

Variable visual habitats may influence the spread of colourful plumage across an avian hybrid zone

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Keywords:

conspicuousness;
hybrid zones;
hybridization;
manakins;
trait introgression;
visual signals.

Abstract

Several studies have shown that hybridization can be a creative process by acting as a conduit for the spread of adaptive traits between species, but few provide the mechanism that favours this spread. In the hybrid zone between the golden- (*Manacus vitellinus*) and white-collared (*Manacus candei*) manakins, sexual selection drives the introgression of golden/yellow plumage into the white species; however, the mechanism for the yellow male's mating advantage and the reasons why yellow plumage has not swept further into the white species remain mostly speculative. We quantified the colour properties of male plumage, the background and the ambient light at the hybrid zone, and allopatric golden and white populations. As measured by the perceived difference in colour between plumage and background, we found that yellow plumage appears more conspicuous than white plumage in the hybrid zone and allopatric golden-collar habitats, whereas white plumage appears more conspicuous than yellow plumage in the allopatric white-collared habitat. These results suggest a mechanism for the unidirectional spread of yellow plumage across the hybrid zone but slowed movement beyond it.

Introduction

Hybridization among individuals from distinct species typically results in less or unfit offspring; however, it can also be a creative evolutionary process by acting as a conduit for the exchange of novel or even adaptive traits between taxa (Anderson & Stebbins, 1954). Only a handful of studies provide evidence for this possibility, with fewer still identifying the mechanism that dictates adaptive trait introgression (see Arnold, 2004; Whitney *et al.*, 2006). For instance, in the classic case of adaptive hybridization between two species of Louisiana iris, hybrids have higher fitness than the parental types in intermediate habitats, presumably because genes for shade tolerance have introgressed from one of the parental species (Arnold & Bennett, 1993). Shade tolerance experiments, however, failed to find a fitness

advantage for hybrids over the shade-intolerant parental phenotype, indicating that the trait that confers a fitness advantage to hybrids and the mechanism that favours the introgression of fitness-enhancing genes remain unclear (Bennett & Grace, 1990).

The closely related golden-collared (*Manacus vitellinus*) and white-collared (*Manacus candei*) manakin form a hybrid zone identified by several steep, concordant genetic and morphometric clines centred near Rio Robalo in Western Panama. By contrast, a cline for yellow plumage is displaced by roughly 50 km to the west, into the white-collared *M. candei* population, where it forms a similar steep cline near Rio Changuinola (Parsons *et al.*, 1993; Brumfield *et al.*, 2001). Adult males in the 50-km stretch between Rio Robalo and Rio Changuinola therefore carry predominantly white-collared *M. candei* alleles but look similar to *M. vitellinus* because of the introgressed yellow plumage (Brumfield *et al.*, 2001).

Along the banks of Rio Changuinola, yellow and white males aggregate in common mating arenas (mixed leks). Our previous work on these mixed leks shows that yellow males, on average, have a fourfold mating

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advantage over white males (Stein & Uy, 2006a), but this mating advantage only occurs in leks where the relative frequency of yellow males is greater than white males. Because yellow males are rare at the leading edge of the plumage cline, frequency-dependent selection provides a possible mechanism for the slowed introgression of yellow plumage into the white population. However, even with frequency-dependent selection mediating the yellow male mating advantage, such a considerable advantage in some leks should drive the spread of yellow plumage yet the plumage cline seems stable near Rio Changuinola (Brumfield *et al.*, 2001). The explicit mechanisms that favour yellow males at the hybrid zone and the slowed movement of yellow plumage beyond the plumage cline remain little understood.

Because signals are perceived in a complex environment, the effectiveness of a signal is dictated by its conspicuousness or how easily it can be detected from background noise. Signal conspicuousness, in turn, is shaped by the physical properties of the habitat where a signal is produced, transmitted and received (Endler, 1992). This is especially true for bright and colourful plumage, which requires an external light source for illumination (i.e. ambient light) and must be discerned against a complex visual background. A geographically variable visual habitat could thus result in signals being more effective in one habitat over another. In this study, we explored the possibility that the visual habitat varies across the *Manacus* complex range, which may then result in certain plumage colours being more effective than others and so explain the observed dynamics of yellow trait introgression. We predict that yellow plumage should be more conspicuous than white plumage at the hybrid zone and allopatric golden-collar habitats, whereas white plumage should be more conspicuous than yellow plumage in the allopatric white-collared habitat.

Materials and methods

The Manacus study system

Male *Manacus* manakins are polygynous and aggregate in mating arenas called leks. Within these leks, each male defends a permanent court, which is a small area on the ground (*ca.* 1 m in diameter) cleared of leaf litter and surrounded on the periphery by at least two saplings. Courts are 1–10 m apart. When a female enters the lek, court-owning males display by hopping back and forth between saplings and over the cleared court, snapping their modified wings and expanding their golden beard and collar feathers (snap grunt display; Chapman, 1935). Females can perch above several courts and view several males simultaneously before joining a male on a court for courtship and mating. Hence, the cleared court serves as the visual background for the bright plumage of males to females (Uy & Endler, 2004). As in most lekking taxa,

there is an extreme skew in male mating success, with one or two males accounting for most of the matings within a lek (Shorey, 2002; Stein & Uy, 2006b). Previous work shows that male centrality within a lek, male body size, and collar brightness were strong predictors of male mating success (*M. manacus*, Shorey, 2002; *M. vitellinus*, Stein & Uy, 2006b).

In the hybrid zone between the golden- and white-collared manakins in Western Panama, the plumage cline is displaced from the morphometric (e.g. overall size) and several genetic clines by 50 km towards the white population (Brumfield *et al.*, 2001). This results in yellow birds between the two clines being similar to white-collared males in morphometrics (e.g. body size and beard length) and carrying predominantly white-collared alleles (Brumfield *et al.*, 2001). Yellow males in the hybrid zone are therefore hybrids, and their distinct morphology led early taxonomists to classify them as a distinct subspecies (*M. vitellinus cerritus*, Ridgley & Gwynne, 1989). White males at mixed leks may similarly carry alleles from both colour forms as a result of hybridization, especially as yellow males have a mating advantage in many of the mixed leks (Stein & Uy, 2006a). In fact, some morphological traits for white individuals in the hybrid zone appear to be intermediate to the pure, allopatric populations. For instance, male *Manacus* manakins have epaulet patches on their wings, and epaulet size for individuals at the plumage cline is intermediate to the epaulet size of pure golden- and pure white-collared males (Brumfield *et al.*, 2001). In addition, there is a slight difference in plumage colour between white-collared males from the hybrid zone and those from allopatric leks (see Fig. 1). Therefore, it is likely that white-collared males at the hybrid zone are also hybrids because they show traits intermediate to the allopatric

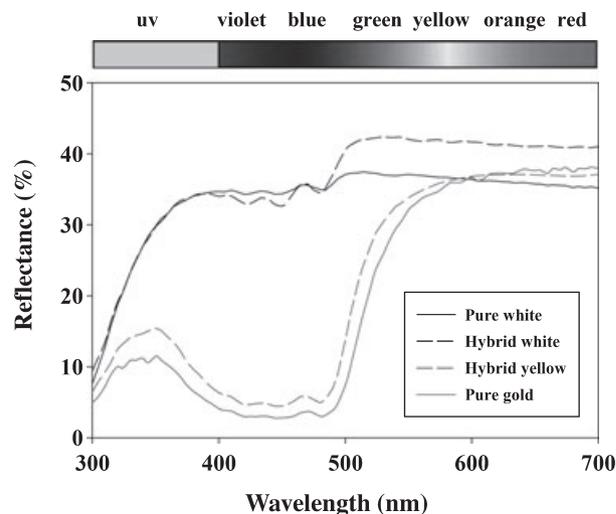


Fig. 1 Mean reflectance of pure white ($n = 11$), hybrid white ($n = 9$), hybrid yellow ($n = 11$) and pure golden ($n = 9$) collars.

golden- and white-collared individuals (see explicit test below).

We monitored 11 courts distributed across two pure white-collared manakin (*M. candei*) leks in La Selva Biological Station, Costa Rica, from 30 April to 18 May 2001 (five courts in the first lek and six courts in the second lek). We monitored 14 courts distributed across two pure golden-collared (*M. vitellinus*) leks in Panama from 2 May to 21 May 2002 – a lek in Soberania National Park consisting of eight courts and a lek in Gamboa Forest consisting of six courts. Finally, along the plumage cline of Rio Changuinola, western Panama, we monitored five leks where both yellow and white males actively competed for the same set of females (mixed leks). We monitored a total of 10 white and 13 yellow courts across these five leks from 17 March to 13 June 2005 (lek 1, three white and two yellow courts; lek 2, two white and one yellow court; lek 3, one white and one yellow court; lek 4, two white and four yellow courts; lek 5, two white and five yellow courts). The general location of the allopatric golden-collared, allopatric white-collared and hybrid zone populations/leks are shown in Fig. 2. For all colour forms, courtship activity at leks was high during our sampling period.

Measuring male morphology and plumage colour

To objectively quantify the spectral and brightness properties of male plumage, we scanned netted males using an Ocean Optics USB2000 spectrophotometer (Ocean Optics Inc., Dunedin, FL, USA) and a Xenon flash light source (Ocean Optics PX-2; as in Uy & Endler, 2004). The tip of a micron fibre-optic probe was housed in a hollow, black anodized aluminum sheath with an angled tip (45° to reduce specular glare) that contacted the bird's plumage. To allow for comparison across different scans, we used a spectrally flat 97% reflecting spectralon white standard (Labsphere) and a dark current reading to standardize each scan. Scans were taken from a ca. 3-mm-diameter circle across 300–700 nm range. For this study, we focused on male collar because this patch is expanded during courtship to females and its properties predict male mating success in golden-collared manakins (Stein & Uy, 2006b). Moreover, this patch is the most obvious trait that differentiates white-collared and golden-collared manakins (Brumfield & Braun, 2001). We scanned a total of nine adult golden-collared and 11 white-collared males in allopatric populations in Panama and Costa Rica respectively. We scanned nine white-collared and 11 yellow-collared males in mixed leks at

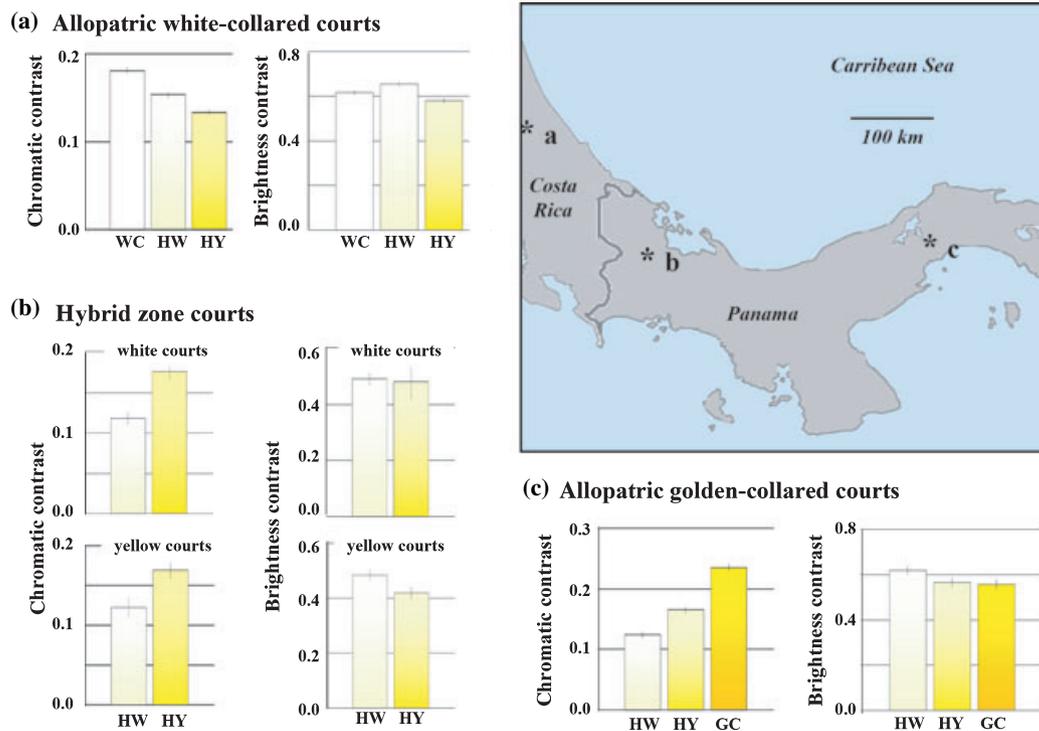


Fig. 2 Conspicuousness of male collars assayed by the perceived difference in colour (chromatic contrast) and brightness properties of male collars against cleared courts at (a) pure white-collared ($n = 11$), (b) hybrid zone ($n = 10$ white and $n = 13$ yellow) and (c) pure golden-collared ($n = 14$) courts. All pairwise comparisons within each population differ significantly (Bonferroni corrected, $P < 0.001$). The map indicates the general locations of the pure white (a), hybrid zone (b) and pure golden (c) populations we monitored.

the hybrid zone along Rio Changuinola. In addition to obtaining reflectance scans at the time of capture, we also took morphological measurements of tarsus, head, tail and beard lengths (mm), which have been shown to vary across the hybrid zone (Brumfield *et al.*, 2001).

To characterize the colour properties of male plumage, we estimated collar brightness, chroma (i.e. colour purity) and hue (i.e. colour). We calculated collar brightness by summing its reflectance from 300 to 700 nm (as in Stein & Uy, 2006b). Because reflectance spectra consist of reflectance at each wavelength that are highly correlated, we used a principal component analysis (PCA) to collapse these values into a few independent variables that summarize spectrum shape (Endler, 1990; Cuthill *et al.*, 1999). We used brightness to standardize all reflectance scans prior to PCA to provide us with PC scores that represent chroma and hue independent of brightness (Cuthill *et al.*, 1999). This is a standard method to handle and analyse spectral data, which we have used in a previous study of golden-collared manakins (Stein & Uy, 2006b).

We used an analysis of variance (ANOVA) to compare and test for differences in colour properties of male collar (e.g. PC scores) and morphometrics (e.g. beard length) between individuals from the allopatric and hybrid zone leks. *Post hoc*, pairwise comparisons between populations were Bonferroni corrected. We also ran a stepwise discriminant function analysis (DFA) to determine how well male plumage colour and morphometrics can correctly classify an individual as either coming from an allopatric site or the hybrid zone. In essence, DFA provides a test for the distinctiveness in plumage colour and morphometrics of males in the hybrid zone.

Measuring the visual habitat: court and ambient light colour spectra

Using the same procedures for measuring plumage reflectance, we measured the colour of the visual background by scanning the cleared courts with a portable spectrophotometer. To obtain an overall estimate of the visual background, we scanned the bare ground of the cleared court every 5 cm along a north-to-south transect bisecting the cleared court (as in Uy & Endler, 2004). In a previous study, we found little variation in the brightness and colour properties of the bare ground within a cleared court (Uy & Endler, 2004).

We measured the ambient light spectra at each court using a portable spectrophotometer and a cosine-corrected sensor (Ocean Optics CC-3-UV), calibrated with a standard light source (LiCor 1800-02, LiCor Environmental, Laurence, KS, USA). A total of five to 10 ambient light scans (i.e. downwelling irradiance) for each court were taken during courtship displays or during periods of high courtship activities (06:00–08:00 or 11:00–15:00 hours). We then calculated the mean ambient light spectra for each court from these irradiance

scans, providing us with an estimate of the typical light condition for each court during displays to females.

In addition, we measured the ambient light along a north-to-south, 100-m transect, 100 m from a lek in mature secondary growth, which is the general habitat type where *Manacus* leks are formed (Ridgely & Gwynne, 1989). Ambient light scans were taken every 10 m along the transect for a total of 10 points during periods of high activity at leks. Because of time constraints and logistical difficulties of working at remote sites, we were only able to conduct one ambient light transect at the allopatric golden-collared site and another at the allopatric white-collared site.

Modelling the perceived conspicuousness of male plumage

To explicitly determine how the visual habitat influences the conspicuousness of male plumage, we modelled how yellow and white plumage would be sensed or perceived by female manakins on a given court during courtship displays. To do so, we first calculated the mean reflectance spectra of male collar for each of the four colour forms (i.e. pure white, hybrid white, hybrid yellow and pure gold), and estimated the radiance spectra of male plumage at each court. We did this by multiplying the collar's mean reflectance with the mean ambient light irradiance at each court. We then estimated the photon capture of the four avian single cones (i.e. violet/ultraviolet, short, medium and long wavelength sensitive cones) using the calculated collar radiance and generalized passerine optical parameters. For the sensory parameters of the model eye, we used ocular media, oil droplet and photoreceptor absorbance parameters from generalized lower passerine eye parameters (Endler & Mielke, 2005). 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 (Goldsmith, 1990; Endler *et al.*, 2005), with each vertex of the tetrahedron representing one of the four avian cone types. This method considers the relative stimulation of the four avian cone classes, and provides an estimate of the perceived hue (colour) and chroma (purity) of an object. There is evidence that birds use a separate and specific cone class called double cones in detecting movement and brightness differences between objects (Campenhauen & Kirschfeld, 1998; Osorio *et al.*, 1999). Hence, we estimated the perceived brightness of a colour patch using double cone optical parameters, which can be approximated by combining the spectral sensitivities of the middle and long wavelength sensitive cones (Hart *et al.*, 2000; Théry & Casas, 2002; Heindl & Winkler, 2003b). Perceived brightness and colour/chroma of the visual background (i.e. cleared courts) were estimated using the same methods.

A signal's conspicuousness depends on the perceived difference in colour and brightness between the signal and the visual background (Leal & Fleishman, 2002; Endler *et al.*, 2005). Hence, to assay the perceived difference in colour properties (chromatic contrast) between the collar and cleared court illuminated by ambient light specific to each court, we calculated the Euclidean distance between male collar and the cleared court in the tetrahedron space (Uy & Endler, 2004; Endler *et al.*, 2005). Achromatic or brightness contrast was estimated as the difference between the perceived brightness of the signal and the court, divided by the sum of the two (see Théry & Casas, 2002; Heindl & Winkler, 2003b; Uy & Endler, 2004).

We calculated the chromatic and brightness contrast values of various plumage types on each court and habitat, which allowed us to determine if certain colour types are more conspicuous than others (i.e. higher contrast). For instance, we calculated and compared the chromatic and brightness contrast values of yellow hybrid and white hybrid collars at each of the 23 hybrid zone courts we monitored. Similarly, on the allopatric courts, we calculated and compared the chromatic and brightness contrast values of their respective pure collars (e.g. mean gold in the golden-collared, and mean white in the white-collared population) with the mean hybrid yellow and white collars. This models a scenario where hybrids expand into the allopatric ranges, and allowed us to compare the conspicuousness of hybrid plumage relative to resident, pure males. For each population or court type (i.e. pure gold, pure white, hybrid white and hybrid yellow), we used a repeated measures ANOVA to test for differences in chromatic and brightness contrast values among plumage types within the same courts, using leks as a between-subject factor. This explicitly tests for the potential confounding effects of leks as individual courts are nested within leks. *Post hoc*, pairwise comparisons of the contrast of plumage types within each population were Bonferonni corrected for multiple comparisons. All tests of significance were two tailed.

Testing for the roles of ambient light and visual background

Observed differences in the perceived contrast of plumage can be shaped by variation in the visual background, ambient light or a combination of both. Therefore, after testing for differences in the perceived contrast of plumage types, we explored the differences in colour and brightness properties of the visual background and ambient light across populations. As with the plumage reflectance spectra, we calculated ambient light and court brightness by summing their irradiance or reflectance from 300 to 700 nm. We also used a PCA to derive indices of chroma and hue independent of brightness for the ambient light irradiance and court reflectance readings (Cuthill *et al.*, 1999). We used an

ANOVA to compare and test for differences in brightness and spectral (i.e. PC scores) properties of ambient light and visual background among populations. *Post hoc*, pairwise comparisons between populations were Bonferonni corrected.

Can active choice of light habitats explain the geographic variation in conspicuousness?

If there is geographic variation among populations in plumage conspicuousness, this may be a result of individuals actively forming leks in specific habitats that best suit their plumage colour. To test for this possibility we estimated the perceived conspicuousness of male collars (see *Materials and methods*) illuminated by ambient light along a transect 100 m away from leks for the allopatric golden- and allopatric white-collared populations. We did not scan the bare ground along the transect. Therefore, we used court reflectance as the visual background for the estimate of perceived chromatic and brightness contrast of male collar along the transects, randomly choosing from the courts we used in the study (without resampling). We then used a one-way ANOVA to test for differences between the perceived chromatic and brightness contrast values calculated from ambient light along the transect with those calculated with ambient light from courts at leks. In essence, these analyses kept background and plumage constant, and allowed us to test for the explicit effects of the differences in ambient light between the random transects and courts in leks.

Results

Male plumage and morphology

Individuals from the hybrid zone and allopatric sites show variation in the colour properties of collars, with individuals from the hybrid zone showing components of the two allopatric forms (Fig. 1). For instance, yellow males from the hybrid zone show a stronger ultraviolet (UV) component than pure golden males, and white males from the hybrid zone have a slight peak in the middle (i.e. yellow) wavelength region. These qualitative observations are supported by more quantitative tests below.

Principal component analysis of standardized collar reflectance extracted three principal components that together explained 98.79% of the variation among males in hue and chroma (PC1, 81.96%; PC2, 11.20%; PC3, 5.64%). Component loadings from PCA of the standardized court reflectance show that PC1 was positively associated with short (i.e. violet to blue) and negatively with long wavelengths (i.e. orange to red), PC2 was positively associated with UV wavelengths, and PC3 was positively associated with UV and medium (i.e. yellow) wavelengths (Fig. 3a).

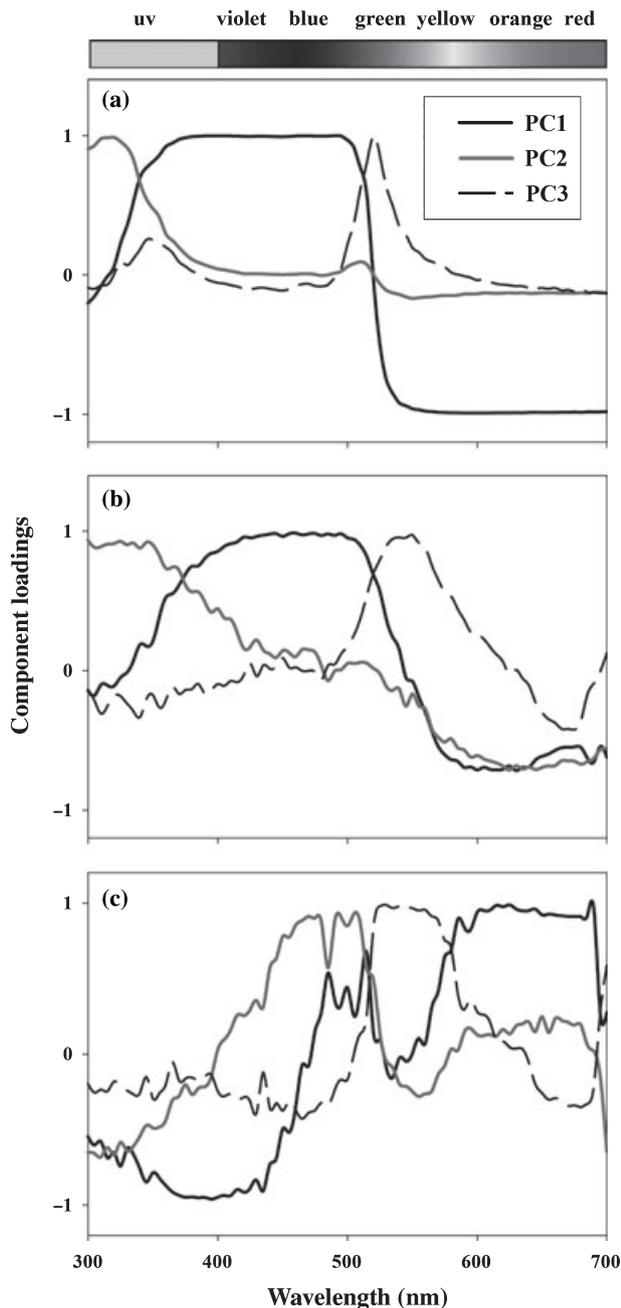


Fig. 3 Component loadings from PCA of standardized (a) collar reflectance, (b) court reflectance and (c) ambient light irradiance.

The ANOVA indicated that birds from the hybrid zone and those from the allopatric sites varied in the spectral properties of male collar (PC1, $F_{3,36} = 416.09$, $P < 0.001$; PC2, $F_{3,36} = 1.01$, $P = 0.40$; PC3, $F_{3,36} = 4.40$, $P = 0.01$). Bonferonni-corrected pairwise comparisons indicated that the PC1 values of pure white collars differed statistically from pure golden and hybrid yellow ($P < 0.001$) collars, with white collars having greater PC1 values or relative reflectance in violet–blue wavelength region (and, conversely, less reflectance in the orange–red wavelength region). PC1 values for pure white collars were generally greater than the PC1 values for hybrid white collars, but this comparison was only nearly significant ($P = 0.07$). PC2 values did not vary among plumage types. Hybrid yellows showed greater PC3 values or reflectance in the UV (300–350 nm) and middle (yellow; 500–550 nm) wavelength regions than pure golden males but this difference was not significant statistically ($P = 0.06$). With respect to morphometrics, individuals from the hybrid zone and allopatric sites varied in tarsus ($F_{3,36} = 4.42$, $P = 0.01$), tail ($F_{3,36} = 29.75$, $P < 0.01$) and beard lengths ($F_{3,36} = 50.76$, $P < 0.01$). Head length ($F_{3,36} = 2.17$, $P = 0.11$) and body mass ($F_{3,36} = 0.44$, $P = 0.73$) did not differ significantly among populations (see Table 1 for descriptive statistics and pairwise comparisons).

The stepwise DFA used beard length, tail length, PC1, PC2 and PC3, and from these extracted three discriminant scores that correctly assigned 38 of the 40 (95%) individuals into their source population or plumage type. Only two white individuals from the hybrid zone were misclassified as white individuals from the allopatric leks. These misclassifications are expected as hybrids should show intermediate spectral and morphological characteristics. In general, however, the DFA indicated that individuals in the hybrid zone were distinct in plumage colour and morphology from individuals in the allopatric sites, and can be distinguished statistically with great consistency. These analyses suggest that yellow- and white-collared birds in the hybrid zone likely carry alleles from pure golden and pure white-collared birds (e.g. yellow hybrids have golden plumage but white-collared morphology).

Geographic variation in perceived conspicuousness of male collar

These spectral differences in collar colour should interact with the visual habitat to result in these signals having

Plumage type	Mass(g)	Tarsus (mm)	Head (mm)	Beard (mm)	Tail (mm)
WC ($n = 11$)	19.77 ± 0.25	$22.54 \pm 0.15a$	29.79 ± 0.11	$11.00 \pm 0.43a$	$36.20 \pm 0.45a$
HW ($n = 9$)	19.50 ± 0.27	$21.98 \pm 0.17a,b$	29.52 ± 0.18	$10.11 \pm 0.47a$	$38.56 \pm 0.91a,b$
HY ($n = 11$)	19.39 ± 0.25	$21.84 \pm 0.15b$	29.87 ± 0.09	$9.91 \pm 0.43a$	$39.55 \pm 0.53b$
GC ($n = 9$)	19.50 ± 0.27	$21.89 \pm 0.17b$	30.04 ± 0.18	$16.89 \pm 0.17b$	$31.58 \pm 0.66c$

For each column/trait, means with different letters indicate significant differences at $P < 0.01$ level (Bonferonni corrected for multiple comparisons).

Table 1 Descriptive statistics (mean \pm standard error) of various morphometrics across the *Manacus* complex range.

Table 2 Repeated measures ANOVA of perceived chromatic contrast of variable plumage against cleared courts at allopatric white-collared (WC), allopatric golden-collared (GC) and hybrid zone visual habitats.

Effect	F	d.f.	P
At allopatric WC courts			
Plumage contrast	87.88	2, 9	< 0.001
Lek	3.22	1	0.106
Lek × plumage	7.66	2	0.021
At hybrid white courts			
Plumage contrast	12.36	1, 5	0.017
Lek	0.91	4	0.525
Lek × plumage	1.40	4	0.356
At hybrid yellow courts			
Plumage contrast	10.55	1, 8	0.012
Lek	3.78	4	0.052
Lek × plumage	8.29	4	0.006
At allopatric GC courts			
Plumage contrast	94.53	2, 11	< 0.001
Lek	4.43	1	0.057
Lek × plumage	2.99	2	0.109

Table 3 Repeated measures ANOVA of perceived brightness contrast of variable plumage against cleared courts at allopatric white-collared (WC), allopatric golden-collared (GC) and hybrid zone courts.

Effect	F	d.f.	P
Allopatric WC courts			
Plumage contrast	6.53	2, 9	0.007
Lek	20.39	1	0.001
Lek × plumage	1.363	2	0.281
Hybrid white courts			
Plumage contrast	0.023	1, 5	0.885
Lek	0.908	4	0.524
Lek × plumage	1.013	4	0.480
Hybrid yellow courts			
Plumage contrast	795.33	1, 8	< 0.001
Lek	0.780	4	0.605
Lek × plumage	0.714	4	0.605
Allopatric GC courts			
Plumage contrast	853.19	2, 12	< 0.001
Lek	0.553	1	0.472
Lek × plumage	0.404	2	0.672

different levels of conspicuousness to intended receivers. We find geographic variation in the perceived chromatic and brightness contrast of yellow and white collars across the *Manacus* range (Tables 2 and 3; Fig. 2). On display courts defended by white and yellow males at the hybrid zone, we found that a typical hybrid yellow collar shows a higher chromatic contrast than a typical hybrid white collar (Table 2; Fig. 2b). Likewise, in courts at allopatric golden-collar leks, typical hybrid yellow and pure golden collars have higher chromatic contrast values than a typical hybrid white collar (Table 2; Fig. 2c). On the

other hand, pure and hybrid white collars have higher chromatic contrast values than a hybrid yellow collars on courts at allopatric white-collar leks (Table 2; Fig. 2a). With regard to achromatic or brightness contrast, white plumage consistently showed the greatest contrast regardless of the visual habitat/population, with the exception of hybrid white courts where yellow and white plumage had similar brightness contrast values (Table 3; Fig. 2).

For most of the comparisons, leks did not factor into the model (Tables 2 and 3). For those that did, variation among leks, as well as interaction effects, within the same population was primarily a result of variation in the magnitude and not direction of contrast differences between plumage types (Table 4). For instance, in allopatric golden-collared courts, the mean contrast values for pure golden plumage and hybrid white plumage were 0.225 and 0.133 respectively. In comparison, in the second pure golden lek, the mean contrast values for pure golden plumage and hybrid white plumage were 0.243 and 0.116 respectively (Table 4). There were two exceptions to this pattern. First, there was a lek by plumage chromatic contrast interaction for hybrid yellow courts, which is driven by one of five hybrid zone lek showing greater contrast for hybrid white instead of hybrid yellow plumage. Similarly, in one of the five hybrid zone leks, hybrid yellow plumage had a higher brightness contrast than hybrid white plumage on hybrid white courts (Table 4).

Factors that influence the geographic variation in plumage conspicuousness

Variation in perceived conspicuousness can be driven by variable visual background, ambient light or both; hence, to infer how these factors may have contributed to the variation in perceived conspicuousness, we compared their spectral and brightness properties across populations (Fig. 4).

Principal component analysis of standardized court reflectance spectra extracted three principal components that together explained 92.89% of the variation among courts in hue and chroma (PC1, 47.32%; PC2, 30.78%; PC3, 14.79%). Component loadings from PCA of the standardized court reflectance show that PC1 was positively associated with short wavelengths (i.e. blue), PC2 was positively associated with UV wavelengths and PC3 was positively associated with medium wavelengths (i.e. yellow; Fig. 3b). The PC scores did not explain variation in long wavelength reflectance because there was little variation in this region among courts. The ANOVA indicated that populations showed some variation in the spectral properties of the cleared court (PC1, $F_{3,44} = 7.18$, $P = 0.06$; PC2, $F_{3,44} = 6.65$, $P = 0.13$; PC3, $F_{3,44} = 11.55$, $P < 0.001$). Bonferroni-corrected pairwise comparisons indicated that the PC3 values of pure white-collared courts differed from pure golden ($P < 0.01$) and

Lek	WC	HW	HY	GC	<i>n</i>
At pure white courts					
WC1	0.197 ± 0.004	0.161 ± 0.005	0.127 ± 0.004	–	5
	0.591 ± 0.013	0.632 ± 0.012	0.522 ± 0.049	–	
WC2	0.211 ± 0.002	0.148 ± 0.002	0.139 ± 0.002	–	6
	0.636 ± 0.008	0.674 ± 0.008	0.627 ± 0.008	–	
At hybrid white courts					
HZ1	–	0.124 ± 0.006	0.162 ± 0.004	–	3
	–	0.481 ± 0.069	0.417 ± 0.073	–	
HZ2	–	0.123 ± 0.020	0.194 ± 0.050	–	2
	–	0.511 ± 0.001	0.722 ± 0.273	–	
HZ3	–	0.113	0.173	–	1
	–	0.526	0.464	–	
HZ4	–	0.140 ± 0.021	0.151 ± 0.017	–	2
	–	0.519 ± 0.046	0.458 ± 0.050	–	
HZ5	–	0.151 ± 0.002	0.208 ± 0.005	–	2
	–	0.435 ± 0.020	0.367 ± 0.021	–	
At hybrid yellow courts					
HZ1	–	0.135 ± 0.002	0.148 ± 0.001	–	2
	–	0.383 ± 0.123	0.313 ± 0.131	–	
HZ2	–	0.119	0.172	–	1
	–	0.491	0.427	–	
HZ3	–	0.096	0.192	–	1
	–	0.578	0.522	–	
HZ4	–	0.170 ± 0.019	0.130 ± 0.016	–	4
	–	0.482 ± 0.030	0.417 ± 0.032	–	
HZ5	–	0.084 ± 0.002	0.205 ± 0.002	–	5
	–	0.461 ± 0.039	0.395 ± 0.042	–	
At pure golden courts					
GC1	–	0.133 ± 0.005	0.155 ± 0.005	0.225 ± 0.005	6
	–	0.634 ± 0.011	0.583 ± 0.013	0.575 ± 0.013	
GC2	–	0.116 ± 0.008	0.172 ± 0.007	0.243 ± 0.007	8
	–	0.607 ± 0.031	0.553 ± 0.033	0.545 ± 0.034	

Table 4 Mean ± SE of chromatic and brightness contrast values for pure white (WC), pure gold (GC), hybrid white (HW) and hybrid yellow (HY) collars against cleared courts categorized by leks within each population.

The first row for each lek indicates chromatic contrast, whereas the second row for each lek indicates brightness contrast. The italicized leks indicate the instances where the direction of difference in contrast values between plumage types is different from other leks within the same population. For each lek, *n* indicates the corresponding number of courts.

hybrid yellow ($P = 0.03$) courts, with white-collared courts having greater PC3 values or reflectance in middle wavelength region. PC1 comparisons indicated a trend ($P = 0.08$) in differences between pure golden and pure white-collared courts, with golden-collared courts showing greater PC1 values or reflectance in short wavelength region. Overall brightness (reflectance) of cleared courts varied across populations ($F_{3,44} = 21.28$, $P < 0.001$). *Post hoc* comparisons indicated that yellow and white hybrid courts did not differ, as well as pure golden and pure white courts. However, yellow and white hybrid courts were significantly brighter than the pure golden and pure white courts ($P < 0.01$ for all comparisons).

Principal component analysis of standardized ambient light spectra extracted three principal components that together explained 94.18% of variation among courts in hue and chroma (PC1, 53.17%; PC2, 21.5%; PC3, 19.51%). Component loadings from PCA of standardized light spectra show that PC1 was positively associated with long wavelengths, PC2 was positively associated with

short wavelengths and PC3 was positively associated with middle wavelengths (Fig. 3c). UV wavelength spectrum had loadings near zero because the ambient light was consistently poor in UV light across all populations (Fig. 3c). The ANOVA revealed that populations varied in the spectral properties of ambient light (PC1, $F_{3,44} = 26.39$, $P < 0.001$; PC2, $F_{3,44} = 1.02$, $P = 0.81$; PC3, $F_{3,44} = 9.15$, $P = 0.02$). For PC1 or the relative amount of long wavelength light, the pure white-collared courts showed significantly lower PC1 values than the other three populations ($P < 0.01$ for all three comparisons). The pure golden-collared population only differed significantly from pure white-collared and hybrid yellow-collared courts ($P < 0.01$). The hybrid white- and yellow-collared courts did not differ significantly from each other ($P = 0.88$). For PC2 or relative abundance of short wavelength light (blue), none of the populations differed significantly ($P > 0.05$). For PC3 or relative abundance of middle wavelength light, only pure golden- and pure white-collared courts differed

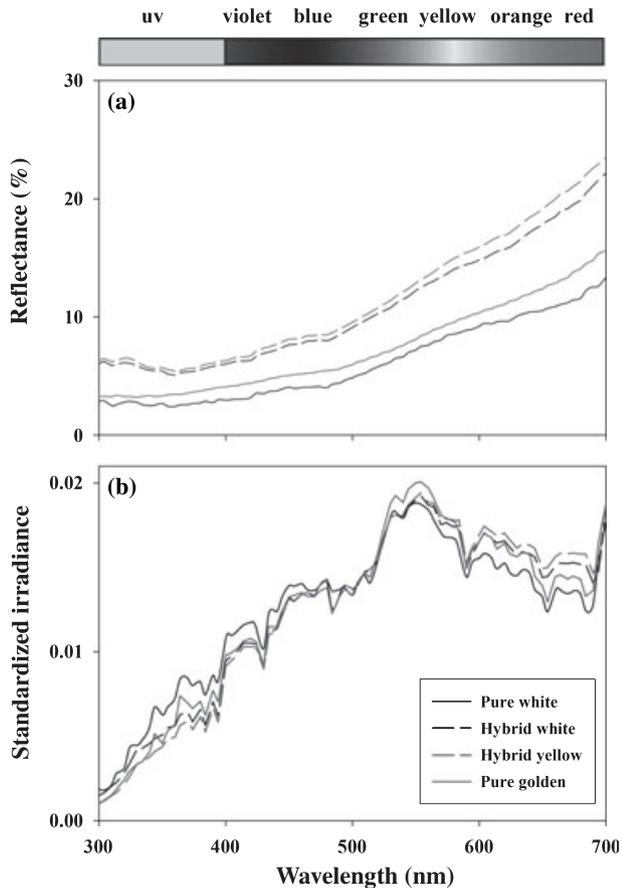


Fig. 4 Spectral properties of the visual habitat: (a) mean reflectance of cleared court (visual background) and (b) standardized (by overall brightness) mean downwelling irradiance of ambient light during displays at pure white ($n = 11$), hybrid white ($n = 10$), hybrid yellow ($n = 13$) and pure golden ($n = 14$) courts.

significantly, with pure golden-collared courts showing greater PC3 values or more green/yellow light ($P = 0.04$). The intensity of ambient light did not vary significantly among populations ($F_{3,44} = 1.04$, $P = 0.38$).

Can active choice of light habitats explain the geographic variation in conspicuousness?

At the allopatric golden-collared site, the perceived chromatic contrast of male collar illuminated by ambient light along the random transect (0.236 ± 0.008 , $n = 10$ transect points) and by ambient light within leks (0.235 ± 0.005 , $n = 14$ courts) did not differ statistically ($F_{1,22} = 0.01$, $P = 0.91$). Similarly, the perceived brightness contrast of male collar along the random transect (0.518 ± 0.047 , $n = 10$ transect points) and within leks (0.558 ± 0.020 , $n = 14$ courts) did not differ statistically ($F_{1,22} = 0.76$, $P = 0.39$).

Similar patterns were found in the allopatric white-collared site. The perceived chromatic contrast of male

collar illuminated by ambient light along the random transect (0.179 ± 0.002 , $n = 10$ transect points) and by ambient light within leks (0.181 ± 0.003 , $n = 11$ courts) did not differ statistically ($F_{1,19} = 0.30$, $P = 0.59$). The perceived brightness contrast values of collar along the transect (0.621 ± 0.010 , $n = 10$ transect points) and within leks (0.616 ± 0.010 , $n = 11$ courts) did not differ statistically ($F_{1,22} = 0.15$, $P = 0.71$).

Discussion

Geographic variation in conspicuousness and the dynamics of trait introgression

Conspicuous visual signals are often attractive to females (Endler & Houde, 1995; Boughman, 2001; Heindl & Winkler, 2003a; Pauers *et al.*, 2004; but see Endler, 1980), and a signal's conspicuousness is influenced by how much it differs from the visual background and how well it matches the spectrum of available ambient light (Heindl & Winkler, 2003b; Leal & Fleishman, 2004; Uy & Endler, 2004; Endler *et al.*, 2005; Heinsohn *et al.*, 2005). If variable visual habitat is shaping the dynamics of the yellow trait introgression, yellow males should be more conspicuous than white males at the hybrid zone and allopatric golden sites, whereas white males should be more conspicuous than yellow males at the allopatric white-collared site. We found that, indeed, comparisons of chromatic or colour contrast values were consistent with these predictions.

We found that yellow collars have higher colour contrast values than white collars on hybrid zone courts, providing a possible mechanism for the general mating advantage of yellow over white males at the hybrid zone (Stein & Uy, 2006a). Likewise, on courts in the allopatric golden-collared leks, hybrid yellow and pure golden collars appear more conspicuous than hybrid white collars. By estimating how hybrid plumage types would appear in the allopatric golden-collar courts, we modelled a scenario where hybrids invade the pure golden population and compete against golden males. These results suggest that white males would be at a disadvantage in allopatric golden-collared courts and should not invade the golden population, which can thus explain the unidirectional spread of plumage from the golden to the white species. By contrast, on courts in allopatric white-collared leks, pure and hybrid white collars appear more conspicuous than hybrid yellow collars. This suggests that white plumage is more effective and possibly more attractive than yellow plumage in pure white-collared courts. This models a scenario where hybrid males invade a pure white population, and suggests that yellow plumage would be at a disadvantage on courts in pure white-collared leks, providing a possible reason why yellow plumage has not swept beyond the hybrid zone despite the mating advantage of yellow over white males within the hybrid zone (Stein & Uy, 2006a).

Two other possibilities have been posited for the slowed movement of yellow plumage beyond the hybrid zone (Brumfield *et al.*, 2001; Stein & Uy, 2006a). First, Rio Changuinola may pose a significant dispersal barrier for yellow males. Genetic data indicating that Rio Changuinola divides the white and yellow forms provide some support for this possibility (Brumfield, 1999; Brumfield *et al.*, 2001). However, in our recent study, we found yellow males on both banks of Rio Changuinola (see Fig. 1 in Stein & Uy, 2006a), indicating the yellow males can cross this river. Instead, a possible explanation for the steep cline near Rio Changuinola is that the visual habitat may change in accord with the plumage cline. That is, the habitat west of the river may favour white signals, whereas the habitat east of the river may favour yellow signals. A more comprehensive and detailed sampling of the visual habitat across this complex's range is needed to test this possibility.

Second, our previous work indicates that the yellow male's mating advantage is found only in mixed leks where yellow males occur in greater frequency than white males. In mixed leks with more white males, yellow and white males had comparable mating success (Stein & Uy, 2006a). This suggests positive frequency-dependent selection for yellow males. Therefore, in regions where yellow male frequency is low, such as the leading edge of the plumage cline, yellow males may not experience a mating success advantage until they reach sufficient numbers, slowing the introgression of yellow plumage. We only measured the ambient light and visual background of courts in five mixed leks for this study; hence, we cannot test for an association between yellow male frequency in a lek and the conspicuousness of yellow plumage. Positive frequency-dependent selection for yellow males, however, is not necessarily an alternative to our findings, and, in fact, may be complementary. That is, both frequency-dependent selection and yellow male conspicuousness disadvantage beyond the hybrid zone slow the movement of yellow plumage into the white species.

Alternatively, the pattern of white collars appearing more conspicuous in white-collared habitats and golden collars appearing more conspicuous in golden-collared habitats may be a result of each species choosing visual habitats that best suit their specific colours. Indeed, there is evidence that animals may choose to display in conditions that best complement their display traits (e.g. Endler & Théry, 1996) or alter their displays based on changes in habitat conditions (e.g. Slabbekoorn & Peet, 2003). In our study, however, we found that the perceived chromatic and brightness contrast values were not different between leks and random ambient light transects in the general habitat, suggesting that *Manacus* manakins do not actively seek specific light habitats that best fit their divergent plumage. These analyses were based on two transects at the two allopatric sites, and a more comprehensive sampling of the visual habitat

across the *Manacus* complex range would provide a more conclusive test of this hypothesis. Our current results, however, are inconsistent with the possibility that individuals are choosing specific light conditions in their general habitat to augment their displays.

We found that white collars consistently had higher brightness contrast values than yellow or golden collars throughout the *Manacus* range, suggesting that differences in brightness contrast cannot explain the overall dynamics of yellow trait introgression. This is not surprising because white plumage reflects a greater spectrum of light than yellow plumage, and thus would appear brighter in most conditions. In our previous work, we found that collar brightness was an excellent predictor of male mating success in an allopatric golden-collared manakin population (Stein & Uy, 2006b). This may be interpreted as inconsistent with our current results, which show that white males are consistently brighter than yellow males yet do not experience a mating advantage in the hybrid zone. However, all the court-owning males in the allopatric golden-collared population we monitored were golden yellow. Females, therefore, are choosing the brightest yellow males. At mixed leks in the hybrid zone, court-owning males are yellow or white, and so females can actively choose between the two colour types. Given the choice between the two colour types, colour contrast may be more important than brightness contrast. Additional work manipulating male plumage at allopatric and hybrid zone leks will provide a more definitive test of this possibility.

Factors that influence the geographic variation in conspicuousness

We found evidence suggesting that differences in both the visual background and ambient light led to the observed patterns of geographic variation in colour contrast. First, we found differences in the relative amounts of short and middle wavelength reflectance of the cleared courts, with golden- and hybrid yellow-collared courts having greater relative reflectance in the short wavelength (blue) region, and pure white-collared having greater reflectance in the medium wavelength (green/yellow) region. Because golden and yellow plumage primarily reflect medium, long and UV light, this would make yellow plumage stand out against golden- and yellow-collared courts but less so on white-collared courts. White plumage reflects across a broader spectrum of light, including the short wavelength region; hence, it should be less conspicuous against golden-collared courts but more conspicuous against pure white-collared court.

Second, we found variation in the spectral properties of ambient light that illuminates the court during courtship displays, especially in the medium and long wavelength spectrum. The ambient light at pure white-collared courts had relatively fewer long wavelength light than pure golden and hybrid courts. Further, the ambient light

at pure golden-collared courts was relatively richer in middle wavelength light than pure white-collared courts, with hybrid zone courts falling between the two allopatric populations. Golden and yellow plumage primarily reflects middle to long wavelength light, which matches the available ambient light and should make yellow plumage more conspicuous in golden-collared and hybrid zone courts.

One final factor that could influence signal conspicuousness is the sensory properties or spectral tuning of conspecifics. In the absence of explicit data on the sensory properties of *Manacus* manakins, we used generalized Passerine optical parameters and assumed that the sensory parameters of individuals across the hybrid zone remained constant. Many studies have used a similar approach (e.g. Heindl & Winkler, 2003b; Endler & Mielke, 2005; Endler *et al.*, 2005; Heinsohn *et al.*, 2005) because closely related avian species show little variation in the sensitivity of specific cones (Hart, 2001a). However, species or populations may vary in the relative abundances of various cone types (e.g. Hart, 2001b), and this should affect an individual's overall spectral tuning (Carleton & Kocher, 2001). Geographic variation in spectral tuning can therefore augment or ameliorate the observed patterns of geographic variation in conspicuousness of male collar across the *Manacus* complex range. Future work should address this possibility by estimating the spectral tuning of various *Manacus* populations and using these empirical parameters in modeling signal perception for this complex.

Conclusions

Without explicit genetic and long-term fitness data on the individuals we monitored, we cannot rule out factors besides sexual selection that can be important in mediating the observed patterns of trait introgression. For instance, outbreeding depression or the breakdown of co-adapted gene complexes through hybridization can limit the spread of a potentially adaptive trait beyond the hybrid zone. Our results, however, are clearly consistent with the possibility that sexual selection and adaptive signal evolution mediate the patterns of trait introgression in this *Manacus* hybrid zone. The yellow plumage of the golden-collared species has spread into the white species (Parsons *et al.*, 1993; Brumfield *et al.*, 2001), and this trait introgression is mediated by sexual selection because in mixed leks at the hybrid zone where both yellow and white males compete, yellow males may account for 80% of matings despite being similar in overall frequency to white males (Stein & Uy, 2006a). Further, females in these leks sampled both white and yellow males before mating, suggesting that female preference for yellow males drives this mating asymmetry. In this investigation, we provide a possible mechanism that explains why yellow males are more attractive to females than white males, and why the

yellow trait has not swept further into the white population. This, along with previous work on this complex (Parsons *et al.*, 1993; Brumfield *et al.*, 2001; McDonald *et al.*, 2001; Stein & Uy, 2006a), adds to the growing evidence that hybridization can play an important role in the evolution of adaptive traits (Grant & Grant, 1996; Arnold, 2004; Whitney *et al.*, 2006).

Acknowledgments

We are very grateful to K. Elliot, M. Halley, C. Neidig, A. Pineda Jr, R. Santos, A. Santos, H. Santos and F. Abrego for their excellent assistance in the field. For help with logistics, we thank M. Braun, R. Brumfield, A. Himler, D. McDonald, and the staff of the Smithsonian Tropical Research Institute and Organization for Tropical Studies. We are grateful to D. Santos and the community of Changuinola Arriba for providing support and granting us permission to work on their land. Autoridad Nacional del Ambiente (Panama) and Ministerio del Ambiente y Energia (Costa Rica) graciously provided permits for our work. We thank J.A. Endler, C. Low, W.T. Starmer, members of the Uy lab and three anonymous reviewers for suggestions that improved this manuscript. This work was funded by the College of Arts & Sciences, Syracuse University, and the National Science Foundation [Biological Informatics Post-doctoral Fellowship (DBI-0074504) and a Research Starter Grant (IBN-0306175) to JACU].

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Received 22 March 2007; revised 23 April 2007; accepted 23 April 2007