Modification of the visual background increases the conspicuousness of golden-collared manakin displays

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Effective visual communication requires signals that are easy to detect, transmit, receive, and discriminate. Animals can increase the probability that their visual signals would be detected by evolving signals that contrast with their visual background. Animals can further enhance this contrast by behaviorally modifying the existing visual background. Male golden-collared manakins (*Manacus vitellinus*) clear leaf litter from the ground to form courts, which are used as display arenas. Using reflectance measures of the signal (male plumage) and the visual background (cleared court and adjacent litter), the irradiance measures of ambient light during display, and published measures of photoreceptor sensitivity of a Passerine, we test the hypothesis that court-clearing augments the contrast between male plumage and the visual background. We find that the chromatic and brightness contrasts of golden patches used during courtship are greater against the cleared court than against adjacent litter. In addition, we find that cleared courts provide a less variable background for these color patches, resulting in displays that consistently contrast the visual background. These results suggest that behavioral modification of the visual background may act to increase the conspicuousness of colorful male plumage during display, providing an explanation for why golden-collared manakins, and possibly other species, build or clear display courts. *Key words:* chromatic contrasts, court-clearing, *Manacus vitellinus*, manakins, signaling, visual signals. *[Behav Ecol]*

Effective communication depends on the efficient exchange of information between or among individuals (see Bradbury and Vehrencamp, 1998). Because information itself has to be carried by signals and signals must be detected and processed by the receiver, the efficient exchange of information, in turn, requires signal designs that are easy to detect, transmit, and receive (Endler, 1992; Fleishman, 2000; Guilford and Dawkins, 1991).

For a signal to be detected, it has to be readily distinguished from background noise. For instance, a visual signal has to represent a nonrandom sample of the visual background in order to be conspicuous to intended receivers (Endler, 1978, 1993a; Lythgoe, 1979). Visual signals can stand out from the background in at least four ways: (1) color, (2) brightness, (3) pattern geometry, and (4) movement contrasts (Bradbury and Vehrencamp, 1998; Endler, 1992, 1993a; Fleishman, 2000). In addition, the degree of contrast between a visual signal and its background is shaped by the interaction between the spectral properties of the signal and objects in the background, the sensory properties of the receiver, and the lighting conditions that illuminate the signal during signal production, transmission, and reception (Endler, 1978, 1992, 1993a,b).

Empirical work on visual signals provides evidence consistent with the hypothesis that signals and signaling behavior have evolved to increase their contrast against the visual background. For instance, Endler and Théry (1996) found that in three lekking avian species, male plumage represents a nonrandom sample of the visual background and that the lighting conditions during display enhance this contrast.

Similar results showing the importance of color or brightness contrast in effective signaling have been shown in other bird (e.g., Andersson et al., 1998; Heindl and Wickler, 2003) and several fish (e.g., Boughman, 2001; Endler, 1983; Fuller, 2002) and lizard (e.g., Fleishman et al., 1993; Leal and Fleishman, 2002; LeBas and Marshall, 2000; Macedonia, 2001) species.

In addition to evolving signals that contrast with the visual background, males can behaviorally enhance the conspicuousness of their color patches in at least three ways. First, males may incorporate postures that highlight specific color patches during display. Several studies and observations provide support for this hypothesis (e.g., Andersson et al., 1998; Clark and Uetz, 1993; Marchetti, 1993). Second, males may choose to display in locations or times of day that best complement their color signals (e.g., Endler, 1978, 1991; Endler and Théry, 1996). Third, males may actively modify the existing visual background to enhance the signal to background contrast. For example, several species of birds such as bowerbirds, widowbirds, cock-of-the-rocks, birds of paradise, peacock-pheasants, and manakins (see Johnsgard, 1994) build or clear courts used as arenas during elaborate courtship displays to females. In addition, males of several cichlid species build conspicuous sand mounds ("bowers") used for spawning and during courtship displays to females (McKaye, 1991; McKaye et al., 1990). These courts may provide a more contrasting background than natural vegetation or litter, making male display traits more conspicuous. The idea that males behaviorally alter their visual background to increase the conspicuousness of their display is intuitive; however, a quantitative test of this hypothesis is lacking.

Selection should favor signaling behavior that maximizes the contrast of signals against the visual background (e.g., Endler 1992; Lythgoe, 1979). Hence, signal design theory makes at least three predictions on how behavioral modification of the background could augment the conspicuousness of male display. First, modification of the background should

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increase the chromatic and brightness contrasts of male signals against the visual background. Second, modification of the background should decrease the variability of the background, thereby creating consistently contrasting signals. If the modified background increases the contrast between a color patch and the background, then having a uniform background would make consistently contrasting signals. Third, modification of the background should reduce the overall contrast of objects that constitute the visual background, thereby making the overall color pattern more conspicuous. Although a specific color patch may be conspicuous, these patches will be viewed in relation to adjacent color patches as well as the entire visual background. In general, a color pattern that contains patches that show high contrast is very conspicuous; however, the conspicuousness of the entire pattern is further influenced by the visual background. A visual background that consists of objects with low contrasts will make the entire male color pattern more conspicuous than if the same color pattern is viewed against a visual background that consists of objects with high contrasts (Endler and Théry, 1996). Thus, altering the background could create a background with overall lower contrast and results in an increase in conspicuousness of the entire male color pattern.

Male golden-collared manakins (*Manacus vitellinus*) clear leaf litter from the ground to form courts, which they then use as arenas for intense courtship displays (Chapman, 1935). Male courtship displays involve rapid hops between saplings and above the cleared court, with males expanding their golden beards and collars (Chapman, 1935) and snapping their wings (Lowe, 1942). Females observe male courtship from the foliage above the courts, so cleared courts would act as backgrounds during display. Hence, court-clearing in golden-collared manakins could increase the conspicuousness of colorful male plumage.

Using reflectance scans of bird plumage and objects from the visual background, along with irradiance measures of ambient light during male displays and published spectral sensitivity of Passerine cones (Hart et al., 1998), we test the predictions of signal design theory in golden-collared manakins and find that the golden patches show greater chromatic and brightness contrasts, and they show lower variability in chromatic and brightness contrasts when viewed against cleared courts than when viewed against natural litter. In addition, the overall contrast of objects in the leaf litter is greater than the overall contrast of the cleared court; hence, court-clearing creates a visual background with lower overall brightness and chromatic contrasts. These results suggest that court-clearing may act to enhance the conspicuousness of elaborate male display in golden-collared manakins.

METHODS

The *Manacus* model system

Golden-collared manakins are sexually dimorphic; adult males have golden collars and beards with black crowns and back, while females and immature males are olive throughout (see Ridgely and Gwynne, 1989). Males are polygynous and congregate in arenas called leks to attract females (Chapman, 1935). Leks consist of six to 15 males, with each male defending a separate and circular court ($\sim$1 m in diam) on the ground (Chapman, 1935). Each court is cleared of leaf and stick litter to expose the ground and encompasses at least two saplings on its periphery. When females arrive, males initiate an intense dance that involves rapid hops between the saplings on their courts, accompanied by loud pops produced by their wings and soft grunt-like vocalizations ("snap-grunt"

display; Chapman, 1935). During this display, males extend their golden beards and expand their golden collars. Females typically view males from above the court ($\sim$1.5–2 m) with the cleared courts as the visual background. Females follow males onto their courts for matings.

From 2 May through 21 May 2002, we monitored two leks in the Republic of Panama, $\sim$30 km east of Panama City: a lek in Soberania National Park (Pipeline Road) consisting of eight active courts, and a lek in Gamboa Forest consisting of six active courts. Courtship activity was high during this period in both leks. Nine court-owning adult males (eight from the lek at Soberania National Park and one from the lek at Gamboa Forest) and four olive-plumed individuals (females or immature males) were mist netted at these leks in 2001 and 2002. Although all 14 courts were monitored in 2002, we restrict our analyses to the nine courts where court-owners were caught and measured. Both leks were found in mature secondary forests adjacent to openings (e.g., creek), which is the typical habitat for *Manacus* leks (Chapman, 1935; Lill, 1974; Ridgely and Gwynne, 1989; Snow, 1962).

Measuring color reflectance and ambient light spectra

Males and females were caught during the mating season with mist nets at or near leks, and they were fitted with a numbered aluminum leg band and unique color leg bands to facilitate identification. We used an Ocean Optics USB2000 spectroradiometer and a Xenon flash light source (Ocean Optics PX-2) to obtain reflectance scans of each bird's color patches. 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 sole source of light for our measures, (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 glare or specular reflection; see Endler, 1990). To allow for comparison across different measures, we used a spectrally flat 97% reflecting spectralon white standard (Labsphere) and a dark current reading to standardize each scan. Scans were taken from an $\sim$3 mm diameter circle at 0.40 nm intervals across 300 to 700 nm, the visible spectrum of most avian species (see Hart, 2001). Reflectance scans were taken for each bird while an assistant held it in place. To gain a general idea of overall plumage color pattern, we scanned the following color patches for each individual: crown, beard, collar, chest, belly, back, rump, primary tail feathers, wing coverts, and epaulets. The size of each color patch was measured for each bird.

To obtain an estimate of the visual background, we scanned the bare ground of the cleared court every five centimeters along a north to south transect bisecting the cleared court ("court transect"). We performed a similar parallel north-to-south transect on the natural litter ("litter transect") adjacent to the cleared court, with the choice of running a litter transect west or east of the court determined randomly by the flip of a coin.

Because the appearance of an object is shaped by the ambient light that illuminates it (Endler, 1990, 1993a,b), we measured the ambient light spectra (irradiance from 300 to 700 nm) during snap-grunt displays at each of the nine display courts we monitored. Ambient light spectra were measured using a portable spectroradiometer and a cosine corrected sensor (CC-3-UV from Ocean Optics, Inc.), calibrated with a standard light source (LiCor 1800–02; see general methods in Endler and Théry [1996]). An average of 9.7 ($\pm$0.5) ambient light spectra during snap-grunt displays were measured for each male/court (range: six to 11 snap-grunt displays per court).

We estimated the perception of a color patch by birds (e.g., female manakins) by explicitly considering the interaction between (1) the ambient light that illuminates the patch during display, (2) the sensory properties of a Passerine retina, and (3) the spectral properties of the color patch. To do so, we first estimated the radiance spectra (light spectrum coming off an object) of a color patch by multiplying the patch's reflectance with the mean ambient light irradiance during the snap-grunt display for each of the nine courts. We then estimated the photon capture of each of the four avian cones using the calculated radiance of the patch and generalized Passerine optical parameters. For the sensory parameters of the model eye, we used ocular media, oil droplet and photoreceptor absorbance parameters from starlings, *Sturnus vulgaris*, another Passerine (Hart et al., 1998). We also used lower Passerine eye parameters (e.g., crow; Endler JA in preparation; Hart, 2001; Odeen and Hastad, 2003), with no qualitative change to our results. We present the data from starlings because more data are available for this species than for lower Passerines. To avoid making assumptions about relative cone abundances or post-receptoral processing, we used the tetrahedral representation of the four relative cone outputs from any object as points in a tetrahedron with height of 1.0 (see Goldsmith, 1990; Vorobyev et al., 1998), with each vertex of the tetrahedron representing one of the four avian cone types. This method reduces the entire stimulus spectrum to relative scores of 0 to 1 for each of the four Passerine cone types, with the sum of these four scores equaling one (for details see Endler [1990] and the Appendix in Fleishman and Persons [2001]). This method controls for patch brightness by only considering the relative stimulation of the four different avian cone classes. The further two points are apart in the tetrahedron, the more they differ in their spectra. The relationship between this distance and perceptual distance is monotonic but not linear, and distances below a threshold are not discriminated (Vorobyev et al., 1998); however, this gives a better prediction of perceived differences between colors than other methods. In addition, at the natural light levels, the observed color pattern components are much further apart than the threshold. Brightness or perceived intensity of a color patch was estimated by multiplying the color patch's radiance spectrum by the spectral sensitivity of each of the four cone types (from Hart et al., 1998), then summing these values across all cone types. Color and brightness of individual objects in the visual background (e.g., litter and cleared court) were estimated using identical methods.

Measuring contrasts

Our general goal is to estimate the conspicuousness of plumage (court-owner and typical female) at each of the nine courts we monitored. To do so, we used the mean lighting condition during the snap-grunt display for each court to calculate the contrast between a court-owner's color patch and objects found on or near his court ($n = 9$ courts). Because males expand their beards and collars during courtship, we focused our analyses on these color patches, as well as on the crown and back, which are the adjacent and intervening dorsal patches (from front to back: beard, crown, collar, and back). Unlike males, females do not own courts and can visit several courts before mating; hence, they cannot be assigned to specific courts. Furthermore, our aim is to determine how females would appear on a cleared versus an uncleared court. Therefore, we took the mean spectral properties of olive-plumed individuals ($n = 4$) caught during the study, then contrasted these with components of the visual background (cleared court and natural litter) for each of the nine separate courts we monitored. This provides us with an estimate of how a typical female plumage would appear at each of the nine courts. In both the male and female plumage estimations, the unit of analysis is the male court.

Chromatic contrast was estimated as the difference in spectral quality between plumage and the visual background. This difference was measured by calculating the Euclidean distance between plumage and the visual background using the cone stimulus scores of a color patch (e.g., X_{uv1} for ultraviolet sensitive cones) and those of the visual background (e.g., X_{uv2} for ultraviolet sensitive cones) for all four cone types:

$$C_c = \sqrt{(X_{UV1} - X_{UV2})^2 + (X_{S1} - X_{S2})^2 + (X_{M1} - X_{M2})^2 + (X_{L1} - X_{L2})^2}$$

where C_c is chromatic contrast, and X_i is the relative stimulus of cone i (for details see Endler [1993a], the Appendix in Fleishman and Persons [2001] and Théry and Casas [2002]). This procedure calculates the differences in the ratio of stimulation of the four avian cone classes that the male color pattern and visual background produce. Thus, objects that are further away in color space (greater C_c or Euclidian distance) are more different (higher contrast) in color than objects that are closer. We quantified the mean contrast value of a color patch against the visual background for each court by taking the individual contrast value of the color patch against a specific object then calculating the mean for the entire court. The relative contribution of each contrast value to the mean was weighted by the relative abundances of the specific object in the visual background.

Brightness contrast between an object and a color patch was calculated as the perceived brightness (intensity from 300 to 700 nm) of a color patch (B_{cp}) minus the perceived brightness of the background (B_b) divided by the sum of these values: $(B_{cp} - B_b)/(B_{cp} + B_b)$ (Endler and Théry, 1996; Fleishman and Persons, 2001). This calculation produces a contrast index value from -1 to 1, with positive values representing signals that are brighter than the background, negative values representing signals that are darker than the background, and values near zero representing signals that are not different from the background. As in the calculations of mean chromatic contrast for each court, objects in the background were weighted according to their frequency.

The coefficient of variation (CV) of chromatic and brightness contrasts for each color patch against the cleared court and against the leaf litter were calculated using the leaf and court transect. This provides a relative measure of the variability of contrast values when the signal is viewed against the litter and when the signal is viewed against the court.

Finally, chromatic and brightness contrasts of adjacent, dorsal color patches (e.g., beard vs. crown, crown vs. collar, collar vs. back, back vs. rump, and rump vs. tail) within a bird were calculated using the same equations (see above). From these, overall color and brightness contrasts were then estimated by calculating the mean contrast values of adjacent patches weighted by their relative size to the entire color pattern. This gives an overall chromatic and brightness contrast values for the entire male ($n = 9$) and female ($n = 4$) color patterns. Likewise, chromatic and brightness contrasts of adjacent objects in the natural litter and regions of the cleared court were calculated to obtain overall contrast values for the two visual backgrounds ($n = 9$ courts). For the overall male color pattern, court and litter contrasts, we used the mean lighting condition during snap-grunt displays for each male at his court. Because females cannot be assigned to specific courts, we calculated the overall color and brightness contrasts of female plumage using the four individuals mist-netted
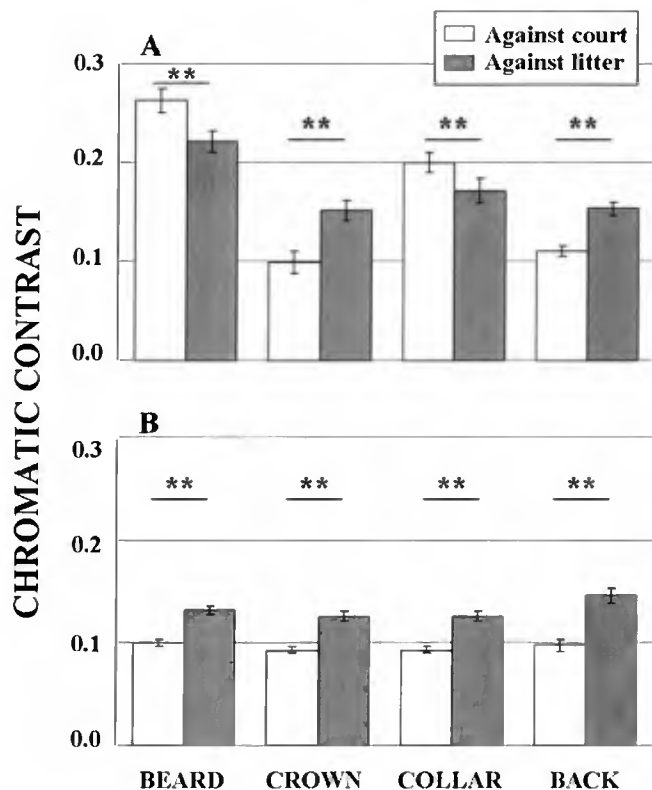
Figure 1
Chromatic contrast of beard, crown, collar, and back against the cleared-court (open bar) and against litter (gray bar) for adult male (A) and female/immature male (B) plumage. Bar graphs show the mean chromatic contrast values ± 1 SE for nine *M. vitellinus* males at their display courts and for the mean female plumage at these nine courts (**$p < .01$).

at the leks and the mean lighting condition during snap-grunt displays for all nine male courts.

Statistical analyses

We used permutation randomization tests involving 50,000 iterations to test for significance of hypotheses (outlined in detail by Manly, 1991). For example, to determine if contrast values of plumage against the cleared court is significantly greater than the contrast values of plumage against natural litter, we first randomly reassigned (without resampling) the mean contrast values of plumage against court and against the litter for the nine courts monitored. We then took the difference in contrast values between the cleared court and leaf litter for each court, and summed these differences (e.g., paired test design for each male). This procedure was iterated 50,000 times to create a null distribution of differences between court and litter contrasts against which we could compare the observed difference between court and litter contrasts for the nine courts. During the iterations, we tallied the number of times that the observed difference between court and litter contrasts arose by chance (including differences that are greater than the observed difference). This provided us with a probability value, and we rejected the null hypothesis of no difference in contrast between court and litter if the probability value was less than 0.05 (Manly, 1991). Similar procedures were used for testing the CV values and overall color pattern contrasts. All tests of hypotheses are two-tailed. Randomization tests were programmed using QBasic 3.0 (Microsoft, Redding, WA).
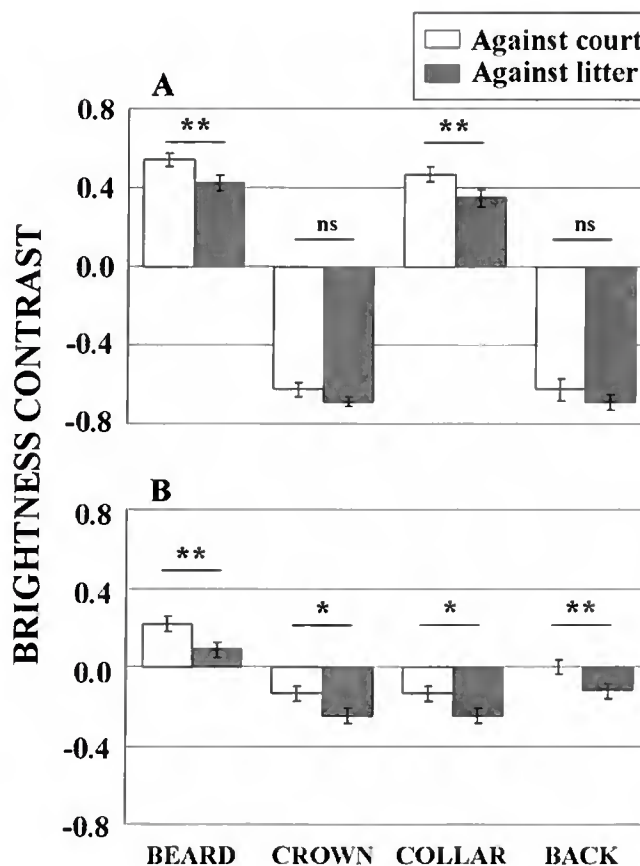

Figure 2
Brightness contrast of beard, crown, collar, and back against cleared-court (open bar) and against litter (gray bar) for adult male (A) and female/immature male (B) plumage. Bar graphs show the mean chromatic contrast values ± 1 SE for nine *M. vitellinus* males at their display courts and for the mean female plumage at these nine courts (**$p < .01$, *$p < .05$).

RESULTS

Chromatic and brightness contrasts

Colorful adult male patches, such as the beard and collar, showed high chromatic (Figure 1A) and brightness (Figure 2A) contrasts against the natural leaf and stick litter. Female color patches, on the other hand, show lower chromatic and brightness contrast against the natural litter (Figures 1B and 2B). When comparing the chromatic contrast of golden beards against the natural litter and against cleared courts (dark brown), contrast against cleared court was significantly greater than contrast against the natural litter (Figure 1A). Similarly, the chromatic contrast of the golden collar against the cleared court is significantly greater than the chromatic contrast of the collar against the litter (Figure 1A). The reverse is found when comparing the black crown and back against the cleared court and against surrounding litter (Figure 1A). For females and immature male plumage, which is drab and olive throughout, the chromatic contrasts of the beard, crown, collar, and back regions against the court are significantly less than the chromatic contrasts against the adjacent litter (Figure 1B).

Likewise, brightness contrast is significantly greater against the cleared court than against the natural litter for the golden beards and collars of adult males (Figure 2A). However, there is no difference in brightness contrast values of black crowns and backs against the cleared court when compared against
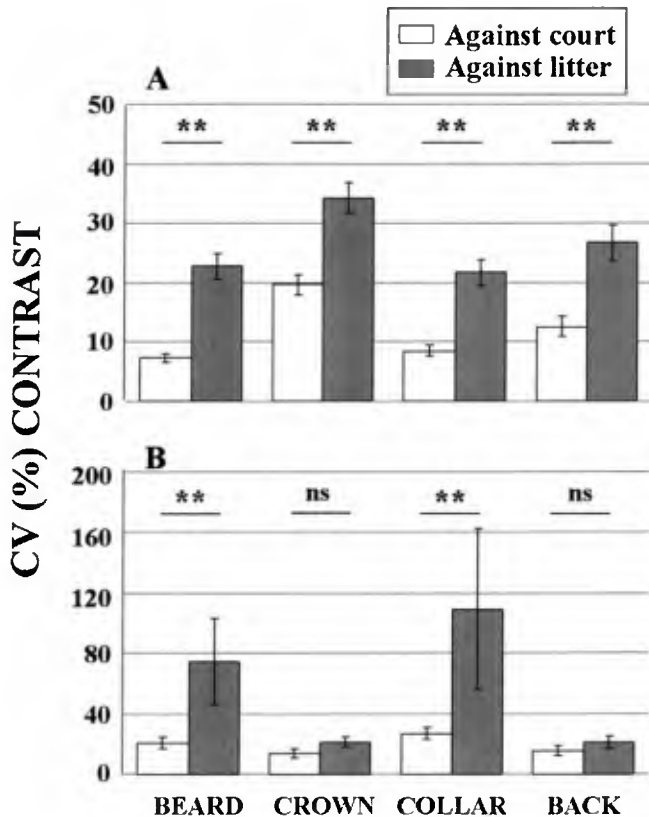
Figure 3
Variability, measured by the coefficient of variation (CV), of chromatic (A) and brightness (B) contrasts of male beard, crown, collar, and back against cleared courts (open bar) and against litter (gray bar) for nine *M. vitellinus* males at their display courts (**$p < .01$).

Figure 4
Mean ($\pm$ SE) overall chromatic (A) and brightness (B) contrasts of adjacent areas (transect every 5 cm) of the cleared court (open bar, $n = 9$), of adjacent leaves and sticks (transect every 5 cm) in the litter (gray bar, $n = 9$), adjacent color patches of males (black bar, $n = 9$), and adjacent color patches of females (stripped bar, $n = 4$). Because females view displaying males from above courts, the analysis of male (and female) color pattern was restricted to dorsal color patches of adult males, which include (anterior to posterior) the beard, crown, collar, back, rump, and tail. All possible pairwise comparisons are different at the $p < .05$ level.

the litter (Figure 2A). Note that black crown and back are darker than both the court and litter. For a typical female plumage, the beard region shows higher brightness contrast when viewed against courts than when viewed against natural litter. On the other hand, the crown, collar and back regions show greater brightness contrast when viewed against litter than when viewed against courts. Note that the female crown, collar, and back appear darker (more negative) against the cleared court than against the litter (Figure 2B).

The variability, measured by the coefficient of variation, of chromatic contrasts of male color patches against the visual background is significantly greater when these patches are viewed against the litter than when viewed against cleared court (Figure 3A). Similarly, the variability of brightness contrasts of male color patches is greater when these patches are viewed against the litter than when viewed against cleared court (Figure 3B).

Finally, the overall brightness and chromatic contrasts of adjacent color patches within an adult male (entire color pattern) is greater than the brightness and chromatic contrasts of adjacent objects in the litter and adjacent regions of the cleared court (Figure 4). When comparing the two background types, the overall brightness and chromatic contrasts of adjacent objects in the litter is greater than those of adjacent regions of the cleared court (Figure 4). This results in the difference in overall chromatic contrast between male color pattern and the cleared court being nearly twice as much as the difference between the male color pattern and the natural litter (0.148 and 0.084, respectively; see Figure 4A). Similarly, the difference in brightness contrast between
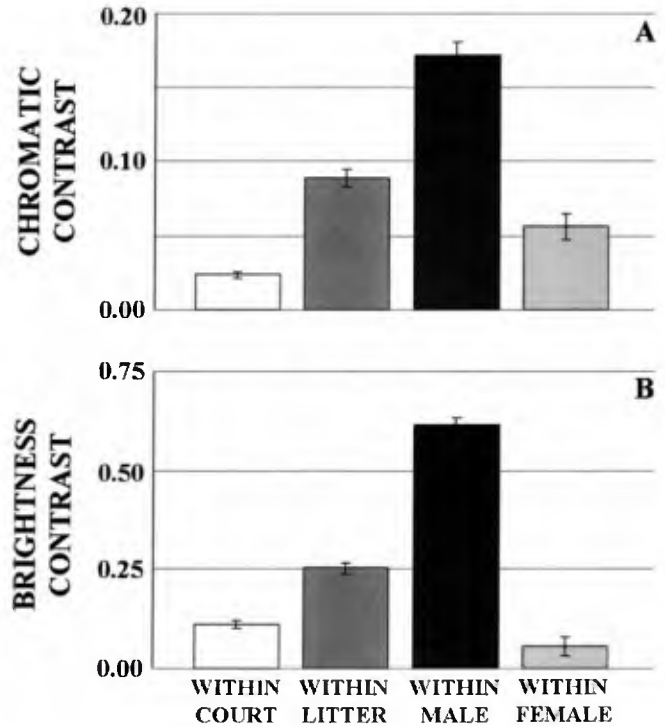
the entire color pattern and the cleared court is much greater than the difference in brightness contrast between the entire color pattern and adjacent litter (0.503 and 0.361, respectively; see Figure 4B). The overall brightness and chromatic contrasts of female plumage (Figure 4), on the other hand, are more similar to the overall chromatic and brightness contrasts of the visual background (for both litter and cleared court).

DISCUSSION

Signal design

Signal design theory predicts that selection should favor visual signals that are conspicuous and easy to distinguish from the visual background (Endler, 1992; Lythgoe, 1979). Recent studies provide support for this prediction, indicating that elaborate male signals differ from the visual background (e.g., Andersson et al., 1998; Endler and Théry, 1996; Macedonia, 2001). Our work provides a quantitative test of this, showing that colorful male plumage contrasts the natural visual background of leaf and stick litter in golden-collared manakins (Figures 1A and 2A). Female (and immature male) plumage, on the other hand, shows relatively reduced contrast against the natural background of leaf and stick litter (Figures 1B and 2B). In fact, the chromatic and brightness contrasts of golden male plumage are about twice as great as those of female plumage against the natural litter (Figures 1 and 2).

In addition to evolving colors that contrast the existing visual background, selection should favor behavioral traits that augment the conspicuousness of male signals. For instance, males can highlight specific components or color patches of their plumage during display. Several avian species, such as ducks, grouse, warblers, bowerbirds, and birds of paradise, incorporate postures that highlight colorful patches on their plumage (see Johnsgard, 1994; Marchetti, 1993). This is also true for several non-avian species, such as Anolis lizards (see Fleishman, 2000; Macedonia, 2001) and guppies (see Houde, 1997), which incorporate complementary postures during display. In golden-collared manakins, males highlight their colorful plumage by expanding their beards and collars during the "snap-grunt" display (Chapman, 1935). When expanded, male beards are 16.89 ± 0.21 mm long, extending well beyond their 8.60 ± 0.15 mm bills.

Because the conspicuousness of a signal is dictated by its visual background (e.g., Heindl and Winkler, 2003), males can further enhance the conspicuousness of their signals by altering the visual background. Signal design theory makes three predictions on how behavioral modification of the visual background could augment the conspicuousness of male display. First, altering the background should increase the chromatic and brightness contrasts of male display against the visual background. Second, altering the background should reduce the variability of the visual background, thereby creating a more consistent signal. Third, altering the background should reduce the overall contrast of objects in the visual background, thereby augmenting the conspicuousness of overall male color pattern. Color patterns that contain contrasting patches would appear very conspicuous (Endler, 1990); however, the conspicuousness of the same color pattern will be reduced if objects in the visual background also show high contrast (Endler, 1978; Endler and Théry, 1996). Hence, reducing the overall contrast of objects in the visual background should augment the conspicuousness of the entire male color pattern.

Golden-collared manakins clear litter from the ground to form circular courts used for courtship displays (Chapman, 1935). Because male display involves hops across the cleared court and females view male display from perches above the court, the cleared court acts as the visual background. Therefore, court-clearing may be an example of how males can behaviorally modify their visual background to augment the conspicuousness of their displays. Our results are consistent with this hypothesis, providing evidence in support of the predictions of signal design theory.

We find that court-clearing augments both the chromatic (Figure 1A) and brightness (Figure 2A) contrasts of male beard and collar, which are the traits expanded and explicitly used during courtship displays (Chapman, 1935). Other traits that are not emphasized during courtship, such as the black crown and back, show the opposite relationship (Figures 1A and 2A). This reversed relationship occurs because the black crown and back match the cleared court better than they do the variable litter, which can consist of dried leaves and sticks of varying colors—bright yellow to dark brown.

Furthermore, cleared courts not only provide a more contrasting background but also a more consistent one. When males initiate their snap-grunt displays, the conspicuousness of their color patches is dictated by the visual background. Therefore, male color patches during display would be most conspicuous if the visual background is consistently different from male color patches. We find that the chromatic and brightness contrasts of male color patches are less variable when viewed against the cleared court than when viewed against natural litter (Figure 3). This makes male plumage consistently conspicuous. A heterogenous back-

ground, like the natural leaf and stick litter, will result in variable contrasts between color patches and the background, with male beards and collars sometimes being highly conspicuous (against dark leaves) and other times relatively cryptic (against bright yellow leaves). Therefore, court-clearing augments signal conspicuousness by reducing the perceived variability of male display.

Lastly, the overall chromatic and brightness contrasts of objects in the litter are two to three times greater than the overall chromatic and brightness contrasts of adjacent regions of the cleared court (Figure 4). The entire male color pattern contains highly contrasting color patches (gold and black), which make males very conspicuous (Endler, 1990; Endler and Théry, 1996). However, the same color pattern would appear less conspicuous if viewed against a background that likewise consisted of objects that show high contrast (Endler, 1978, 1990, 1992). Conversely, the same color pattern would appear more conspicuous when viewed against a background that consisted of objects that show low contrast. Court-clearing creates an overall background with low chromatic and brightness contrasts, making the entire male color pattern more conspicuous. In sum, our observations suggest that court-clearing may have evolved or is maintained because it augments the conspicuousness of male display by increasing its chromatic and brightness contrasts, reducing the variability of the visual background, and reducing the overall contrast of objects that constitute the visual background.

Female color patterns

The chromatic and brightness contrasts of the olive plumage of females are generally greater when viewed against adjacent litter than when viewed against the cleared court (Figures 1B and 2B)—a pattern opposite that of colorful male patches. Females typically watch males from above the courts during courtship visits but will follow males onto the courts for mating (Chapman, 1935; Uy JAC, personal observations). Although there has been no record of predation at manakin leks, and matings only last for a few seconds, it is possible that cleared courts provide an advantage to females by making them less conspicuous when they join males on the court for matings, thereby reducing the risks of predation. These observations suggest the intriguing possibility that court-clearing may provide simultaneous advantages to males and females—males appear more conspicuous to females during courtship, while females appear less conspicuous to potential predators during matings.

Alternative explanations of court-clearing

Court-clearing or court-building may also function to signal a male's ownership/attendance of a court-site or the quality of the court-owner himself. For instance, in bowerbirds males build ground structures called bowers, the quality of which is influenced directly by aggressive male-male interactions (e.g., bower destructions; Borgia, 1985). Females, in turn, use aspects of the bower to assess potential mates. In manakins, males do not directly influence aspects of the cleared court; however, the size or placement of courts may be subject to male-male aggression. Therefore, this hypothesis predicts that male manakins with better-kept or larger courts are more aggressive and thus more attractive to females. This possibility remains to be tested in manakins; however, it is not mutually exclusive to the hypothesis that males clear courts to enhance the conspicuousness of their elaborate plumage. The idea that courts function as a signal of male quality or territory ownership addresses

the content of the signal—what is the court signaling to conspecifics? In contrast, the hypothesis that court-clearing enhances male conspicuousness addresses the design of a signal—how can a signal be effectively perceived by receivers? Therefore, both hypotheses could work synergistically. Court-clearing may have evolved to enhance male displays and was later co-opted by females in mate choice, or it first evolved as a signal for mate choice and is maintained (or elaborated) because of the positive effects on male conspicuousness.

Conclusion

Our results suggest that court-clearing in golden-collared manakins acts to increase the visual contrast of elaborate male signals, while possibly reducing predation on females who are assessing potential mates. Several other avian groups, such as bowerbirds, birds of paradise, pheasant-peacocks, and widowbirds, clear or build courts on which males display to visiting females (see Johnsgard, 1994). Bowerbirds additionally use their courts as platforms to present decorations, such as fruits, flowers, and shells, which are attractive to visiting females (e.g., Borgia, 1995; Gilliard, 1969; Uy and Borgia, 2000). In fishes, several species of colorful cichlids build sand mounds ("bowers"), which are visually distinct from the natural floor (McKaye, 1991). These bowers are used primarily for spawning; however, male courtships to females also occur above these structures (McKaye et al., 2001). Similar to golden-collared manakins, court-clearing in these fish and avian species may also act to enhance signal conspicuousness by augmenting the contrast between elaborate male coloration and the visual background and by reducing the variability of the visual background.

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