



Unidirectional Introgression of a Sexually Selected Trait across an Avian Hybrid Zone: A Role for Female Choice?

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UNIDIRECTIONAL INTROGRESSION OF A SEXUALLY SELECTED TRAIT ACROSS AN AVIAN HYBRID ZONE: A ROLE FOR FEMALE CHOICE?

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Abstract.—Hybridization can be an evolutionary creative force by forming new polyploid species, creating novel genetic variation or acting as conduits of potentially advantageous traits between hybridizing forms. Evidence for the latter is often difficult to find because alleles under positive selection can spread rapidly across a hybrid zone and sweep to fixation. In Western Panama, an avian hybrid zone between two species of manakins in the genus *Manacus* exists where the unidirectional introgression of bright, yellow plumage into a white population provides evidence for the importance of hybrid zones as conduits of advantageous traits. Several lines of indirect evidence suggest that sexual selection favoring yellow plumage drives this asymmetrical spread, but more direct evidence is lacking. Along the edge of the hybrid zone, both yellow- and white-collared manakins are found in the same mating arenas or leks and compete for the same females (“mixed leks”), providing us with a unique opportunity to understand the dynamics of yellow plumage introgression. We studied these mixed leks to determine whether yellow males have a mating advantage over white males and, if so, whether the mating advantage is driven by male-male interactions, female choice, or both. We found that yellow males mated more than white males, suggesting that sexual selection favoring yellow males can, indeed, explain the spread of yellow plumage. However, we found that this advantage occurred only in mixed leks where the frequency of yellow males is greater than white males. This suggests that the advantage of yellow males may depend on the presence of other yellow males, which may slow the rate of introgression in leks where yellow frequency is low such as in areas where yellow males are beginning to colonize the white population. This, along with the geographic barrier posed by major rivers in the hybrid zone, may initially limit or slow the spread of yellow plumage. Finally, we found that yellow and white males were similar in aggression and body size, and held comparable positions within leks. Because these traits or factors are often important in or dictated by aggressive male-male interactions, these comparisons indicate that male-male interaction is not the primary mechanism for the spread of yellow plumage. However, white and yellow males received similar numbers of courtship visits from females but differed in the number of matings, suggesting that females actively rejected white in favor of yellow males. Our results indicate that sexual selection by female choice has driven the unidirectional introgression of yellow plumage into the white population, providing a mechanism for how hybrid zones act as conduits of novel and advantageous traits.

Key words.—Hybrid zones, *Manacus*, manakins, plumage, sexual selection, unidirectional introgression.

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Hybrid zones are regions where genetically distinct populations meet, mate, and produce hybrids (Barton and Hewitt 1985). Hybrid zones often contain narrow, coincident changes in the frequency of diagnostic characters between populations, which are called clines (Barton and Hewitt 1985). Although hybridization and the formation of hybrid zones are relatively widespread phenomena in nature (Harrison 1990), their role in evolution remains equivocal.

Hybridization can either hinder or promote species diversification and adaptation (reviewed in Arnold 1997; Barton 2001; Lexer et al. 2003). Hybridization limits speciation and adaptation by permitting gene flow between diverging populations or diluting unique gene complexes of already diverged species (see Turelli et al. 2001). However, hybridization can act as a creative process in evolution in several ways. First, hybridization can promote speciation through the spontaneous formation of new recombinant individuals or polyploid species (reviewed in Dowling and Secor 1997; Rieseberg 1997). For instance, hybridization between two species of tiger salamander (*Ambystoma jeffersonianum* and *A. laterale*) resulted in the instantaneous creation of a new allopolyploid species (*A. tremblayi*; Spolsky et al. 1992). Second, hybridization can create unique genetic variation that facilitates evolution or adaptation. For instance, hybridization between three species of *Geospiza* finches resulted in in-

creased additive genetic variation two to three orders of magnitude greater than those created by mutation alone (Grant and Grant 1994). Third, hybridization and selection against hybrids can exaggerate species differences when hybrids are at a disadvantage (i.e., reinforcement). For instance, Sætre, et al. (1997) found that novel plumage traits have evolved in areas where two species of *Ficedula* flycatchers overlap, which, in turn, reduces the hybridization. Finally, hybridization can act as a conduit for the introduction of new and potentially advantageous alleles or traits into another population (Anderson and Stebbins 1954; Arnold 1992, 1997; Barton 2001). Growing empirical evidence supports the role of hybridization in aiding speciation and adaptation (reviewed in Dowling and Secor 1997; Rieseberg 1997). In contrast, even though theoretical work has shown that hybridization can act as an important conduit for adaptive traits (Pialek and Barton 1997; Buerkle et al. 2003), empirical evidence for this remains scant (Arnold 2004). This paucity of empirical evidence may be due to the difficulty in detecting alleles under positive selection while they spread across a hybrid zone and rapidly sweep to fixation (Barton 1979; Hewitt 1988).

The closely related golden- (*Manacus vitellinus*) and white-collared (*M. candei*) manakins form a hybrid zone identified by several steep, concordant genetic and morphometric clines

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A golden-collared manakin (*Manacus vitellinus*) expanding his collar and beard during a courtship display to a female. • Adam C. Stein and J. Albert C. Uy, p. 1476.

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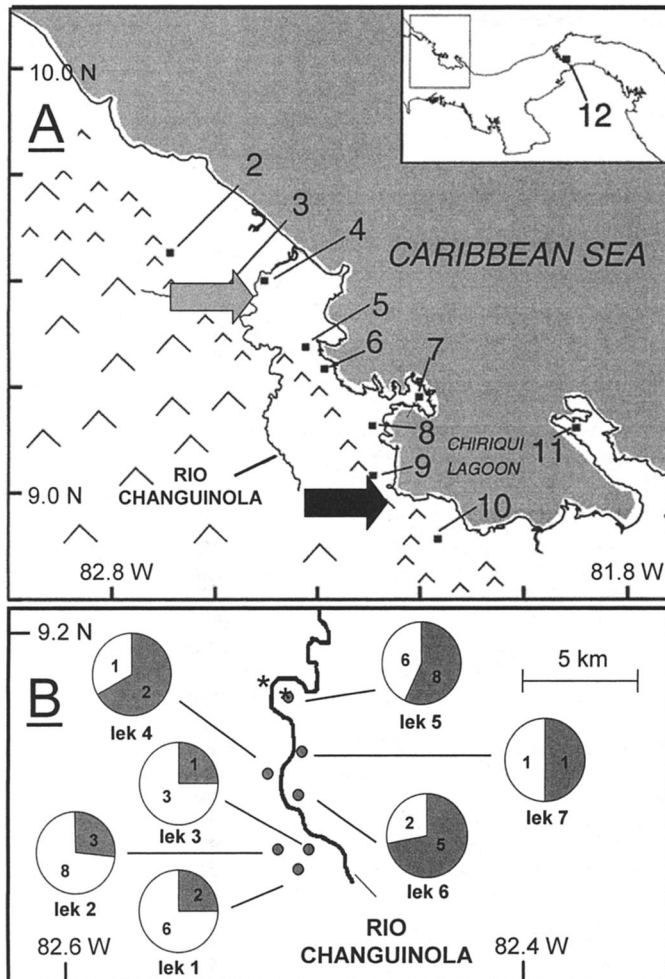


FIG. 1. (A) Location of the genetic, morphometric, and plumage clines of the golden- and white-collared manakin hybrid zone (from Brumfield et al. 2001). The black arrow indicates the region of concordant and coincident clines in several neutral alleles and morphometric traits along Rio Robalo. The gray arrow indicates the shifted yellow plumage cline along Rio Changuinola. The area between populations 9 and 4 is the region where male birds are genetically and morphometrically *Manacus candei* (white-collared manakin) but superficially resemble *M. vitellinus* (golden-collared manakin) due to the introgressed yellow plumage. (B) Location and male color ratios of the seven mixed leks used in our study along the Rio Changuinola. Gray and white sections in the pie charts represent proportion of yellow and white males, respectively. Numbers within the pie charts indicate number of yellow or white males within the mixed lek. The asterisks indicate localities of the two mixed leks sampled by McDonald et al. (2001).

centered near Rio Robalo in the Bocas del Toro province of Panama (Parsons et al. 1993; Brumfield et al. 2001; see Fig. 1). In 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 along Rio Changuinola. Adult males in the 50 km stretch between Rio Robalo and Rio Changuinola are thus genetically and morphometrically *M. candei* but look similar in color to yellow *M. vitellinus* males (Brumfield et al. 2001). Several lines of evidence suggest that the yellow plumage has actively spread through the Rio Robalo clines and into the white population

(Parsons et al. 1993; Brumfield et al. 2001; R. T. Brumfield, pers. comm.). First, it is more likely that a few genes (i.e., associated with plumage) can spread through a hybrid zone than a suite of genes and traits. Second, the genes and traits forming the Rio Robalo clines are likely neutral, while colorful plumage is likely under intense sexual selection (Parsons et al. 1993; McDonald et al. 2001). Therefore, sexual selection may be responsible for the introgression of yellow plumage into the white population, and this complex may provide evidence for the role of hybrid zones as conduits of adaptive traits.

The most probable explanation for the observed shift of the plumage cline relative to the other coincident clines is either genetic dominance of yellow plumage or sexual selection favoring yellow males (Brumfield et al. 2001). Directly testing for dominance is difficult in a long-lived species like manakins, but indirect evidence suggests that dominance is an unlikely mechanism for the observed spread of yellow plumage (Parsons et al. 1993; Brumfield et al. 2001). For instance, using the observed frequency of white males within the hybrid zone, a simple genetic dominance model shows that yellow plumage would have to be controlled by a minimum of 12 unlinked loci to displace the plumage cline by the observed distance of 50 km (Brumfield et al. 2001). This is considerably higher than those shown in other species (e.g., Johnson and Brush 1972; Rohwer and Wood 1998). Alternatively, sexual selection favoring yellow plumage can drive the differential introgression of yellow plumage into the white population. McDonald et al. (2001) showed that yellow males are more aggressive than white males; therefore, if the observed aggression leads to a mating advantage, then sexual selection via male-male competition can explain the introgression of yellow plumage into the white population. However, there is no direct evidence demonstrating that the more aggressive yellow males have a sexual advantage. Evidence showing a mating advantage for yellow males would provide more direct support for the hypothesis that sexual selection favoring yellow males explains the shift in plumage cline.

If sexual selection is indeed driving the introgression of yellow plumage, it could operate through female choice, male-male interactions, or both. Male-male interactions could be the primary mechanism driving the introgression of yellow plumage if the yellow plumage is linked to advantageous behavioral traits used in male-male interactions and if such advantages lead to increased reproductive success (e.g., Kallioinen et al. 1995; Rohwer and Wood 1998; Pearson and Rohwer 2000). This has been observed in other hybrid zones where there is an asymmetrical movement of a more aggressive species into the other species' range (e.g., Mallards and American black ducks, Brodsky et al. 1988; black-capped and Carolina chickadees, Bronson et al. 2003). Alternatively, female choice for yellow plumage may provide yellow males with a mating advantage and facilitate the spread of yellow plumage into the white population.

Along the displaced plumage cline on the banks of the Rio Changuinola both color forms compete within the same mating arenas or leks for the same set of females (mixed leks; McDonald et al. 2001). These mixed leks provide an opportunity to understand the explicit mechanism underlying the introgression of yellow plumage into the white population.

We studied males in these mixed leks to test whether yellow males have a mating advantage over white males and, if so, to determine what factors influence this advantage and whether the mating advantage is due to male-male interactions or female choice for yellow males. If male-male interaction is the primary mechanism in this sexual advantage, traits or factors linked to male-male interactions should differ between color forms. For instance, yellow males should (1) be more aggressive than white males, (2) control more central territories in leks, (3) be larger than white males, and/or (4) direct matings to them through direct courtship disruptions (e.g., Trail 1985). On the other hand, if female choice for yellow males is the primary mechanism for this sexual advantage, white and yellow males should receive a similar number of on-court courtships from females, but yellow males should mate more than white males. This would suggest that females actively reject white in favor of yellow males. Finally, we explored factors that could influence the mating and aggressive interactions in these mixed leks, including lek size and the ratio of color forms within each mixed lek.

MATERIALS AND METHODS

Study Taxa

The genus *Manacus* consists of four closely related species that are very similar in behavior, morphology, and habitat preference but differ dramatically in color of male plumage (Brumfield and Braun 2001; Höglund and Shorey 2004). *Manacus manacus* (white-bearded manakin) and *M. candei* (white-collared manakin) have white collars and beards, whereas *M. aurantiacus* (orange-collared manakin) has an orange collar and beard, and *M. vitellinus* (golden-collared manakin) has a golden/yellow collar and beard. Females and immature males of each species, in contrast, are olive in color and visually indistinguishable. The four species are mostly allopatric throughout their range but have narrow zones of sympatry where ranges overlap. In these sympatric zones, hybridization occurs, and hybrid zones are formed between the white-collared and golden-collared, and the white-bearded and golden-collared forms (in Panama and Colombia, respectively). Phylogenetic analyses indicate that (1) these taxa form a recently diverged, monophyletic group; (2) white collars and beards are the likely ancestral states; and (3) the orange- and golden-collared forms are independently derived (Brumfield and Braun 2001; Höglund and Shorey 2004). Although it is possible that the hybrid zones were formed during the incipient stages of species divergence, evidence from this and other avian species suggests that they were more likely formed during secondary contact after a period of isolation (Parsons et al. 1993; Brumfield and Braun 2001; Brumfield et al. 2001). First, the golden- and white-collared manakins, which form the hybrid zone in Bocas del Toro, Panama, are not sister taxa (Brumfield and Braun 2001). This suggests that these species diverged in isolation and secondarily formed their hybrid zone. Second, the Bocas del Toro region is a transition site or contact zone for several pairs of other closely related avian species (e.g., *Glaucidium* hermits, *Anthracoceros* hummingbirds, *Gymnopithys* antbirds, and *Tangara* tanagers; see Olson 1993), indicating the region's general

importance as a site for secondary contact between divergent avian species. This current work focuses on the well-characterized hybrid zone between the white- and golden-collared manakins in Bocas del Toro, Panama (Parsons et al. 1993; Brumfield et al. 2001; Fig. 1).

Males of all *Manacus* species aggregate in arenas called leks, where each male clears and defends a permanent court roughly one meter in diameter and surrounded on the periphery by at least two saplings. Male courts are spaced roughly 2–10 m apart, and each lek can consist of two to 15 males. Based on behavioral observations of banded males in an allopatric population of the golden-collared manakin, as well as observation of leks in the white- and golden-collared hybrid zone, adult males do not move between leks. Furthermore, once courts are established and females are visiting leks for courtships and matings, there are little to no changes in court ownership, or the addition of new males (Stein and Uy 2006; A. C. Stein and J. A. C. Uy, unpubl. data).

When a female enters the lek, court-owning males initiate courtship by rapidly hopping back and forth over the cleared court while emitting soft gruntlike vocalizations and loud pops by snapping their wing feathers ("snap-grunt display"; Chapman 1935). During this snap-grunt display, males expand their bright collars and beards. Females can perch above several courts and simultaneously view several males before joining a male on a court for courtship and/or mating (Uy and 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 (Shorey 2002; Stein and Uy 2006). Because almost all time intervals between matings were several hours to days (Stein and Uy 2006), it is unlikely that direct female copying is driving this skew in male mating success. Finally, previous work shows that male centrality within a lek, male body size, and, most importantly, collar brightness are strong predictors of male mating success (*M. manacus*, Shorey 2002; *M. vitellinus*, Stein and Uy 2006).

Do Yellow Males Have a Mating Advantage over White Males?

From 17 March to 13 June 2005, we studied seven mixed leks in the Republic of Panama on Rio Changuinola, about 20 km southwest of the town of Almirante (Fig. 1). All leks were found in mature secondary forests adjacent to openings (e.g., riverbanks), which is the typical habitat for *Manacus* leks (Chapman 1935; Ridgley and Gwynne 1989; Uy and Endler 2004). Individuals were caught with mist nets at or near the lek sites, and were fitted with a numbered aluminum leg band and a unique combination of color leg bands to facilitate identification. At the time of capture we took standard morphological measurements of tarsus, wing, head and tail lengths (mm), bill dimensions (mm), and body mass (g). We measured and banded a total of 19 adult yellow and 24 adult white males. Ownership of courts by specific males was verified using each male's unique color leg bands.

To determine whether yellow males have a mating advantage over their white counterparts, we monitored 13 pairs of banded males, with each pair consisting of one white and one yellow court-owning male across six of the seven mixed leks we found. Because local landowners cleared the trees in

lek 7 after our mount presentation experiments (see below), we could only monitor leks 1 to 6 for our analysis of mating success (see Fig. 1). We monitored two pairs in lek 1, two pairs in lek 2, one pair in lek 3, one pair in lek 4, five pairs in lek 5 and two pairs in lek 6. To control for male position on leks, which has been shown to play an important role in determining male mating success in *Manacus* manakins (Shorey 2002; Stein and Uy 2006), pairs were chosen based on their proximity to one another and position within the lek (i.e., adjacent yellow and white males were used). Observations for each pair were done simultaneously from a distance of 8–12 m from each of the courts, and hidden from the two focal males' view. Behavioral observations were 2 h in duration and conducted between 0630–0830, 1200–1400, and 1400–1600, which coincide with the peaks in mating and courtship activity in *Manacus* spp. (A. C. Stein and J. A. C. Uy, unpubl. data). Each pair was monitored for a total of 28 h with minor discrepancies due to weather (mean = 28.08 \pm 1.02 h).

What Mechanisms Drive the Mating Advantage?

If there is a difference in the number of matings and courtships between yellow and white males, the mating advantage can be driven by female choice for specific males, certain males winning in aggressive male-male interactions, or both. To test for the role of female choice, we compared the number of courtships and matings of the 13 banded pairs we observed. We defined "matings" as on-court visits by females that resulted in a copulation. We defined "courtships" as on-court visits by females that did not result in a mating. We differentiated these two behaviors because on-court visits that resulted in copulations (i.e., mating) may not be assessment visits (e.g., females are returning for copulations after a decision has been made). In contrast, on-court visits that did not result in copulations (i.e., courtships) are most likely assessment visits, with the female either rejecting the sampled male or deferring a decision until other males are sampled (e.g., Uy et al. 2001). Evidence that yellow and white males differ in number of matings, but not in number of courtships, would suggest that females are visiting both male types but actively rejecting one in favor of the other.

To assess the role of male-male competition in generating the potential difference in male mating success between yellow and white males, we quantified four factors or traits known to be linked to male-male competition in lekking species, and tested whether these factors differed between yellow and white males. The factors we quantified and compared include: (1) behavioral aggression (e.g., Moss et al. 1994), (2) court placement on leks (e.g., Gratson et al. 1991; Fiske et al. 1998), (3) courtship disruption rate (e.g., Trail 1985), and (4) male body size (e.g., Clutton-Brock et al. 1988; Shorey 2002).

To test for differences in behavioral aggression, we conducted taxidermic mount presentation experiments using a protocol previously used by McDonald et al. (2001) in *Manacus* manakins. We presented taxidermic mounts to 17 white and 17 yellow court-owning males across seven mixed leks (Fig. 1). Of the 34 subject males in this experiment, 31 were banded, which facilitated individual identification and court

assignment. Court ownership and plumage color were confirmed for the remaining three unbanded males through behavioral observations. Because only a single male clears and defends a court, and male territories are stable once courts are established (Stein and Uy 2006; A. C. Stein and J. A. C. Uy, unpubl. obs.), we were confident that the same unbanded male controlled each court for the duration of our mount presentation experiments. Four observers presented subject males with two taxidermic mounts: adult white-collared (white form) and adult golden-collared (yellow form) manakins. Each mount was prepared in a neutral pose and, to ensure that the response was not due to a particular mount condition, we used two different mounts for each color form and randomized which mount was used during a presentation. We also randomized the order of mount presentation for each subject male. The interval between mount presentations was at least one day (mean = 2.77 days \pm 2.36). Observers were located approximately 10 m from the edge of the court and each presentation was preceded by a 30-min observation to assess the impact of variation in background activity (e.g., weather). After this observational period, observers then placed the mount 25–50 cm from the edge of the cleared court. Data collection began once the subject male was within 5 m of the court and continued for 30 min. Presentations were conducted during peak courtship and mating activity times of *Manacus* manakins, which is between the hours of 0600–0800 and 1200–1600 (A. C. Stein and J. A. C. Uy, unpubl. data).

We observed and recorded the incidence of physical attacks by males, which is when the subject male makes direct contact with the mount (as in McDonald et al. 2001). Physical attack of a mount has been used as an assay of male aggressiveness in many avian taxa (e.g., Pearson and Rohwer 2000; Alonso-Alvarez et al. 2004), including manakins (e.g., McDonald 1993; McDonald et al. 2001). Each subject male had an opportunity for two physical attacks, one for each mount presented. We used percentage of attacks per opportunity to compare responses for the binary attack variable among replicate subject males. This resulted in possible attack percentages of 0%, 50% (attack one mount), and 100% (attack both mounts; as in McDonald et al. 2001). McDonald et al.'s (2001) mount experiments in *Manacus* showed that males ignored heterospecific mounts (i.e., thrush, *Catharus ustulatus*), and responded less aggressively to adult and juvenile/female mounts. Because of these results, we felt it unnecessary to present female *Manacus* and heterospecific (*C. ustulatus*) mounts in our experiment.

Court placement in the lek is a result of aggressive male-male interactions and, in many taxa, lek centrality is correlated with male mating success (e.g., Gratson et al. 1991; Fiske et al. 1998). If male-male competition and lek centrality are the mechanisms for the mating advantage of yellow males, we expected yellow males to control courts closer to the center of the lek. Within each lek, we measured male centrality by establishing a reference point in the lek and taking the distance and bearing from there to the center of each male's court. Courts were then plotted on an x-y graph, and the center of the lek was then determined as the median of the x and y coordinates of all males. The distance from this point and the male's court was then calculated (see Stein and

Uy 2006). To pool across leks, we standardized the distances in each lek to a mean of zero and a standard deviation of one (e.g., Gratson et al. 1991; Pryke et al. 2001). We used all 47 court-owning males in leks 1 through 6 (Fig. 1). Forty-one of the 47 court owners were caught and banded, allowing for direct identification and confirmation of court ownership. The remaining six males were not caught, but court ownership and male plumage color were confirmed through behavioral observations.

To test for the possibility that yellow males direct females away from white males through direct interference during courtship, we tallied the occurrence of courtship disruptions for the 13 white and 13 yellow males across six leks monitored for mating success. Finally, to determine whether yellow males were larger than white males, which may result in yellow males winning aggressive interactions, we used the morphometric data collected from court-owning yellow ($n = 19$) and white ($n = 22$) males caught at mist nets around the seven leks we monitored. Because morphometric traits are often correlated (e.g., Shorey 2002; Stein and Uy 2006), we performed a principal component analysis to collapse these variables into fewer, orthogonal variables that serve as indices of male body size. We then tested for differences in these indices between yellow and white males.

Possible Factors That Influence Social Interactions in Mixed Leks

Social dynamics in a lek can be influenced by several factors. For instance, lek size has been shown to positively correlate with the per capita attractiveness of males within a lek (e.g., Lank and Smith 1992) and the mixed leks we monitored varied in size (Fig. 1); hence, we tested for the effects of lek size on the differences between yellow and white males in number of mating and courtships, position in the lek, and level of aggression. Similarly, the frequency of color forms varied among the leks we monitored (Fig. 1), and this may influence specific interactions within leks; thus, we tested for the confounding effects of color ratio on the differences between yellow and white males in number of matings and courtships, position in the lek, and level of aggression.

Finally, differences in the amount of time we monitored each lek may affect the overall number of matings and courtships we observed, so we tested for the possible effects of unequal sampling of each lek in our comparisons of mating and courtship success between yellow and white males.

Statistical Analyses

We tested for differences in mating and courtship success between yellow and white males using a repeated-measures (i.e., paired comparison of adjacent white and yellow males) analysis of variance (ANOVA), with mating and courtship success log-transformed to meet the assumptions of this parametric test. To test for potentially confounding effects of lek size and ratio of yellow to white males within a mixed lek, we used a repeated-measures analysis of covariance (ANCOVA) with lek size and ratio of yellow to white males as covariates, color (yellow vs. white) as a fixed factor, and log-transformed mating and courtship success as dependent variables. Similarly, we tested for the effects of observation time

on our comparisons by running a repeated-measures ANCOVA with total observation time for a lek as a covariate, color (yellow vs. white) as a fixed factor, and log-transformed mating and courtship success as dependent variables. We ran this test separately because any biases introduced by variation in observation time among leks would indicate a potential problem with our methods and not be biologically relevant (unlike lek size and color form ratio).

To test for differences in aggression (i.e., attack rate) we used an ANCOVA, with arcsine-transformed attack rate as the dependent variable, color as a fixed factor, and lek size and frequency of yellow males as covariates. To test for a nonrandom distribution of court placement on the lek, we compared the standardized distance from the center of white versus yellow males using an ANCOVA, with lek size and frequency of yellow males as covariates. We performed a principal component analysis on male morphometrics to collapse these correlated variables into orthogonal variables that serve as indices of male body size. We then used the principal components to test for differences in body size between yellow and white males using a multiple analysis of variance (MANOVA). Finally, we compared the courtship disruption rate of yellow versus white males, quantified from our behavioral observations of the 13 pairs of white and yellow court-owning males. Statistical analyses were performed using SPSS 11.5 (SPSS Inc., Chicago, IL). All tests of significance are two-tailed. Means and standard deviations are presented as mean \pm standard deviation.

RESULTS

Do Yellow Males Have a Mating Advantage over White Males?

The size of the seven mixed leks we monitored varied from two to 14 males per lek (7 ± 4.40 males). Frequency of yellow court-owning males in these mixed leks varied from 0.25 to 0.72 (0.46 ± 0.20). Lek size, location, and yellow-to-white proportions for each of the seven leks we monitored are shown in Figure 1. The distribution of matings and courtships across leks are presented in Figure 2.

As predicted by the sexual selection model, yellow males received more matings than white males ($F_{1,12} = 6.174$, $P = 0.029$; Fig. 2A), with yellow males receiving a total of 14 matings and white males receiving only three matings. When considering the potential effects of lek size and proportions of color forms within each lek, we found a significant interaction between color form and frequency of yellow males (Table 1). Exploring this interaction, we found that the mating success of yellow males increased with an increase in frequency of yellow males in mixed leks. In contrast, the mating success of white males did not change with a change in frequency of color forms (Fig. 3). Lek size was not a significant covariate in this analysis (Table 1). The total amount of observation time for a given lek was not a significant covariate ($F_{1,11} = 0.32$, $P = 0.583$), suggesting that unequal sampling of the six leks did not influence our mating success comparisons.

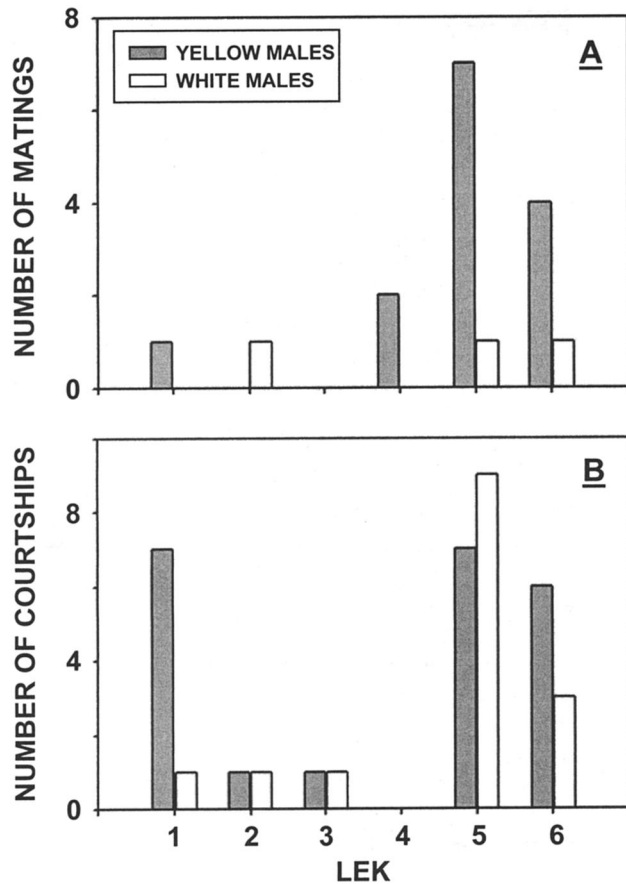


FIG. 2. The distribution of (A) matings and (B) courtships by females among yellow and white males across six mixed leks.

What Mechanisms Drive the Mating Advantage?

Yellow and white males received a similar number of courtships from females ($F_{1,12} = 0.14$, $P = 0.715$; Fig. 2B), with yellow males receiving a total of 22 courtships and white males receiving 15 courtships. Lek size and frequency of yellow males within each lek were not significant covariates (Table 1). The total amount of observation time for a given lek was not a significant covariate ($F_{1,11} = 0.32$, $P = 0.583$), suggesting that unequal sampling of the six leks did not influence our courtship comparisons.

Analysis of the attack data revealed that yellow and white males did not differ statistically in their tendencies to attack a mount ($F_{1,28} = 0.002$, $P = 0.969$). Of the 17 white males, four attacked one of the mounts (one attacked the white and three attacked the yellow mount), and two attacked both of the mounts (mean attack rate = 0.24 ± 0.36). Of the 17 yellow males, six attacked one of the mounts (four attacked the yellow and two attacked the white mount), and only one attacked both of the mounts (mean attack rate = 0.24 ± 0.31). Lek size ($F_{2,28} = 1.024$, $P = 0.3721$) and frequency of yellow males within each lek ($F_{2,28} = 1.370$, $P = 0.271$) were not significant covariates.

We found no statistical difference between white and yellow males in the placement of their courts within each lek ($F_{1,38} = 0.965$, $P = 0.332$). Lek size ($F_{2,38} = 0.207$, $P =$

TABLE 1. Repeated-measures ANCOVA of mating and courtship data for 13 pairs of yellow and white males. The dependent variable was number of matings or courtships, the fixed factor was male color (yellow vs. white), and the two covariates were frequency of yellow males within each lek (frequency) and the number of males found in each lek (lek size). Bold indicates significance.

Effect	$F_{1,10}$	P
Matings		
Male color	0.264	0.618
Color and frequency	5.324	0.044
Color and lek size	0.284	0.606
Courtships		
Male color	1.1551	0.241
Color and frequency	0.233	0.64
Color and lek size	1.254	0.289

0.814) and frequency of yellow males ($F_{2,38} = 1.977$, $P = 0.152$) were not significant covariates.

Principal component analysis on male morphometrics extracted three principal components that together explained 58.63% of the variation related to male size (PC1, 23.39%; PC2, 20.09%; PC3, 15.14%). Component loadings indicate the relationship between specific principal components and male morphology: PC1 was positively associated with beak width (0.58), beak length (0.61), and tail length (0.79); PC2 was positively associated with body mass (0.68), tarsus length (0.40), and wing length (0.68); and PC3 was positively associated with head length (0.65) and negatively associated with tarsus length (-0.55). Results from the MANOVA did not detect any statistical differences between yellow and white males in any of the three principal components (PC1: $F_{1,39} = 1.091$, $P = 0.303$; PC2: $F_{1,39} = 0.516$, $P = 0.477$; PC3: $F_{1,39} = 0.114$, $P = 0.737$). Finally, we did not observe any courtship disruptions during the 39 observed courtships among the 13 pairs of court owners we monitored.

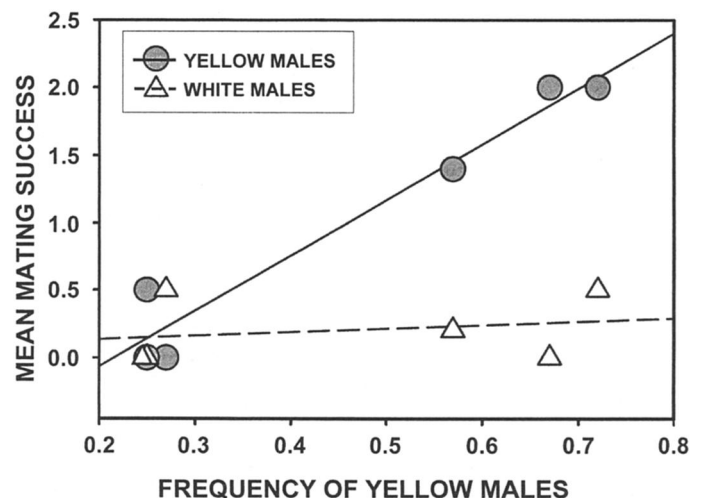


FIG. 3. Correlation between the frequency of yellow males in a mixed lek with the mean mating success of yellow (Pearson correlation, $n = 6$ leks, $r = 0.974$, $P < 0.001$) or white (Pearson correlation, $n = 6$ leks, $r = 0.231$, $P = 0.660$) males within mixed leks. Lines are drawn to visualize the association between mating success and frequency of color forms.

DISCUSSION

Sexual Selection as an Explanation for the Plumage Cline Shift

We found that yellow-collared males had a mating advantage over white-collared males (Table 1), providing evidence that sexual selection is associated with the observed cline shift in male plumage color across this hybrid zone. Given that many studies have shown the importance of bright plumage in reproductive success (e.g., Johnsen et al. 1998; Sheldon et al. 1999; McGraw et al. 2001), including our recent work in pure yellow leks of the golden-collared manakin (Stein and Uy 2006), these results are not surprising. However, we found that this mating advantage occurred only in leks where yellow males were at a higher frequency than white males (Table 1 and Fig. 2), suggesting the possibility of positive frequency-dependent selection favoring yellow males.

Positive frequency-dependent selection has been shown to maintain steep and stable clines in warningly colored *Heliconius* butterfly (Mallet and Barton 1989) and *Partula* snail (Johnson et al. 1987) hybrid zones. Similarly, in the *Manacus* hybrid zone, positive frequency-dependent selection for yellow males may influence the rate and differential spread of yellow plumage into the white population (Brumfield et al. 2001). At the leading edge of the plumage cline, yellow males should be relatively rare and hence would not experience a significant mating advantage over white males. When the frequency of yellow males finally increases (e.g., via drift, or nonrandom association based on male color), then yellow males would realize a mating advantage over white males and the yellow trait could sweep into the white population. The 50-km zone between the plumage and morphometric/genetic clines, where all males are yellow except genetically and morphometrically white *M. candei*, may be a region where yellow plumage has swept after leks reached higher yellow frequencies (see Fig. 1). Rio Changuinola, where the introgression of yellow plumage abruptly stops, has been posited as a geographic barrier that prevents the yellow plumage from further sweeping into the white population (Brumfield et al. 2001). Our results of a positive frequency-dependent selection on yellow males suggest an additional or alternative mechanism that could slow the introgression of the yellow plumage into the white population during the early stages of trait introgression. The genetic and morphometric clines centered 50 km west of the plumage cline, in contrast, are not under frequency-dependent selection (i.e., selectively neutral; Brumfield et al. 2001) and are thus either stationary or moving at a much slower and consistent rate. Additional sampling is needed to measure the temporal and spatial stability of these clines.

Our finding that yellow males gain a significant advantage when their frequency within a lek is greater than white males may be interpreted as evidence that females are not choosing and yellow males are receiving more matings solely because they are more abundant in a lek. However, this is not the case for our study. First, in three mixed leks where the frequency of white males is greater than yellow males, white males did not have a mating advantage over yellow males (Fig. 3). This suggests that it is not simply the relative abun-

dances of males that dictate male mating success. Second, we observed females actively visiting both white and yellow males, yet primarily choosing yellow males. This indicates active choice for yellow males, especially in mixed leks with higher frequency of yellow males.

Alternatively, genetic dominance of yellow plumage may cause a shift in plumage clines when the underlying allele frequencies are actually coincident. This explanation has been used to explain the shifted plumage clines in *Dendroica* warbler (Rohwer and Wood 1998) and *Gymnorhina* magpie (Hughes 1982) hybrid zones. Captive breeding experiments and crosses are required to explicitly test the genetic dominance hypothesis; however, at least two lines of evidence indicate that sexual selection is the better explanation for the displaced plumage cline. First, Brumfield et al. (2001) made a logical and convincing argument that limits the utility of genetic dominance as an explanation for the shifted plumage cline. By comparing the frequency of white males observed within the hybrid zone to the expectation under a simple genetic dominance model, Brumfield et al. (2001) concluded that given the extremely low frequency of white males within the hybrid zone (<0.005 in populations 4–8 in Fig. 1), yellow plumage would have to be controlled by a minimum of 12 unlinked loci in order to displace the plumage cline by the observed distance of 50 kilometers. This required number of loci controlling plumage traits is considerably higher than those documented in other species (Johnson and Brush 1972; Buckley 1987; Rohwer and Wood 1998). Second, and more importantly, we now have more direct evidence showing that yellow males indeed have a mating advantage over white males, at least in mixed leks with greater frequency of yellow males. This provides concrete support for the sexual selection hypothesis. Note, however, that evidence for the sexual selection hypothesis does not indicate that dominance is not an important factor in the yellow plumage introgression. Most likely, yellow plumage introgression is a result of complex interactions among various factors, which include strong sexual selection for yellow traits and possibly partial dominance of yellow plumage.

Mechanisms that Drive the Yellow Mating Advantage

Sexual selection results from females actively choosing specific males or males preventing other males from gaining access to females (Darwin 1871). Hence, the mechanism causing the sexual advantage of yellow males can operate through female choice, male-male interactions or both. Using mount presentation experiments, McDonald et al. (2001) found that yellow males were generally more aggressive than white males in pure yellow or white leks in allopatric regions and the hybrid zone (population 5 in Fig. 1). If yellow plumage is linked to male aggression, this result is consistent with the possibility that male-male competition is the primary mechanism by which sexual selection is driving the unidirectional spread of yellow traits across the *Manacus* hybrid zone. However, McDonald et al. (2001) did not determine whether increased aggression indeed leads to higher mating success for yellow males, or how aggression may differ in leks where white and yellow males naturally interact.

Our observations of males at mixed leks provide a unique

opportunity to directly determine the relative roles of female choice and male-male interactions in creating a mating advantage for yellow males. If male-male interaction is the mechanism by which yellow males are gaining a reproductive advantage over white males, we expect to detect differences between yellow and white males within the mixed leks in factors that are linked to success in male-male interactions, including: (1) aggression, (2) position in the lek, (3) body size, and/or (4) tendency to disrupt courtships. We failed to find a statistical difference between yellow and white males in any of these factors.

First, our mount presentation experiments in the mixed leks showed no statistical difference in attack rate, a measure of aggressiveness, between white and yellow males. We used the same protocol and comparable sample size as McDonald et al. (2001), who found considerable difference in aggressiveness between yellow and white males in pure white or pure yellow leks. McDonald et al. (2001) observed nine attacks of a possible of 34 with yellow males in pure yellow leks. We observed a similar attack rate with the yellow males in mixed leks, where subjects attacked eight of a possible 34. We observed that white males in mixed leks also attacked a total of eight of 34 times, which is statistically greater than McDonald et al.'s (2001) observations of only two of a possible 34 times ($\chi^2 = 4.48$, $df = 1$, $P < 0.05$) in pure white leks. McDonald et al.'s (2001) study focused on males at pure leks, which may explain our different results. They did, however, run preliminary experiments on two white and two yellow males in two mixed leks (see Fig. 1). They found a trend toward increased aggressiveness in white males at mixed leks relative to white males from pure white leks. This is consistent with our results from a larger set of males across six mixed leks, showing similar levels of aggressiveness between yellow and white males. As McDonald et al. (2001) point out, interactions and experience with aggressive yellow males at mixed leks may result in white males becoming more aggressive. If such is the case, plumage color may not necessarily be linked to aggression. In fact, Day et al. (2006) found that juvenile golden-collared manakins implanted with testosterone, a hormone that mediates aggressive behavior (e.g., Delville et al. 1996), increased their courtship activity but did not result in juveniles molting into the golden plumage. Note, however, that Day et al.'s (2006) results differ from other studies, where a direct link between testosterone and male plumage has been found (e.g., Collis and Borgia 1992).

Second, we failed to detect a statistical difference in lek centrality between yellow and white males, suggesting that yellow plumage does not provide an advantage when competing for more attractive territories. This is true even when considering lek size and the frequency of yellow to white males within mixed leks as covariates. Third, yellow and white males did not differ statistically in body size. Previous studies within this hybrid zone found that hybrid males, although similar to yellow *M. vitellinus* in plumage color, are virtually indistinguishable from white *M. candei* in several morphometric measures (e.g., body size, wing length; see Parsons et al. 1993; Brumfield et al. 2001). Results from our morphometric comparisons are consistent with this. However, we tested for a difference in body size between yellow

and white males because body size has been shown to be an important aspect in determining the outcome of male-male interactions (reviewed in Andersson 1994) and has been a significant correlate of male mating success in *Manacus* manakins (Shorey 2002; Stein and Uy 2006). Finally, we did not observe disruptions during any on-court courtships in the *Manacus* mixed leks, indicating that direct male-male aggression during courtships does not influence the outcome of mate choice. In fact, in a more detailed study of golden-collared manakin leks, we also failed to find courtship disruptions from the 241 courtships among 22 males we observed with automatic video cameras (Stein and Uy 2006). In another lekking bird, however, males can influence the outcome of matings through courtship disruptions (Guianan cock-of-the-rock; Trail 1985).

Because yellow and white males did not differ in traits or factors linked to male-male competition, female preference for yellow plumage may be an alternative mechanism explaining the mating advantage of yellow over white males. In support of this possibility, we found that yellow and white males received a similar number of courtship visits from females, yet yellow males received more matings than their white counterparts. This suggests that females are actively rejecting white males after courtships. In fact, we directly witnessed females initiating courtships with white and yellow males, then choosing to mate with yellow males (A. C. Stein and Uy, J. A. C. unpubl. data). Furthermore, lek size or ratio of yellow to white males did not affect female visitations of white and yellow court owners. This suggests that the mating advantage experienced by yellow males in leks with high frequency of yellow males was a result of females choosing yellow over white males, and not merely yellow males receiving more courtships from females.

Although we have evidence suggesting that female choice for yellow males drives the yellow male advantage in these mixed leks, we lack information to explain the frequency-dependent advantage of yellow males. In the *Partula* land snail hybrid zone, individuals must match in shell chirality (i.e., direction of shell coiling) for effective mating, thus the necessity for assortative mating selects against individuals of the rare chiral form (Johnson et al. 1987). This maintains the steep cline between two snail populations that differ in shell chirality. In contrast, male and female manakins are not under such anatomical constraint, and thus the advantages of yellow males must be a result of active female choice. One possibility is that the higher frequency of yellow males in some leks enforces female preferences for yellow plumage. Before joining individual males for on-court courtships, female manakins alight on vegetation above the courts and watch several males display (Uy and Endler 2004). The cumulative effects of multiple yellow males simultaneously displaying may augment the per capita attractiveness of yellow males. This possibility is supported by work in other avian species in which additional stimuli (e.g., calls) from conspecifics within a colony promotes sexual activity (royal penguins, Waas et al. 2000) or increases ovarian development in females (e.g., ring doves, Lott et al. 1967).

Additional work is needed to reveal the specific mechanisms that dictate the positive interaction between male color and frequency of yellow males, and to determine what factors

influence the frequency of each color form within a lek. However, even without direct knowledge of the underlying mechanisms influencing the frequency-dependent advantage of yellow males, our results provide strong support for the hypothesis that sexual selection by female choice has driven the unidirectional spread of yellow plumage into the white population.

Female Choice and Hybrid Zones

Our results suggesting that females are choosing males with sexual signals of heterospecifics are contrary to the expected rationale that female choice should favor signals that facilitate mating with conspecifics (Paterson 1985), as seen in two hybridizing species of *Ficedula* flycatchers (Sætre et al. 1997). In other hybrid zones where female choice is the mechanism of unidirectional introgression of traits, females are often from the rarer species, and are unable to find conspecific mates and so “settle” for a heterospecific male (Moyer 1981; Avise and Saunders 1984; Avise et al. 1997). This may lead to the introgression of alleles that are not necessarily advantageous into a population. Female manakins, however, chose heterospecific traits even when males possessing conspecific traits were available. Thus, yellow plumage is advantageous to males who possess it.

When understanding the evolution of elaborate traits and the accompanying female preferences, studies often assume that the trait and preference emerged within the population and eventually reached fixation (see Andersson 1994). Our results suggest the interesting alternative that display traits, and possibly female preferences for the trait, may have originated from another population and spread secondarily into a given population. Although this does not address the ultimate origin of a trait and preference, it does provide a mechanism for the evolution of elaborate displays and preferences for a given population. The role of migration and hybridization as a source of genetic variation has long been appreciated (e.g., Jaenike 1973; Grant and Grant 1994), but its potential role in the evolution of elaborate displays is relatively unexplored. Our study indicates that an attractive secondary sex trait and possibly the female preference associated with it originated from an adjacent population, providing evidence for hybrid zones as an important source for attractive and adaptive display traits.

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