generalized forest-shade light environment and a visual background consisting of green vegetation. However, manakins might further enhance or reduce the conspicuousness of their ornaments through modification of the visual background or by displaying in particular light environments. Even within forests, a number of different light environments are recognized (Endler 1993), and manakins may seek out particular subsets of the light environment for their sexual displays to further enhance the conspicuousness of their plumage ornaments (Théry 1987; Théry and Vehrencamp 1995; Endler and Théry 1996; Heindl and Winkler 2003*a*, 2003*b*). Although green vegetation is a common visual background in forests, at least one species of manakin is known to enhance the conspicuousness of its sexual displays through modification of the visual background by clearing a display court (Uy and Endler 2004). We were unable to take into account such species-specific modification of the display environment in our analyses, which suggests that the patterns we document here are quite general and may even underestimate of the strength of selection for signal efficacy in manakin plumage ornaments. Moreover, support from other comparative studies suggests that the visual environment may have a widespread influence on ornamental plumage coloration in birds (McNaught and Owens 2002; Gomez and Théry 2004).

Multiple Plumage Patches and Within-Plumage Contrast

Because many species of manakin have multiple colored plumage patches, we were interested in whether the degree of within-individual plumage contrast increased with increasing sexual dichromatism. Males exhibited significantly higher chromatic and achromatic contrast between plumage patches than did females. Moreover, both chromatic and achromatic within-individual plumage contrast increased significantly with sexual dichromatism in males but not females. These data therefore support the predictions of our second hypothesis, suggesting that sexual selection has favored the evolution of multiple, contrasting plumage patches in manakins. Our findings have important implications for the evolution of elaborate sexual ornaments in animals. Within-individual contrast can increase the conspicuousness of male plumage displays at short viewing distances while not necessarily increasing, and sometimes even decreasing, conspicuousness at longer viewing distances (Endler 1990; Endler and Théry 1996; Heindl and Winkler 2003*a*; Théry 2006). Thus, by increasing contrast between plumage patches, male manakins become more conspicuous to nearby females but not necessarily to distant predators. Thus, the evolution of multiple colored plumage patches may offer a partial resolution of the conflict between selection for conspicuous intraspecific sexual displays and selection for predation avoidance through crypsis (Heindl and Winkler 2003*a*; Théry 2006).

Mechanism-Based Variation

We found that colors produced by different mechanisms resulted in different levels of chromatic and achromatic contrast against the background. Under forest-shade illumination and viewed against a background of green vegetation, carotenoid colors resulted in the largest values of chromatic contrast, followed by phaeomelanin colors and blue structural colors. Because forest-shade illumination is rich in middle wavelengths of light (fig. 1*B*), carotenoid and phaeomelanin colors, which peak at longer wavelengths, will be conspicuous against a green vegetation background. Although noniridescent blue structural colors resulted in relatively high chromatic contrast against the background under these conditions, they might result in higher contrasts in light environments that are richer in

short wavelengths (Endler 1993). However, reanalysis of our data revealed that even under blue-sky illumination, carotenoid colors resulted in the greatest amount of chromatic contrast against the background (S. M. Doucet, D. J. Mennill, and G. E. Hill, unpublished data). Our findings therefore suggest that the background against which a color is viewed has a potentially greater influence on conspicuousness than the light environment, a phenomenon that probably results from the fact that variation in light environment influences the color of both the plumage patch and the background in similar ways. White structural colors and eumelanin colors resulted in the lowest values of chromatic contrast. Because these colors reflect more evenly across the spectrum, forest-shade illumination induces a relative increase in reflectance at middle wavelengths and relative decreases in reflectance at long and short wavelengths, giving them a greenish appearance resulting in low chromatic contrast against the green vegetation. High values of achromatic contrast can result from signals that are either much darker or much brighter than the visual background. Because eumelanin and white structural colors are, respectively, the darkest and brightest colors found in manakins, these same color mechanisms resulted in the highest values of achromatic contrast against the background. Similar patterns have been documented in other studies (e.g., Endler and Théry 1996; Heindl and Winkler 2003*b*). Our data therefore support the predictions of our third hypothesis, suggesting that colors produced by different mechanisms differ in their degree of contrast against the background.

Our findings have important implications for the evolution of sexual ornaments. Theory predicts that sexual selection will favor the evolution of ornaments that exhibit an optimal balance between signal efficacy and signal content (Schluter and Price 1993). Several studies suggest that colors produced by different mechanisms may differ in signal content (McGraw and Hill 2000; McGraw et al. 2002; Jawor and Breitwisch 2004), and we show here that colors produced by different mechanisms also differ in chromatic and achromatic conspicuousness. Thus, the most conspicuous signals may not be the most informative, which may result in a trade-off between selection for signal efficacy and selection for signal content. In most animals, acuity for color detection is typically inferior to acuity for brightness detection (Endler 1978). In birds, this may result from the fact that double cones, which are thought to be used for achromatic signal detection, occupy a large cross-sectional area for photon catch (Hart 2001). Because individual signals cannot maximize both chromatic and achromatic contrast against the background, signals that maximize chromatic contrast will be easier to detect at shorter viewing distances, whereas signals that maximize achromatic contrast will be detectable at longer viewing distances (Endler 1978; Endler and Théry 1996; Heindl and Winkler 2003*b*). Thus, quality-indicating signals, which necessarily require assessment from short distances, should optimize chromatic contrast. Indeed, in our study, carotenoid coloration, a known quality indicator in a number of bird species (Hill 2006), exhibited the highest level of chromatic contrast and only moderate achromatic contrast. Conversely, signals that necessitate long-range transmission should optimize achromatic contrast (Heindl and Winkler 2003*b*; Théry 2006). For example, the black and white plumage patches found in many species of manakins may be particularly efficient as amplifiers (sensu Hasson 1991) of longer-range signals such as behavioral displays. Bright blue colors in manakins showed intermediate levels of chromatic and achromatic contrast and may be effective as either short- or long-distance signals. Thus, when used individually, particular types of plumage ornaments may optimize efficacy, content, or some combination of the two, depending on the distance from which these signals are perceived. A comparative analysis of the types of signals used in short-range and long-range communication would provide an interesting test of this hypothesis.

Multiple Benefits of Multiple Patches

In addition to increasing signal efficacy through increased conspicuousness, the evolution of multiple plumage patches may also increase signal content. Because patches that differ in color are often produced by different mechanisms, the evolution of multiple color-producing mechanisms may also be under strong selection for signal content. Different plumage patches, particularly those produced by different mechanisms, have been shown to differ in signal content (McGraw and Hill 2000; McGraw et al. 2002; Jawor and Breitwisch 2004). Multiple plumage patches may thereby reveal different aspects of male quality to discriminating females (Candolin 2003; van Doorn and Weissing 2004). Thus, the evolution of multiple plumage patches may be a means by which manakins can simultaneously increase the signal efficacy and signal content of their plumage ornaments. Interestingly, various combinations of red, black, white, and blue are common in manakins and appear to have evolved independently in a number of lineages (Prum 1997).

In summary, we have shown here that sexual selection for signal efficacy has probably had a strong influence on the evolution of manakin plumage ornaments. This conclusion necessarily implies that the signal environment has had an important influence on signal design in the Pipridae (Endler and Théry 1996; Heindl and Winkler 2003*a*, 2003*b*; Uy and Endler 2004), and other studies suggest that this may be a widespread pattern in birds (McNaught

and Owens 2002; Gomez and Théry 2004). We also show that plumage colors produced by particular mechanisms may optimize either efficacy or content and may be more effective signals at particular viewing distances. However, the combination of multiple plumage patches may allow manakins to optimize both efficacy and content in their plumage ornaments. Although manakins as a group may experience particularly strong sexual selection, many of the patterns we describe here will potentially apply to any sexually selected ornament. Moreover, signals that maximize conspicuousness by increasing signal-to-noise ratio will be important not only in visual communication, but in all signaling modalities, including acoustic and chemical communication (Bradbury and Vehrencamp 1998). Whenever possible, studies should consider aspects of both signal efficacy and signal content, as even within-species selection is likely to act simultaneously on both of these properties of signal design.

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