Loss of sexual dimorphism is associated with loss of lekking behavior in the green manakin *Xenopipo holochora*

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Manakins (Pipridae) are well know for elaborate male sexual displays and ornate plumage coloration, both of which are thought to have evolved as a consequence of lekking breeding, the prevalent mating system in the family. Less attention has been paid to a handful of 'drab' manakin species, in which sexual dimorphism appears to be reduced or absent. Using character reconstruction, we show that these 'exceptions to the rule' represent phylogenetically independent cases of losses in sexual dimorphism, and as such could provide a focal group to investigate the link between changes in morphology and in life history (e.g. mating system). We take a first step in this direction by focusing on two subspecies of the putatively monomorphic green manakin *Xenopipo holochlora* to formally confirm that the species is sexually monomorphic in size and plumage color and test the prediction that sexual monomorphism is associated with the loss of lekking behavior in this species. Our results show that size dimorphism is present but limited in the green manakin, with substantial overlap in male and female morphometric measures, and that sexes are largely monochromatic (including from an avian perspective), despite marked coloration differences between subspecies. Behavioral observations indicate that males do not form leks and do not engage in elaborate sexual displays, that there is no stable pair bond formation, and that females provide parental care alone. These findings are consistent with the idea that changes in mating behavior may have driven changes in morphology in Pipridae, and we encourage similar studies on other drab manakins to better understand this relationship.

Sexual dimorphism refers to the presence of obvious phenotypic intraspecific differences between males and females, such as in coloration (i.e. sexual dichromatism) or other aspects of morphology. Although sexual dimorphism may arise as the result of natural selection (Shine 1989, Badyaev and Hill 2003), sexual selection is frequently invoked as the main force driving these differences (Darwin 1871, Andersson 1994). In fact, degree of sexual dimorphism is a commonly used indicator of sexual selection intensity (Owens et al. 1999, Nadeau et al. 2007, Medina and Francis 2012), an assumption generally supported by correlations between sexual dimorphism and intensity of sperm competition (Bennett and Owens 2002), rate of evolution of genes involved in plumage coloration (Nadeau et al. 2007), or degree of polygyny (Payne 1984, Dunn et al. 2001; but see Burns 1998, Friedman et al. 2009).

The use of a phylogenetic perspective has been instrumental to our understanding of the evolutionary forces that shape sexual dimorphism across bird species. It is now clear, for example, that changes in the degree of sexual dimorphism can be caused by either increases or decreases in either male or female traits such as size (Karubian and Swaddle 2001) or plumage elaboration (Burns 1998, Hofman et al. 2008, Friedman et al. 2009, Johnson et al. 2013, Karubian 2013, Price and Eaton 2014). In addition, such comparative studies provide a powerful way to investigate the relative role life history traits such as mating system play in the evolution of sexual differences. For example, in oropendolas and caciques (Icteridae), size dimorphism increases with degree of polygyny (Webster 1992), and even though these birds are largely sexually monochromatic, plumage color changes faster in polygynous lineages compared to monogamous lineages (Price and Whalen 2009). Among grackles and allies (another clade in the family Icteridae), socially monogamous species are significantly less dichromatic than species with other mating systems, but other life history traits such as migratory status and breeding latitude seem to influence patterns of sexual dimorphism as well (Price and Eaton 2014). In some groups, gains or increases in sexual dimorphism have been causally associated

with evolutionary transitions from monogamy to lekking or non-lekking polygyny (Oakes 1992, Lislevand et al. 2009). Taken together, these studies corroborate the long-held observation that when changes in mating systems increase the intensity of sexual selection, males and females tend to become more distinct in sexually-selected traits such as size or plumage color. On the other hand, reductions in sexual dimorphism have been investigated mostly in the context of females becoming more elaborated, and thus more similar to males, perhaps as a result of sexual or social selection on females, or correlated evolution with male traits (Burns 1998, Hofman et al. 2008, Friedman et al. 2009, Johnson et al. 2013, Price and Eaton 2014). Cases in which reduced sexual dimorphism ensues from both sexes being relatively non-elaborated, however, are much more rare in nature and less well understood.

Manakins (Pipridae) are Neotropical birds well known for their lek breeding systems and the ornate plumage and displays of males (Snow 2004). Lekking males experience intense sexual selection, as evidenced by their strong variation in reproductive success (Payne 1984, Mackenzie et al. 1995, DuVal and Kempenaers 2008). In the Pipridae clade, consisting of 52 species in 13–15 genera (Snow 2004, Ohlson et al. 2013), lekking is an ancestral trait and thought to have promoted the evolution of strong sexual dimorphism in morphology and sexual displays found in most manakins (Prum 1994). Male plumage evolution seems to conform to a Fisherian model, with rapid and unconstrained changes and little convergence among taxa (Prum 1997). On the other hand, females, which provide all the parental care, are without exception unornamented in plumage, with drab colors varying in shades of olive and green, likely resulting from natural selection to avoid nest predation. Departing from this general pattern, male ornamentation is largely reduced or absent in a few species – most notably, among the 'true' manakins, those traditionally included in the genus *Chloropipo* (olive manakin *C. uniformis*, green manakin *C. holochlora*, yellow-headed manakin *C. flavicapilla*). *Chloropipo* has recently been shown to be a polyphyletic genus (Ohlson et al. 2013) and thus potentially provides instances of losses in sexual dimorphism that are phylogenetically independent. As such, these species are especially valuable for our understanding of the mechanisms behind the evolution of sexual dimorphism in manakins and, potentially, other taxa. Unfortunately, 'drab' manakins are also among the least studied (Prum 1994, Snow 2004), and the ecological and behavioral correlates of reduced or absent sexual dimorphism are largely unknown.

Here, we provide data on two of the four recognized subspecies of the green manakin (former *C. holochlora*, currently *Xenopipo holochlora* according to the American Ornithologists' Union, Chesser et al. 2013): the *litae* subspecies from the western Andes in Colombia and Ecuador, and the *holochlora* subspecies from the eastern Andes in Colombia and Peru. These birds occupy humid lowland and foothill forests and have males and females that to the human eye are identical in their green plumage and general morphology. Yet, cryptic dichromatism (in which color differences are visible to birds but not to humans) has been shown to be common among putatively monochromatic passerines (Eaton 2005, 2007), raising the question of whether green manakins are truly monochromatic from an avian perspective. Similarly, the species is considered monomorphic in size (Snow 2004), but because of the difficulty in identifying males from females in the field based on plumage, it is possible that existing differences in structural morphology have been overlooked. Virtually no information is available on their mating behavior (Prum 1994, Christian 2001, Snow 2004), but the putative lack of sexual dimorphism suggests absence of strong sexual selection and a possible change to non-lekking polygyny or even monogamy.

As such, our objectives were three-fold. By first focusing on the whole manakin clade, we aimed 1) to confirm that the putatively monochromatic/nearly monochromatic manakins underwent reversals from an ancestral state of dichromatic sexes, and how many times such transitions happened in the family. Then, by focusing specifically on the green manakin, we aimed 2) to formally confirm that the species is sexually monomorphic in size and coloration and, assuming that this is the case, 3) provide behavioral data to test the hypothesis that lekking behavior was lost in this species.

Methods

Sexual dichromatism evolution in manakins

We reconstructed ancestral character states of sexual dichromatism by mapping this trait onto the recent molecular manakin phylogeny provided in Ohlson et al. (2013). Placement of *X. holochlora* and other putatively monochromatic or nearly monochromatic manakins is well-supported in this phylogeny (Bayesian posterior probabilities and maximum likelihood bootstrap values > 97 and > 89, respectively). We reconstruct character states with Mesquite 2.75 (Maddison and Maddison 2011) using both the maximum likelihood and parsimony with unordered states methods (as both methods produced similar results, we only report the ML results here). For these analyses, we used human-perceived measures of dichromatism, which have been shown to be appropriate proxies of avian-perceived dichromatism in the context of comparative studies (Armenta et al. 2008, Seddon et al. 2010). We determined dichromatism states for all 36 manakin and 5 flycatcher outgroup species included in the phylogeny based on illustrations and descriptions found in Snow (2004). Character states were coded as: 0 = sexes are monochromatic from a human perspective; 1 = sexes are nearly monochromatic (defined by sexes being similar in general plumage coloration but differing in shade [one case: *Chloropipo flavicapilla* females are duller] or having coloration differences restricted to a single part of the body [two cases: *Tyranneutes virescens* and *Lepidothrix iris* females are similar to males but have less yellow on crown or lack the shiny opalescent crown, respectively]); 2 = sexes are dichromatic (i.e. visible color differences are present in more than one part of the body). We also conducted this same analysis by coding dichromatism simply as present (1) or absent (0), in which case all taxa that had been previously coded 'nearly monochromatic' were coded as 'dichromatic'. In all cases where different subspecies or races exist, the nominate taxon was considered.

Size dimorphism in *X. holochlora*

We tested for size dimorphism in *X. holochlora* using measures taken from live birds in the field. These analyses were limited to the western *litae* subspecies as we did not have comparable measurements of the eastern *holochlora* subspecies. From a larger pool of birds captured in ground-level mist-nets between 2004 and 2006 at Bilsa Biological Station (79°45′W, 0°22′N, 330–730 m a.s.l., Esmeraldas Province, Ecuador) as part of a community-wide avian study (for details, see Carrasco et al. 2013 and Durães et al. 2013), we randomly chose 64 individuals without any obvious out-lier measurements. All individuals were banded with color band combinations and/or unique-numbered aluminum bands. Standard morphological measurements were taken, always by the same observer (LC), and included tarsus length, wing chord, tail length, bill depth, bill width and exposed culmen (measured with calipers to the nearest 0.1 mm), and body mass (measured with a scale to the nearest 0.1 g). Each individual was captured and measured 1–8 times during the course of the study, and multiple measurements were averaged within individuals. A small blood sample (~50 µl) was taken by puncture of the brachial vein and stored in lysis buffer for subsequent molecular sexing in the lab using the primers 2550F (Fridolfsson and Ellegren 1999) and MSZ1R (Sehgal et al. 2005) (see Supplementary material Appendix 1 for details). Among the 64 birds, 39 were genetically sexed as males and 25 as females.

Morphological variables were checked for normality and variance homogeneity prior to analysis; no transformations were necessary to meet parametric assumptions. We examined the ability of morphological variables to differentiate males and females using discriminant analysis (DA), which seeks to extract underlying gradients of variation in which such variation is maximized among sample groups (McGarigal et al. 2000). Only variables that were significantly or marginally significantly different between males and females, according to Student's *t*-tests, were included in the DA; these included all morphological variables with exception of body mass, for a total of seven variables (Table 1). We used the Mahalanobis distance from each point to each group multivariate mean to predict group membership (McGarigal et al. 2000). From the total of 64 sexed birds, 3 were excluded from the DA for having missing data

Table 1. Average (and standard deviation) of morphological traits for male and female green manakins *Xenopipo holochlora litae* from northwest Ecuador. Sexes were compared with Student's *t*-tests; values between parentheses represent the percent difference between males and females (negative values indicate that males have smaller values). All units are in mm, except for body mass, in grams.

Trait	Males (n = 39)	Females (n = 25)	*t*-ratio	p-value
Body mass	16.3 ± 1.0	16.7 ± 1.1	−1.609	0.110 (−2%)
Tarsus length	15.0 ± 0.7	14.5 ± 0.8	2.596	**0.012** (3%)
Wing chord	68.7 ± 2.7	65.8 ± 3.2	3.882	**0.003** (4%)
Tail length	47.5 ± 2.2	44.2 ± 2.0	5.855	**<0.001** (7%)
Bill height	4.3 ± 0.2	4.4 ± 0.3	−1.898	0.062 (−2%)
Bill width	5.0 ± 0.6	5.3 ± 0.7	−2.021	**0.048** (−6%)
Culmen	7.5 ± 0.3	7.7 ± 0.4	−2.825	**0.006** (−3%)
Exposed culmen	10.7 ± 0.6	11.1 ± 0.7	−1.958	0.055 (−4%)

for 1–2 morphological traits. Of the remaining 61 birds, we included 51 (34 males, 17 females) as training points, after removing ten randomly chosen individuals (5 of each sex) to validate model accuracy. These analyses were conducted using JMP, ver. 10.0.2 (SAS Inst.).

Differences in plumage reflectance between sexes and subspecies

We measured plumage reflectance on the crown, back, tail, wing coverts, wing edging, breast, belly, bill, and chin of 112 *X. holochlora* specimens (87 *holochlora* and 25 *litae* individuals; 73 males, 39 females) loaned from four institutions (see Acknowledgements) using an Ocean Optics S2000 fiberoptic spectrometer with a PX-2 pulsed xenon light source (Ocean Optics, Dunedin, FL). Two people collected different subsets of the data on different spectrophotometers (same model). Instead of attempting to standardize by data collector and equipment, we analyzed the data sets separately and refer to them by their place of data collection (LSU or UCLA). We calibrated the spectrometer with a WS-1 diffuse reflectance standard. We took each reading at a 45° angle to the feather, with the sensor and light source positioned a standardized distance away from the feather through the use of a metal attachment over the sensor. With respect to positioning of the 45°-angled sensor relative to how the feather barbs lie, all readings were taken perpendicular to the feather barbs rather than parallel to them. We took three readings for each plumage area (crown, back, etc.).

We used Tiger Spectre ver. 1.7 (<https://pantherfile. uwm.edu/pdunn/www/Spectre/Spectre.html>) to 1) analyze readings between 300 and 700 nm, 2) average the three readings per plumage area, and 3) calculate brightness, hue, and chroma values for each plumage area with respect to the human visual system. We conducted Student's *t*-tests to determine if there were significant univariate differences in brightness, hue, or chroma for each plumage area between sexes (partitioning by subspecies) and between subspecies. These tests were conducted separately for the data collected at UCLA and LSU. We applied a Bonferroni correction by converting p-values to *q*-values (Newson 2010) using Stata 11 (Stata Corp.). We also assessed sex and subspecies differences using multivariate principal components analyses of brightness, hue, and chroma values for all plumage areas. We tested for differences between sexes and subspecies for all PCs with an eigenvalue greater than 1.

To ensure that our plumage reflectance analyzes did not overlook differences perceived by birds but not by humans, we re-analyzed the UCLA data subset according an avian visual model, following methods detailed in Smith et al. (2008). Reflectance spectra were converted into bird-specific cone excitation estimates (E_j) using typical cone λ_{max} values (wavelengths of maximum absorbance) for violet sensitive passerines, and E_j were used to calculate relative cone contrasts and coordinates in tetrahedral color space (Endler and Meilke 2005). E_j values calculated under five different ambient light environments (early-late, open-cloudy, woodland shade, forest shade, and small gap) were similar, so results are presented for the forest shade light environment only. To test for differences in tetrahedral color space between sexes and between subspecies, we employed the nonparametric

statistics program LSED-MRPP (Endler and Meilke 2005), which reports an effect size or disparity value (K, a measure of distance in tetrahedral color space) and associated p value. Color patterns can be considered different enough to be perceived by birds with V-type cones if $K > 0.01$, easily distinguished if $K > 0.05$, and completely different if $K > 0.2$ (Endler et al. 2005). For LSED-MRPP models yielding statistically significant results, we subsequently used analysis of distance (AOD in Stata, see Smith et al. 2008 for details) to determine which specific reflectance variables were responsible for the differences.

Behavior

Focal behavioral observations were made in 2006–2008 on a *litae* population in Bilsa Biological Station as part of a study focused on describing the basic biology of the species (PM and JK unpubl.). General methods involved capture in mistnets and marking of green manakins with color plastic leg bands for individual identification; opportunistic observation of individuals and radio-telemetry to aid in focal behavioral observations (two males, two females, and two individuals of unknown sex were equipped with BD-2N transmitters [0.55 g, Holohil, Ontario, CA] attached to the back with a Rappole harness, Rappole and Tipton 1991); systematic nest searching and description of basic nesting biology and parental care. This work was conducted in all months of the year at our long-term study site.

Results

Sexual dichromatism evolution in manakins

Ancestral character state reconstruction indicates that sexual dichromatism is the most likely ancestral state in the manakin clade, and that reversals to monochromatism likely occurred independently in all drab manakin species included in the Ohlson et al. (2013) phylogeny (Fig. 1). This finding holds using both the binary classification scheme (which treats only *X. holochlora* and *C. uniformis* as monochromatic) as well as with the 3-point scale (in which *C. flavicapilla* and *L. iris* are included as nearly monochromatic); *Lepidothrix villasboasi* was also assigned a score of '2: nearly monochromatic', but it was not included in the Ohlson et al. (2013) phylogeny. Because females in all manakins have drab colors, losses in dichromatism are presumably driven by reductions in male plumage ornamentation.

Size dimorphism in *X. holochlora*

In western green manakins *X. h. litae*, males are generally larger than females (longer tarsi, wings, and tails), but females have larger bills (Table 1). Despite considerable overlap between males and females in morphological space (Fig. 2), a discriminant function comparing morphological variables between sexes was significant (Wilks' $\lambda = 0.492$, $p < 0.001$) and correctly sexed 43 of the 51 (84%) individuals included as training points. The function was slightly more accurate at identifying females (88%) than males (82%), indicating that males are more variable in morphometric traits than females.
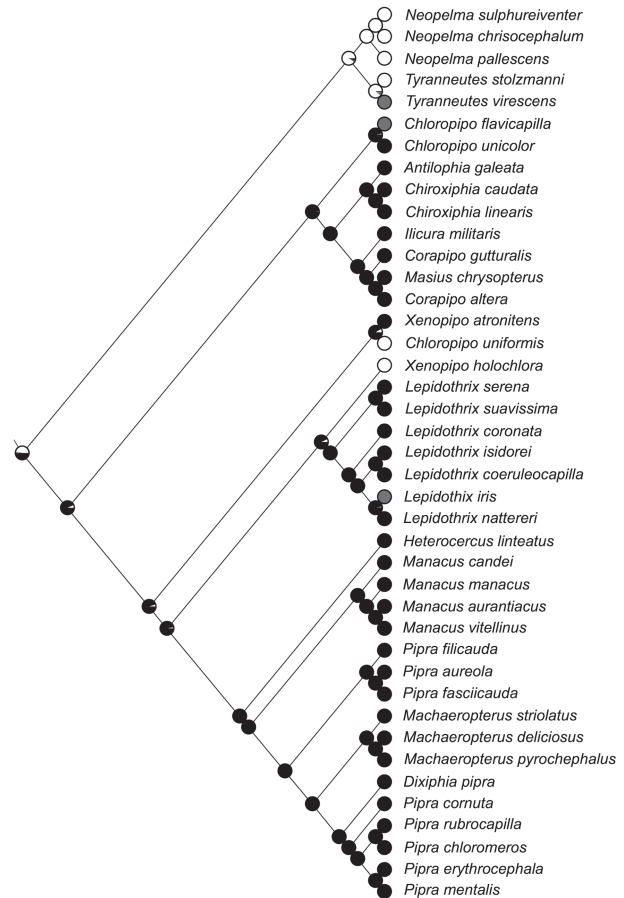

Figure 1. Reconstruction of ancestral states of sexual dichromatism in manakins (Pipridae) and five outgroup taxa (*Neopelma* and *Tyranneutes* spp.), mapped onto the molecular phylogeny of Ohlson et al. (2013) and determined using a maximum likelihood method. Dichromatism states are coded as: white = sexes are monochromatic from a human's perspective; gray = sexes are nearly monochromatic (sexes are similar in coloration but differ in shade or differences are restricted to a single part of the body); black = sexes are dichromatic. Colors in pie charts indicate the relative likelihood of different ancestral states at each node.

The function correctly sexed 80% of the 10 individuals used to validate the model; one of the five individuals of each sex was misclassified.

Differences in plumage reflectance between sexes and subspecies

There were few significant differences between sexes in plumage brightness, hue, or chroma; none was significant after Bonferroni correction (Supplementary material Appendix 2, Table A1). In contrast, there were highly significant differences in plumage spectra between the *holochlora* and *litae* subspecies (pooling sexes for each subspecies, given the lack of sexual dichromatism; Supplementary material Appendix 2, Table A1). Multivariate analyses using PCA revealed a similar pattern where subspecies, but not sexes, were differentiated in PC space, especially in axes that explained most of the variation (Fig. 3). The LSU data showed some evidence for sex differences on the lower PCs, but this pattern was not significant after Bonferroni correction and was
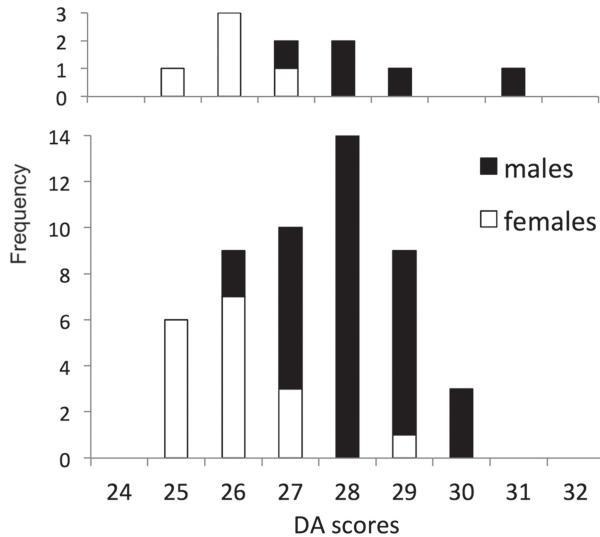
Figure 2. Scores of a discriminant analysis differentiating males (n = 39) and females (n = 22) of western green manakins *Xenopipo holochlora litae* based on seven morphological variables; the upper histogram shows scores of additional 5 males and 5 females used to validate the model. The discriminant analysis model was able to sex green manakins with 84% of accuracy, but there is considerable overlap on scores received by males or females.
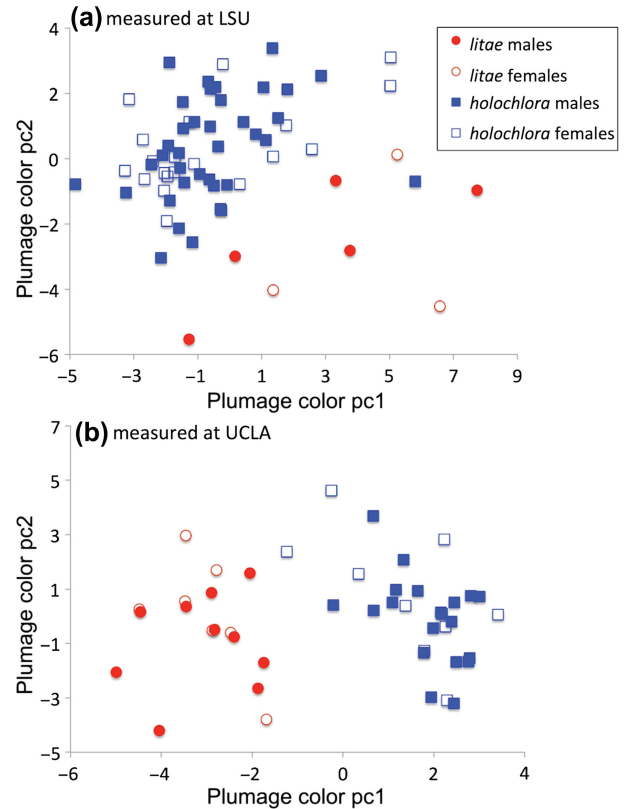

Figure 3. Scores for the two main axes of principal component analyses describing plumage color of male and female green manakins of two subspecies (*Xenopipo holochlora holochlora* and *X. h. litae*) as measured at two different institutions, (a) LSU and (b) UCLA. There are marked differences between subspecies but not between sexes.

not replicated in the UCLA data (Supplementary material Appendix 2, Table A1). Interpreting these axes using variable loadings (Supplementary material Appendix 2, Table A2 and A3), for the UCLA data PC1 (26% of variation explained) generally described a trade-off between brightness and hue, on the one hand, and chroma on the other, for most plumage patches. PC2 (15%) described hue and chroma of the bill, breast, belly, crown, and chin. For the LSU data, PC1 (29%) described a trade-off between chroma and hue, on the one hand, and brightness on the other, while PC2 (13%) described hue of the crown, back, tail, wing, and breast. In general, these reflectance measures indicate that *litae* has more pigmented plumage because it has higher chroma (more saturated color) and less brightness (more saturated colors reflect less light).

Adoption of an avian visual model produced qualitatively similar results. The sex difference disparity value was statistically significant ($K = 0.003$, $p = 0.016$), but below the $K = 0.01$ threshold for color differences to be perceived by birds. K values were still below this threshold if sex differences were tested separately by subspecies (*holochlora* $K = 0.0086$, $p = 0.0013$; *litae* $K = 0.0046$, $p = 0.06$). On the other hand, the two subspecies presented color disparity well above the threshold of detection ($K = 0.039$, $p < 0.0001$) and just below the threshold of being easily distinguishable to the birds (i.e. $K = 0.05$). A posteriori analyses of distance revealed that most patches differed in reflectance between subspecies (crown, back, tail, wing coverts, and breast feathers).

Behavior

We found 27 active nests of the western green manakin, of which 21 were successful in fledging young. Nesting was concentrated in two periods, between the months of September and November and between February and May,

corresponding to the dry and rainy seasons, respectively. Over 50 h of observation on these nests revealed that only one individual, presumably the female, builds the nest, incubates the eggs and feeds the nestlings; we were able to ascertain this despite the fact that we did not always have the focal nesting birds individually marked, since we never saw two individuals close or at an active nest at the same time, and banded individuals at nests were always identified as females, never males.

We did not find any evidence for lekking behavior during > 600 h of radio-tracking, focal observations and opportunistic observations. Males were never observed in aggregations or engaging in sexual displays, and only rarely vocalized within hearing or sight distance from each other. Rather, our observations suggest that males hold solitary territories. We did not find any evidence for pair bond formation, and most male territories were centered in upland areas away from creeks and rivers, whereas all nests were located along waterways. In sum, the population of green manakins at Bilsa does not form classical or exploded leks, and it appears unlikely that females nest inside male territories.

Discussion

Manakins have been the subject of intensive behavioral study for decades (Snow 2004 and references herein) and

have provided a valuable focal group for evolutionary (Cheviron et al. 2005), ecological (Durães et al. 2007), and neurophysiological (Fusani et al. 2007) research. Most studies have concentrated on the 'showy' species, in which highly ornamented males engage in elaborate sexual displays at leks. Yet, exactly because of the fact that they are outliers in the clade, the drab manakin species may provide unique opportunities for understanding the ultimate and proximate causes of sexual dimorphism. This study confirms previous suspicions that lekking behavior is absent in the green manakin (Prum 1994), suggesting that this species may serve as an 'exception that proves the rule' that mating systems are a major evolutionary force shaping patterns of sexual dimorphism (Payne 1984, Dunn et al. 2001).

Size dimorphism exists in green manakins, with males being larger in body size, but it is weak, with considerable overlap between the sexes. This is not necessarily surprising, as most manakin species present little dimorphism in size, which has been attributed to the agility required for the elaborate flight displays of males (Payne 1984, Oakes 1992). However, it seems that green manakins have reduced size dimorphism even compared to other (dichromatic) manakin species. For example, Ryder and Durães (2005) used similar methods to ours to investigate size dimorphism in the wire-tailed manakin *Pipra filicauda* and found that the overall discriminatory power of morphometric variables was higher for this strongly dichromatic manakin than for green manakins (94 vs 84%), suggesting that monochromatic manakins may have sexes that are structurally more similar as well.

Interestingly, both Ryder and Durães (2005) and the present study showed that, despite males in both species being generally larger than females, females have larger bills, suggesting that different body parts may be under different selection regimes in each sex. We see two possible, non-mutually exclusive causes for this pattern. First, males may be under selection for more slender bills that optimize song production (smaller beaks can produce faster songs and broader frequency bandwidths, Podos 2001). Green manakin vocalizations are infrequent and inconspicuous (unpubl.; Snow 2004), yet it is possible that this pattern was selected in other manakins and simply conserved in this species. Alternatively, broader and larger bills may be selected in females for foraging optimization. Manakins are primarily frugivores, but also incorporate arthropods in their diet (Fair et al. 2013), and the relative importance of fruits and arthropods may differ between sexes (Buitrón-Jurado 2008). In particular, female manakins, which provide all the parental care, feed young chicks heavily with arthropods (PM and JK unpubl.).

Between the two sub-species isolated by the Andes mountains, there was well-defined divergence in plumage coloration, which may be indicative of incipient speciation (Campagna et al. 2012). Within each subspecies, however, sexual dichromatism was virtually nonexistent. This is perhaps even more surprising given how widespread cryptic dichromatism was shown to be among putatively monochromatic passerines (Eaton 2005, 2007). The fact that lekking behavior was lost in green manakins suggests that relaxation of sexual selection pressure on males promoted their change to a female-like drab coloration, whose production may bear lower physiological costs than bright plumage (Hill 1996, Huggins et al. 2010) and/or be better for predation avoidance (Promislow et al. 1992). All eight recognized species of *Lepidothrix*, the sister genus of *X. holochlora*, are dichromatic and lek-breeders, but dichromatism is reduced in several of them (*L. iris*, *L. villasboasi*, some subspecies of *L. coronata*; Snow 2004). Interestingly, *Lepidothrix* spp. also present relatively simple sexual display repertoires compared to other manakins (Prum 1990, Anciães et al. 2009, Durães 2009), suggesting that sexual selection may have been generally relaxed in the *Xenopipo–Lepidothrix* clade, and reached its low in the monochromatic, non-lekking green manakins. This is supported by the observation that male reproductive skew increases with display complexity across manakin species (B. Loiselle pers. comm., RDB et al. unpubl.). Yet, currently there is no data on reproductive skew among male green manakins that provides a direct measure of the intensity of sexual selection in this species.

Traditionally, sexual dimorphism has been assumed to result chiefly from directional selection on increased male ornamentation, as documented in the context of mating systems that exert strong sexual selection on males (Oakes 1992, Lislevand et al. 2009). More recently, a growing body of work has made clear that changes in female plumage can also be a major factor underlying patterns of dichromatism in birds (Burns 1998, Hofman et al. 2008, Friedman et al. 2009, Johnson et al. 2013, Price and Eaton 2014), calling into question the use of sexual dichromatism as a proxy for the intensity of sexual selection acting on males. The two main situations in which this would be true, however, do not seem to apply to manakins. The first one are cases in which reduced sexual dichromatism arises from females becoming ornamented like males, suggesting that sexual selection is acting on both sexes or that changes in females are correlated with changes in males (Hofmann et al. 2008, Price and Whalen 2009). Female manakins, however, are without exception unornamented. The second situation is when changes in the degree of sexual dichromatism can be explained by other factors rather than sexual selection, such as migratory behavior (Friedman et al. 2009) or differences in ecological pressures (Johnson et al. 2013). Yet, all manakins are non-migratory, and both dichromatic and monochromatic species commonly coexist in the same habitat. As such, while we recognize that this may not be the case with all bird clades, sexual selection on males remains the most likely factor underlying the evolution of sexual dichromatism in manakins.

Bird plumage color is a highly labile trait (Price and Birch 1996) and there is no a priori reason to expect that gains of sexual dimorphism would be any more common than losses over evolutionary time. Yet, cases of decreased male elaboration, and consequent loss of dimorphism, associated with weakened sexual selection seem to be rare in birds, and remain poorly understood (Lislevand et al. 2009). Comparative and species-level studies addressing the evolutionary and life history correlates of monomorphic species with dimorphic ancestors are a powerful yet still relatively under-utilized tool for understanding the processes underlying interspecific phenotypic variation. In the present study, we show that reductions in sexual dichromatism occurred independently at least two, and maybe as much as five, times among

manakins. We predict that, as in the green manakin, lekking has been lost in these other species with reduced or absent sexual dimorphism (olive manakin *C. uniformis*, yellow-headed manakin *C. flavicapilla*, and potentially some *Lepidothrix* species). We urge focused study on the life histories, mating systems, and direct measures of sexual selection (e.g. male reproductive skew) on these species, as well as some of their closest dimorphic but less-known relatives (e.g. jet manakin *C. unicolor*, black manakin *Xenopipo atronitens*).

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