

Dancing in the rain: selective drivers of variability in Neotropical manakins

by

Elsie Hulda Shogren

B.S., Cornell University, 2012

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

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Division of Biology  
College of Arts and Sciences

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## **Abstract**

The overarching goal of this dissertation is to understand how natural and sexual selection interact to drive trait and behavioral evolution. Under challenging abiotic conditions, natural selection is expected to constrain sexual selection, resulting in evolutionary tradeoffs in behavior, morphology, and genetics. In the tropics, precipitation is the main axis of climatic variability, but relatively little is known about the functional relationships between rain and endotherm biology. I focus on how precipitation influences Neotropical birds at multiple levels of biological organization from macroevolutionary patterns across clades to individual behavior within populations. In manakins (Pipridae), a family of sexually-selected Neotropical birds, males perform elaborate courtship displays. Despite consistency of mating system, the direction of sexual size dimorphism (males larger or smaller than females) varies among species. I determined the relative importance of abiotic environmental selection and sexual selection associated with courtship display drove patterns of sexual size dimorphism across 22 species of manakin. Males tended to weigh less than females in species where courtship display involved more aerial elements, suggesting that sexual selection for agility has shaped body size in these species. However, in species found in rainier environments, males had longer wings than females indicating that abiotic constraints also affect morphological evolution in this clade. These types of macroevolutionary patterns are likely shaped by associations between demography and local environmental variation. Consequently, I tested the prediction that inter-annual variation in rainfall influenced estimates of apparent survival using a seven-year capture-mark-recapture dataset for seven Neotropical montane forest bird species. The response to rainfall varied among species; apparent survival decreased following years of heavier rain in three species and increased in two species. Thus, demographic effects of annual precipitation are contingent upon

other aspects of species' ecology and life history. Reduced annual apparent survival may disproportionately limit the strength of sexual selection in long-lived species in which age-graded social hierarchies determine reproductive success. Elevated mortality can reduce reproductive skew by increasing turn-over of dominant individuals resulting in more males gaining opportunities to reproduce. To link abiotic selection to reproductive skew, I sampled White-ruffed Manakins (*Corapipo altera*) at seven sites varying in precipitation regime. Among populations, reproductive skew, measured by the ratio of nucleotide diversity on the Z chromosome relative to autosomes ranged from 0.53 to 0.56. Reproductive skew was lowest in the populations subject to high and relatively aseasonal rainfall. This suggests that the intensity and timing of precipitation can constrain sexual selection and shape the genetic diversity of a population. Population-specific sources of selection could also influence the stability and scope of male interactions within a population. Male White-ruffed manakins display at sites clustered in "leks." Individual investment in display behavior is strikingly variable, and males interact frequently on their own and nearby sites. To test whether competition, cooperation, or individual quality drive variation in male behavior, I manipulated the social environment by both increasing acoustic signaling and by temporarily preventing nearby males from displaying. Focal males reduced their investment in vocalization when the acoustic signal was experimentally increased, and females visited focal logs more frequently when nearby logs were covered, but other behaviors remained unchanged. These results are consistent with the hypothesis that males cooperate to advertise display sites, and that likely, condition or quality underlies variation amongst males in other display behaviors. The dissertation as a whole reveals the importance of abiotic, environmental context in studying and interpreting the individual, population-level, and species-level patterns of sexually selected behaviors and morphology in Neotropical birds. By

linking ecological abiotic constraints to the evolutionary trajectories of tropical organisms, this dissertation highlights the complex interactions of natural and sexual selection in the evolution of some of the tropics' most charismatic animals.

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## **Dedication**

To Gram and Grandpar. Thank you for instilling a sense of wonder, a love of learning, and a desire to see the world.

## Chapter 1 - Introduction

The diversity of organisms in the world are a testament to the power of the evolutionary processes that have resulted in such fascinating forms. Despite steady advances, disentangling the effect of multiple selective pressures shaping organisms is difficult (Maan and Seehausen 2011). The overarching theme of this dissertation is an examination of how two core evolutionary processes interact with and constrain one another. Sexual selection is a powerful evolutionary driver of morphology and behavior, because individuals bearing certain traits produce more offspring (Andersson and Simmons 2006, Seddon et al. 2013). However, sexual selection operates against the pervasive background of natural selection; when naturally-selected reductions in fitness outweigh the benefits of sexually-selected traits or behaviors, natural selection will limit the strength of sexual selection (Kokko et al. 2002). While this concept is frequently applied to extreme expression of discrete traits, natural selection is a constant selective pressure that is always expected to have some bearing on the strength of sexual selection (Liker and Székely 2005, Cornwallis and Uller 2010). Through this dissertation I aim to shed light on how natural selection constrains and interacts with sexual selection at multiple biological levels.

The tradeoffs between fitness costs and benefits exerted by natural and sexual selection are especially important in species with mating systems which allow for high variance in reproductive success. The traits associated with reproductive behavior in these systems are a rich area of research, and often there are dramatic differences in among species, populations, and individuals in their investment and expression of sexually-selected traits even when the strength of sexual selection might be expected to be consistent and directional. This surprising variation may be due to the continuous influence of natural selection and limitations imposed by

environment and abiotic conditions (Candolin et al. 2016). It is therefore imperative that studies of sexual selection acknowledge the ecological context in which organisms are seeking mating opportunities (Twiss et al. 2007, Miller and Svensson 2014). By incorporating abiotic natural selective constraints in studies of sexually selected traits and behaviors, we can gain a more complete understanding of the evolutionary processes generating such remarkable biodiversity.

The tropics are a hotspot of biodiversity and selection via biotic interaction has long been the focus of studies in this region (Mittelbach et al. 2007). Due to mild year-round temperatures, abiotic sources of selection have not been viewed as important in the tropics relative to the temperate zone where seasonality in temperature is extreme. However, precipitation is highly seasonal in most tropical regions, and rainfall regime underlies much of the variation in vegetation composition, structure, and productivity throughout the tropics. As such, it is beginning to be recognized as a potentially powerful source of natural selection (Boyle et al. 2020 *in press*). In particular, studies of avian demography, development, and physiology have documented responses to both increased precipitation and prolonged dry seasons (Blake and Loiselle 2015, Brawn et al. 2017). Variation in demography and fitness associated with rainfall can influence individuals' investment in pursuing mating opportunities. Precipitation is therefore relevant to understanding constraints on sexual selection in the tropics. To date, integration of precipitation as an abiotic selective force in studies of sexual selection has been lacking.

Manakins (family Pipridae) are a clade of Neotropical birds well known for traits and behaviors resulting from sexual selection. Males perform courtship displays and have highly variable reproductive success while females care for young. Although this lek mating system is ubiquitous among species in Pipridae, variation in display-associated behavior also suggests variation in the strength or nature of sexual selection across the clade (Prum 1990). In addition,

habitat preferences vary within and between species, from wet to dry, montane to lowland forests (Kirwan and Green 2011). This variation in abiotic natural selection potentially constrains the scope of sexual selection in manakins, explaining some of the species-, population- and individual-level differences in courtship behaviors, social interactions, and display investment. Indeed, recent research has attributed a critical role to precipitation patterns in shaping behavior and demography of several manakin species. For example, in Amazonia, Wire-tailed manakin males had higher estimates of apparent survival and were in better condition following dry El Niño years than wetter La Niña events (Ryder and Sillett 2016). In Panama, Lance-tailed manakins that hatched in wetter, La Niña years developed more external lesions from insect parasites, reducing their likelihood of fledgling. However, those that did successfully fledge were more likely to recruit to the population the following year (Jones and DuVal 2019). Meanwhile, chicks hatched in drier El Niño years had higher growth rates (Jones and DuVal 2019). Variation in precipitation clearly plays a role in shaping individual fitness and population demography of manakins, and the consequences of this source of natural selection for sexually-selected traits and behaviors remains unclear.

A species in which precipitation influences physiology and fitness is the White-ruffed manakin (*Corapipo altera*). *Corapipo altera* responds negatively to temporal increases in rain. During drier periods of the year, males display for females in montane tropical rainforests. However, during heavy rainfall in the non-breeding season, many males migrate to lower elevations (Boyle et al. 2010). When those males return in the subsequent breeding season, females are less likely to mate with them (Boyle et al. 2011). Additionally, physiological assays provide evidence that storms incur short-term fasting (Boyle et al. 2010). This indicates that heavy rainfall limits the ability of these small birds to access their food although it is plentiful

(Boyle 2010). Thus, storms and rainfall are an environmental factor that directly and indirectly influences the behavior and physiology of a strongly sexually selected bird. Environmental constraints on sexually selected behavior in this species may have consequences for individual fitness and inter- and intra-population differences in behavior of individuals at display sites as males balance the physiological costs incurred by precipitation.

My dissertation aims to elucidate when and how the natural selective forces of precipitation and other features of the abiotic environment constrain the strength of sexual selection in tropical birds. I tackled this question at multiple levels of biological organization, from the community and clade to population and individual levels. Although I test more specific hypotheses and predictions relevant to each level, my chapters collectively advance our understanding of how interacting selective pressures drive evolutionary processes.

### ***Chapter 2 – Dancing drives evolution of sexual size dimorphism in manakins***

Variation in morphology across a clade provides an opportunity to test predictions of how natural and sexual selection have interacted to shape the species-level traits within that taxonomic group. In many animals, males and females differ in size. Evidence exists for both sexual selection and environmental or natural selective constraints influencing patterns of size dimorphism in vertebrate taxa. Surprisingly, the manakin clade comprises both species in which males are larger than females and species in which males are smaller than females. Additionally, the displays of male manakins range from simple hops to complex aerial maneuvers, while the environment in which they perform their displays also varies widely in elevation and precipitation. I tested whether patterns of sexual size dimorphism are associated with sexual selection for agility and/or environmental constraints in 22 species of manakin, using a phylogenetic framework. I found that males tended to be smaller than females in species with more aerial display, likely due to sexual selection for agility. However, dimorphism in wing length was more strongly associated

with environmental variables. Thus, within a single species, different aspects of morphological dimorphism are shaped by alternative sources of selection; sexual selection via courtship and natural selection due to the environment.

### ***Chapter 3 – Apparent survival of tropical birds in a wet, premontane forest in Costa Rica***

Macroevolutionary patterns can be driven by evolutionary responses to local environmental variation. Mortality is the putative mechanism by which rain acts as a source of selection, but we have very few data with which to evaluate that crucial link. Thus, characterizing demography and population dynamics is a critical first step to understanding how environmental variables influence life history and behavior. To test the prediction that rain influences apparent survival, I used a seven-year capture-mark-recapture dataset from a tropical avian community in an exceptionally rainy montane forest. Of the seven species for which demographic estimates could be calculated, apparent survival increased in wetter years in two species, and decreased in three species. The variation in responses within an avian community emphasizes the probability of species-level adaptation to different precipitation regimes and is surprising given the exceptionally rainy conditions at this site. This chapter therefore highlights the potential for precipitation to play a context-specific role in shaping life history and evolution of species in the tropics.

### ***Chapter 4 – Genetic evidence of environmental constraints on the strength of sexual selection across populations of a Neotropical bird***

When precipitation influences demography of populations (e.g., via reducing apparent survival), the relative strength and importance of sexual selection may be diminished due to these environmental limitations. A key measure of the strength of sexual selection is reproductive skew, i.e., the degree of variance in reproductive success of males. Directly measuring degree of reproductive skew to determine the importance of environmental constraints on sexual selection

is logistically difficult via methods that rely on direct measures of male reproductive success through paternity analyses. To overcome this challenge, I adapted an indirect measure of reproductive skew used previously in only a few inter-specific studies of sexual selection in birds. Because male birds carry two copies of the sex chromosome (Z) whereas females only carry one, reductions in male effective population size associated with reproductive skew disproportionately reduces genetic diversity of the Z chromosome relative to autosomes in a population. I predicted that population-level variation in male reproductive skew would manifest as differences in the relative genetic diversity of Z chromosomes and autosomes because the fewer males that co-opt reproductive opportunities, the lower the effective population size and genetic diversity of sex chromosomes. Thus, the ratio of sex chromosome to autosomal genetic diversity (Z/A) is an indirect metric of reproductive skew and the strength of sexual selection within populations. In *Corapipo altera* I tested the prediction that reproductive skew would be constrained by heavy precipitation in all or some seasons of the year, sampling three sites on the Caribbean slope of Costa Rica and four on the Pacific slope. Reproductive skew was lowest at sites subject to heavy rainfall throughout most of the year. This suggests that natural selection in the form of consistently high year-round rainfall exerts a constraint on the scope for sexual selection in this species, potentially acting via lower survival and higher turnover of reproductively successful males. To understand how underlying genetic diversity might influence the Z/A diversity metric, I also quantified strong genetic differentiation of individuals sampled on different slopes, although whole-genome nucleotide diversity was similar at all sites. Thus, local abiotic and environmental conditions can have important effects on the evolutionary trajectory of a population.

***Chapter 5 – Spread the word: male manakins cooperate with neighboring competitors to advertise presence of display sites***

White-ruffed manakins are a long-lived species and social hierarchies and relationships among males are critical components of display behavior. Environmental effects on demography may also influence the stability of male-male interactions and their behavior at display sites. Within populations, males vary widely in lek attendance and rates of display. Understanding the basis of individual variation in male behavior within a population may help us understand how demography and behavioral evolution are related. I manipulated the social environment at display sites in two experiments to test whether individual variation was driven by cooperative or competitive interactions among males, or by inherent variation in individual male quality. Males decreased their vocalization effort in response to artificially increased manakin acoustic signal, suggesting that they cooperate in advertising the presence of a display area to prospective female visitors, minimizing individual effort. When I prevented displays at neighboring sites, female visitation to the focal display site increased, despite rates of other behaviors not changing. These results are consistent with the hypothesis that males cooperate with neighbors to advertise the presence of their display sites, but female assessment and preference is based upon individual differences in male quality. The social stability necessary to support the evolution of cooperative male-male interactions is a key factor when considering how demographic variation is influenced by abiotic conditions.

## ***Chapter 6 – Conclusions and implications***

In my final chapter, I discuss the overall conclusions of my dissertation. I consider the implications my findings have for understanding how variation in selection and environment can influence evolution at multiple biological levels. Finally, I emphasize novel contributions of this dissertation and identify important areas for future research.

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## **Chapter 2 - Dancing drives evolution of sexual size dimorphism in manakins**

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## **Abstract**

Body size mediates life history, physiology, and inter- and intra-specific interactions. Within species, males and females frequently differ in size, reflecting divergent selective pressures and/or constraints. Both sexual selection and sex-related differences in environmental constraints or life-history trade-offs can drive sexual size dimorphism, but the causes of dimorphism are rarely tested empirically. Manakins (Pipridae), a family of Neotropical birds comprising ~50 species, exhibit both male- and female-biased size dimorphism. Males perform courtship displays ranging from simple hops to complex aerobic manoeuvres. Manakins are also distributed across strong environmental gradients of precipitation and elevation. We tested associations between sexual size dimorphism and both (a) sexual selection for agility and (b) environmental constraints by analysing morphological, behavioural, and environmental data for 22 manakin species in a phylogenetic framework. Sexual dimorphism in mass was most strongly related to agility, with males being lighter than females in species performing more aerial display behaviours. However, wing length dimorphism was more strongly associated with environmental variables, suggesting that different sources of selection act divergently on different aspects of body size. This combination of results highlights both the strength of sexual selection in shaping morphology—even atypical patterns of dimorphism—while demonstrating the importance of abiotic sources of selection and ecological consequences of body size evolution.

## Introduction

Body size is fundamental to an animal's life history, physiology, and ecology, influencing everything from the speed of cellular reactions to the environments in which it can live (Blanckenhorn 2000, Brown et al. 2004, Gardner et al. 2011). Shifts in body size within lineages are often associated with differences in habitat, foraging strategy, and distribution (Olson et al. 2009, Baker et al. 2015). Even within species, size can vary dramatically, however. Intraspecific niche-partitioning may lead to sexual dimorphism just as it shapes interspecific differences; males and females may differ in size to reduce competition for food by adopting divergent foraging strategies (Pearson et al. 2006, Pérez-Camacho et al. 2018). Alternatively, fecundity selection can lead to sexual size dimorphism when larger females are capable of producing more or higher quality offspring or can better tolerate environmental conditions associated with sex-linked behaviours (Fokidis et al. 2007, Scharf and Meiri 2013). Despite strong natural selection on body size, sexual selection can also drive sexual size dimorphism (Blanckenhorn 2005). In birds and mammals sexual selection typically results in males that are larger than females (Lindenfors et al. 2007, Székely et al. 2007). Selection for male-biased sexual size dimorphism may be due to direct competition between males for access to mates and advantages conferred by being larger and heavier (Blanckenhorn 2005, Lindenfors et al. 2007). Alternatively, females may choose males based on size-related traits (Hudson and Fu 2013, Vanpé et al. 2017). When sexual selection is strong, males are typically larger than females; the reverse is rare but is known to occur in species under selection for speed or agility (Székely et al. 2007, Soulsbury et al. 2014).

The morphological, behavioural, and reproductive diversity of birds is ideal for testing whether environment or mating success is more strongly associated with interspecific variation

in sexual size dimorphism. When mating systems and foraging strategies are similar among closely related taxa, the direction of sexual size dimorphism is usually also consistent (either male-biased or female-biased; Dale et al. 2007). However, Neotropical manakins (family Pipridae) are an intriguing exception, containing both species in which males are the larger sex, and species where females are larger. Thus, this family provides an excellent opportunity to test hypotheses regarding the evolution of sexual size dimorphism.

Manakins are a family of small-bodied (9 – 25 g) suboscine passerines distributed throughout the Neotropics. All ~51 species are mainly frugivorous and are found exclusively in tropical forests (Anciães and Peterson 2009, Kirwan and Green 2011). Many species inhabit hot lowland forests, but some are distributed up to > 2000 meters above sea level. They also live in habitats that vary dramatically in rainfall, from dry savanna woodlands to incredibly wet montane forest. Manakin research has largely centred around the astounding species-specific mating displays performed by males (Prum 1990, Fusani et al. 2014, Villegas et al. 2018). Most species have lek mating systems (Höglund and Alatalo 1995), in which males display at clustered display sites (Prum 1990, Kirwan and Green 2011). Males provide no parental care and derive all reproductive success from their ability to attract and copulate with females assessing their displays (DuVal and Kempnaers 2008, Barske et al. 2015). Reproductive skew among displaying males is driven by female choice; male-male competition has resulted in the evolution of striking behaviours, cooperative alliances, and the maintenance and defence of display sites (McDonald 1989, Ryder et al. 2009, Jones et al. 2014). The displays themselves are diverse and range from exaggerated postures which accentuate certain plumage patches to high speed aerial dives and flips too rapid for the human eye to see (Prum 1990, Lindsay et al. 2015). Some displays involve mechanical sounds or “sonations” produced through rapid wing or body

movements, either while perched or mid-flight (Prum 1998). In some species, socially dominant alpha males are accompanied by subordinate males in coordinated displays. In such cases, males generally adhere to strict social hierarchies and only alphas have the opportunity to mate (DuVal 2007, Jones et al. 2014, Boyle and Shogren 2019). Previous studies of sexual size dimorphism in the family demonstrated that male manakins tend to be smaller than females in small species and larger than females in large species, following Rensch's rule of allometry (Payne 1984). Payne (Payne 1984) also discovered that wing length and body mass are not correlated in males, although they are in females, suggesting that the direction of sexual selection may vary by sex and/or trait. Thus, the causes of the unusual variation in sexual size dimorphism in manakins remains unknown, especially because previous work did not account for shared evolutionary history in the analysis of size dimorphism.

The importance of display for male fitness suggests that sexual selection may drive patterns of sexual size dimorphism. Although sexual selection typically results in larger males than females, some behavioural traits can result in smaller males being favoured (Blanckenhorn 2005). For example, birds with lower mass relative to size are more manoeuvrable and agile due to lower wing loading and less energy being required to perform acrobatic displays (Altshuler and Dudley 2002, Dudley 2002). Consistent with this, female Golden-collared Manakins (*Manacus vitellinus*) preferentially mate with males that perform certain display behaviours more rapidly (Barske et al. 2011). Thus, if sexual selection for agility drives size dimorphism in manakins, we predicted that males would be lighter than females in species with more aerial, acrobatic displays.

As small endotherms with high energetic demands, manakins are also subject to strong abiotic selective pressures driven by elevation, precipitation, and climatic seasonality which

could shape patterns of sexual size dimorphism. Environmental constraints and differences in male and female behaviours (e.g., aerobic display vs. parental care) may influence size-dependent responses to climatic conditions. In the tropics, temperature varies little over the year at a given locality but declines with increasing elevation (Janzen 1967, Clark et al. 2015). Additionally, heat tolerance and body size are correlated in birds because surface area to mass ratio and conductance increase with decreasing body size; the smallest birds must expend the most energy to maintain stable internal temperatures (Calder 1974, McKechnie and Wolf 2019). In colder environments, birds are likely under selection to conserve body heat, particularly during inactive periods such as incubation (James 1970). Thus, we predicted females would be larger than males in species inhabiting colder, high elevation environments. Conversely, larger males are expected to have higher heat tolerance (Barske et al. 2013), and we predicted that males would be larger than females in species living in hot, low elevations, especially in species that experience high metabolic rates during aerobically taxing displays.

The seasonality and quantity of rainfall are increasingly recognized as potent selective forces in the tropics, affecting survival and reproductive behaviour of many bird species (Brawn et al. 2017, Gaiotti et al. 2019). The frugivorous diet of manakins necessitates frequent foraging to maintain energy reserves (Witmer and Van Soest 1998), and at least one species (*Corapipo altera*) shows evidence of fasting and altitudinal migration in response to seasonal rain storms (Boyle et al. 2010). If fasting endurance constraints influence sexual size dimorphism, we predicted that males would be larger than females both in cold, high elevation environments and in more rainy and seasonal environments. Disproportionate selection on males could occur if increased energy stores are necessary for males to survive cold or rainy conditions while maintaining display sites (Boyle et al. 2011, Jones et al. 2014). Additionally, the propensity to

evolve aerobic display may be subject to abiotic constraints. Therefore, we tested whether species with more aerial displays were associated with specific environmental conditions. Furthermore, selection or constraints on female mass may be more important than selection on males in shaping patterns of sexual size dimorphism. Thus, we separately tested how female mass varied with the environment.

Avian body mass fluctuates depending on age, season, or time of day (Cucco and Bowman 2018, Sikora and Neubauer 2018). However, mass critically influences manoeuvrability and wing loading in agile displays, is largely composed of thermogenic muscle, and correlates with fat storage (Witter and Cuthill 1993, Dietz et al. 2007, Milbergue et al. 2018). Therefore, it provides a direct and relevant measure of sexual size dimorphism for testing the above predictions. We also tested whether less plastic metrics of dimorphism were associated with the same set of biotic and environmental selective pressures. Wing length affects flight ability, with shorter, rounder wings associated with more manoeuvrable flight but reduced endurance (Phillips et al. 2018). Thus, we predicted that males of species performing more aerobic displays would have shorter wings than females. Tarsus is a standard skeletal measure of size and in manakins it may be under sexual selection due to leaping display elements in some species (Prum 1990). Therefore, we predicted that male tarsus length would be larger relative to females in species with more aerobic displays. We collected morphological data for ~ half the species of Pipridae and used phylogenetically corrected analyses to test the above predictions.

## **Methods**

### **Data**

We collected measurements of mass (g), tarsus (mm), and wing length (mm) from individuals in definitive plumage and/or sexed by brood patch or molecular methods for as many species as

possible. Most individuals were measured during the breeding season when males display. We excluded data from the few females suspected to be carrying an egg in their oviduct because their weight was not representative of normal mass. We calculated the mean value of each metric for each sex, then calculated trait- and species-specific indices of sexual size dimorphism that scale symmetrically around zero (Lovich and Gibbons 1992, Smith 1999). When males were larger, this index is calculated as  $(\text{larger sex}/\text{smaller sex}) - 1$ . When females were larger, the index is calculated as  $-1 \times [(\text{larger sex}/\text{smaller sex}) - 1]$ . Thus, species with male-biased size dimorphism have positive index values whereas species with female-biased size dimorphism have negative index values.

We developed a metric of display agility for each species, based on comprehensive, peer-reviewed descriptions of display behaviour (Table 2.1). Modifying a previously-published display complexity score (Lindsay et al. 2015), in our agility score we allocated a point for each unique aerial behavioural element included in each species' display repertoire and summed up the points. These included such behaviours as leaps between perches, stylized flight patterns, and high-speed dives. Thus, behaviours during which males remained perched – e.g., bowing or fluttering their wings – did not contribute to the score. We considered aerial display elements performed by multiple males in coordination as well as aerial movements involving sonations to require an added degree of agility (Prum 1990, 1994, Lindsay et al. 2015). Therefore, we added an additional point for each of these coordinated or acoustic aerial behaviours and summed all points to calculate each species' total agility score.

To characterize the climatic niche of each species, we used locality data from natural history specimen records compiled by Anciães and Peterson (Anciães and Peterson 2009). We imported localities into ArcGIS (ESRI 2011) and obtained environmental values (averaged from

1970 – 2000) for each point from Worldclim bioclimatic surfaces (Fick and Hijmans 2017). We extracted 13 variables hypothesized to influence thermoregulation and/or fasting endurance: annual precipitation, precipitation seasonality (coefficient of variation of monthly totals), precipitation during the wettest, driest, warmest, and coldest months, annual mean temperature, diurnal temperature range, annual temperature range, maximum and minimum temperatures, and elevation. We averaged values for each variable by species for every locality record, and also included an absolute maximum for elevation because high elevations potentially represent the strongest constraints on thermoregulation and fasting endurance.

## **Analyses**

We conducted all analyses in R (R Core Team 2018, version 3.5.1). First, we assessed the degree and inter-specific variability of sexual size dimorphism among the three morphological metrics. To account for evolutionary relatedness of taxa, we corrected for non-independence of data using a well-resolved manakin phylogeny (Leite et al. *in review*). We reduced the dimensionality of the environmental variables for each species using phylogenetic principal components analysis in the package *phytools* (Revell 2012) to derive two principal components for subsequent analyses (Supplemental Table 2). We performed phylogenetic generalized least squares regression in the *caper* package (Pagel 1999, Orme et al. 2012). We used a maximum likelihood estimate of phylogenetic signal (Pagel's lambda,  $\lambda$ ), thereby allowing the phylogenetic correction in the regression model to match the strength of the phylogenetic signal (Freckleton et al. 2002). We evaluated a set of *a priori* models to test predictions regarding the drivers of sexual size dimorphism. We constructed a candidate model set that included single factors of agility score and two principal components of environmental variables. We also evaluated models including additive and interactive combinations of agility score and environmental principal components.

We evaluated model sets using four different response variables: dimorphism in mass, dimorphism in tarsus length, dimorphism in wing length, and female mass (independent of male mass). Finally, to test whether aerobatic display is associated with certain environmental conditions, we analysed models in which agility score was the response variable while the environmental principal components and mass dimorphism were the predictor variables. We used Akaike's information criteria corrected for small sample sizes (AICc) in the package *MuMIn* to assess fit of models to the data, and considered  $\Delta\text{AICc}$  values of  $< 2$  competitive (Burnham and Anderson 2002). We also assessed Rensch's rule, plotting the relationship between male and female phylogenetically independent contrasts of the log mean values of each morphological trait (Abouheif and Fairbairn 1997).

## Results

We analysed morphological data for 2914 individuals representing 22 species in 12 different genera (Table 2.1). Our median sample size was 33 males and 29 females (male range: 2 – 615, female range: 2 – 334). We gathered mass data for all 22 species, wing measurements for 19 species, and tarsus measurements for 14 species (Table 2.1). Indices of mass sexual size dimorphism varied substantially, ranging from  $-0.16$  to  $+0.13$ . By contrast, wing dimorphism values ranged only from  $-0.04$  to  $+0.08$  and tarsus dimorphism ranged from  $-0.04$  to  $+0.10$  (Figure 2.1). In 10 species, females were heavier than males, but had smaller wing and tarsus measurements (Table 2.1). Scores for agility ranged from 0 (in species not known to display for females, eg., *Cryptopipo holochlora*), to 14 (in *Chiroxiphia lanceolata*, a species in which males perform complex cooperative aerial display manoeuvres; Table 2.1).

We reduced the 13 environmental variables to two principal components which collectively explained 72% of the variance (Table 2.2). Variables loading positively on the first

component (PC1; 44% of variance) related to temperature range (diurnal and annual) and mean elevation whereas precipitation in the coldest month and minimum temperature loaded negatively. Seasonality of precipitation variable loaded positively on the second component (PC2; 28% of variance) while the remaining precipitation variables loaded negatively.

Sexual size dimorphism in mass was best explained by the single main effect of agility score, carrying 47% of the model weight (Table 2.3). Consistent with the sexual selection hypothesis, males were generally smaller than females in species having more aerial display behaviours ( $\beta = -0.010$ , 95% CI:  $-0.021, 0.001$ ; Figure 2.2, 95% confidence intervals calculated using R package *evomap*, Smaers). The difference between sexes in wing length was negatively associated with PC2 (Table 2.3); males had longer wings than females in less seasonal and wetter environments but shorter wings in drier and more seasonal environments ( $\beta = -0.007$ , 95% CI:  $-0.012, -0.001$ ; Figure 2.3). All other wing size dimorphism models were  $>2.5$  AICc below the top model. Neither tarsus dimorphism nor female mass were clearly correlated with the variables we tested; both metrics were equally well explained by each of the single effect models (agility score, PC1, and PC2; Table 2.3). Using agility score as the response variable, multiple models were competitive (Table 2.3). Additive, interactive, and single effects of sexual size dimorphism and PC1 were present in all of the four models within  $2 \Delta AICc$  units. Negative relationships between agility score, sexual size dimorphism and PC1 suggest that agility score is lower in species with male-biased size dimorphism inhabiting colder, higher elevation environments (Figure 2.4). The slope of the relationship between phylogenetic independent contrasts of log male and log female values was  $< 1$  for all morphological traits, indicating that as body size increases, male-biased sexual size dimorphism becomes more pronounced, as

predicted by Rensch's rule (mass:  $\beta = 0.831$ , 95% CI: 0.683 – 0.979; wing:  $\beta = 0.880$ , 95% CI: 0.787 – 0.973; tarsus:  $\beta = 0.849$ , 95% CI: 0.705 – 0.992; Figure 2.5).

## Discussion

Manakins are subject to strong sexual selection, with female choice and male-male competition directly and dramatically influencing reproductive success of males. The variability of sexual size dimorphism across the clade is therefore surprising. In most lekking or sexually-selected avian species, males are significantly larger than females and use display behaviours to further accentuate their size (e.g. sage grouse, turkeys, peacocks; (Höglund and Alatalo 1995)). We tested whether sexual selection for agility (via either female choice or male-male competition), or environmental constraints (acting via thermoregulation or fasting endurance) explained components of body size dimorphism in the manakin clade. Agility score was the best predictor of sexual dimorphism in mass, with females tending to be heavier than males in species performing more aerial display, consistent with sexual selection driving female-biased dimorphism in some species in this clade. However, many manakin displays do include postures in which they “inflate” their throat feathers, potentially appearing larger (Prum 1990). Thus, the negative relationship between display agility and sexual size dimorphism in mass may represent a trade-off in response to sexual selection where species are responding differentially to selection for larger vs. more agile males.

Agility itself was negatively related to both sexual size dimorphism and temperature/elevation. This suggests that while selection for agility is still clearly associated with selection for lighter males, species performing more aerobic displays also tend to be found in warmer, lower elevation environments. Female mass was not strongly associated with either the agility of males or the climatic variables we examined, despite exhibiting the same range of

variation as male mass. Dimorphism in wing and tarsus length varied much less than mass dimorphism, and tarsus dimorphism was not strongly associated with either agility or environment. However, sexual dimorphism in wing length did vary along climatic gradients, consistent with the environmental constraints hypothesis. In more rainy environments, males had longer wings than females. The relationships between male and female morphological traits are consistent with Rensch's rule – males tend to be larger than females in large species and smaller than females in small species.

Environmental variation influenced both degree of aerobic display and dimorphism in wing length, and the relationship between abiotic conditions and these variables requires further interpretation. Colder, higher elevation environments seem to constrain the evolution of aerobic displays, potentially due to thermoregulatory constraints that favour larger body sizes. In these species sexual selection for agility may trade-off with sexual selection for larger males. Rainy environments are associated with male-biased dimorphism in wing length. This result is surprising, as we would expect wing morphology to be related to agility in aerobic display movements. In fact, a previous study of five sympatric manakins observed that manoeuvrable and hovering flight displays were characteristic of species in which males had lower wing loading and longer hand wing index (Théry 1997). However, longer wing length in males may be the result of fasting endurance constraints. For example, males may undertake more direct or rapid flight to forage during or following rainfall. Three and possibly more species of manakin migrate altitudinally during the non-breeding season; in at least one of those species males are more likely to migrate than females (Boyle et al. 2010), and longer wings may be adaptive for such long-distance flights.

Despite the impressive level of taxonomic sampling we achieved, inferences about the drivers of sexual dimorphism are subject to some caveats. First, given that our hypotheses relating to thermoregulation and fasting represent immediate physiological challenges, we assumed that the traits we measured reflect selection imposed by current environmental conditions rather than historical sources of abiotic selection. Second, due to the availability of high-speed video for some but not all species, the accuracy of our agility score likely varies by species because some display manoeuvres occur too quickly for the human eye to detect. Additionally, our point-score system equates multiple different types of display behaviours and it is possible that the scoring does not reflect the relative difficulty of all behaviours (e.g., highly coordinated display). However, such issues would tend to reduce rather than magnify the biological signal in results; our methods represent a standardized, reproducible approach that could be expanded upon as new behavioural data becomes available.

This study leverages a large, field-collected morphological dataset and detailed behavioural information from a charismatic group of Neotropical bird to understand the evolution of sexual size dimorphism. We expand on previous studies of size dimorphism in manakins by incorporating a phylogenetic comparative framework, considering multiple axes of size dimorphism, and testing whether variation in environment constrains evolution of sexual size dimorphism (Mendenhall et al. 2010, Ribeiro et al. 2015). Our alternative-hypothesis-testing framework sheds light on the fact that although sexual selection on display is important for the evolution of sexual dimorphism in mass, other morphological differences are more strongly influenced by environmental constraints. Across many taxa, dramatic differences between the sexes are often attributed to male-male competition, female choice, or fecundity selection without considering alternative drivers of dimorphism. We observed that in many species, males

are lighter than females, while being the same size or slightly larger in tarsus and wing length (Figure 2.1). Thus, sexual selection does not always consistently drive sexual size dimorphism in the same direction. In this system, mass seems to be under stronger sexual selection than other aspects of morphology; using structural size (e.g., tarsus, wing length) to infer the strength of sexual selection would thus lead to erroneous conclusions. Degree of sexual size dimorphism should therefore only be used as a proxy for the strength of sexual selection when the selective forces shaping size dimorphism are well known and understood.

This and other studies of sexual size dimorphism provide insight into the selective forces that shape body size, a fundamental trait with far-reaching implications for a species' ecology and evolution. Even when sexual selection is the main driver of male reproductive success, body size evolution is still subject to environmental constraints that may shape morphology in unexpected ways. Considering the multiple evolutionary forces at play within and across taxa is critical to understanding how organisms may evolve in changing selective regimes and how body size itself may shape and be shaped by life history strategies.

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## Tables

**Table 2.1** Summary of data analysed for each species

Species	Agility Score	Mass SSD	Wing SSD	Tarsus SSD	♀ Mass (g)	Species mass (g)	N♀	N♂	Agility Score Source	Morphological Data Source
<i>Neopelma chrysocephalum</i>	1	0.088	0.079	0.033	15.04	16.17	9	56	(Davis 1948), (Snow 1961), (Alonso and Whitney 2003)	Ungvári
<i>Antilophia bokermanni</i>	2	0.024	0.020	0.030	20.42	20.64	37	29	(Gaiotti et al. n.d.)	Gaiotti
<i>Antilophia galeata</i>	1	-0.014	0.024	-0.025	19.10	19.02	15	6	(Marini 1992)	Gaiotti
<i>Chiroxiphia lanceolata</i>	14	-0.111	0.026	0.059	19.17	18.18	30	32	(Lindsay et al. 2015)	DuVal
<i>Chiroxiphia pareola</i>	11	-0.039	0.038	-0.021	18.95	18.71	6	3	(Lindsay et al. 2015)	White
<i>Ilicura militaris</i>	7	0.065	...	...	11.44	12.10	5	37	(Snow and Snow 1985)	Marini
<i>Corapipo altera</i>	11	-0.157	0.000	...	12.75	11.63	334	615	(Jones et al. 2014)	Boyle
<i>Corapipo gutturalis</i>	7	-0.145	0.030	-0.039	8.49	7.91	23	27	(Lindsay et al. 2015)	Stouffer
<i>Lepidothrix coronata</i>	10	-0.165	0.035	0.033	9.85	9.26	149	109	(Lindsay et al. 2015)	White
<i>Lepidothrix serena</i>	5	-0.054	-0.031	0.049	10.43	10.07	75	159	(Prum 1985), (Théry 1990)	Stouffer
<i>Cryptopipo holochlora</i>	0	-0.025	0.044	0.034	16.70	16.50	25	39	(Ribeiro et al. 2015)	Ribeiro et al. 2015
<i>Heterocercus aurantiivertex</i>	6	-0.008	0.031	-0.011	21.05	20.97	2	2	(Alonso 2000)	Ungvári
<i>Manacus candei</i>	7	0.047	-0.001	...	17.62	17.94	32	20	(Lindsay et al. 2015)	Boyle
<i>Manacus manacus</i>	5	0.021	...	0.105	16.65	16.90	6	17	(Snow 1962a), (Lill 1974)	Cestari
<i>Manacus vitellinus</i>	7	0.121	0.039	0.047	16.91	18.46	29	91	(Lindsay et al. 2015)	Barske
<i>Pipra fasciicauda</i>	6	-0.040	0.011	...	16.18	16.14	12	23	(Robbins 1983)	Scholer

Species	Agility Score	Mass SSD	Wing SSD	Tarsus SSD	♀ Mass (g)	Species mass (g)	N♀	N♂	Agility Score Source	Morphological Data Source
<i>Pipra filicauda</i>	7	-0.141	0.012	-0.005	15.57	14.33	121	216	(Schwartz and Snow 1978), (Prum 1985), (Heindl 2002)	Ryder
<i>Ceratopipra chloromeros</i>	7	-0.051	-0.023	...	17.18	16.82	107	77	(Tello 2001)	Scholer
<i>Ceratopipra erythrocephala</i>	4	-0.108	-0.036	-0.024	11.97	11.48	96	69	(Snow 1962b)	Stouffer
<i>Ceratopipra mentalis</i>	4	-0.039	-0.020	...	15.24	15.08	81	34	(Lindsay et al. 2015)	Boyle
<i>Ceratopipra rubrocapilla</i>	4	0.131	...	...	11.75	12.98	2	8	(Castro-Astor et al. 2004)	Anciães
<i>Dixiphia pipra</i>	10	-0.096	0.000	...	13.62	13.30	36	13	(Lindsay et al. 2015)	Boyle

Agility score = calculated score of species' agility; Mass, Wing, Tarsus SSD = calculated index of sexual size dimorphism for relevant morphological trait; ♀ Mass = female mass averaged for every species; N♀, N♂ = number of females and males for each species; Agility score source = literature describing display behavior which underlies agility score; Data source = author or source providing morphological data.

**Table 2.2** Phylogenetic principal components of environmental variables

<b>Environmental Variables</b>	<b>PC1</b>	<b>PC2</b>
Annual Precipitation	-0.47	-0.85 <sup>a</sup>
Precipitation of Wettest Month	-0.21	-0.58 <sup>a</sup>
Precipitation of Driest Month	-0.46	-0.79 <sup>a</sup>
Precipitation of Warmest Month	0.25	-0.90 <sup>a</sup>
Precipitation of Coldest Month	-0.87 <sup>a</sup>	-0.34
Seasonality of Precipitation	0.45	0.74 <sup>a</sup>
Annual Mean Temperature	-0.84 <sup>a</sup>	0.23
Maximum Temperature	-0.39	0.48
Minimum Temperature	-0.96 <sup>a</sup>	0.14
Diurnal Temperature Range	0.82 <sup>a</sup>	-0.18
Annual Range of Temperature	0.88 <sup>a</sup>	0.05
Mean Elevation	0.71 <sup>a</sup>	-0.16
Maximum Elevation	0.50	-0.55 <sup>a</sup>
<b>% variation explained</b>	<b>43.75</b>	<b>28.10</b>

Loading of environmental variables on phylogenetic principal components 1 and 2 (PC1 and PC2) Cumulative variance explained by PC1 and PC2 is 71.85%. Environmental variables contributing significantly (>0.5) to principal component denoted by <sup>a</sup>

**Table 2.3** Model results for each sexual size dimorphism variable, including all models within 2  $\Delta$ AICc units of top model

Response Variable	Model	$\Delta$ AICc	weight	$\beta$	95% CI	$R^2$
<b>Mass sexual size dimorphism</b>	Agility	0	0.52	-0.010	-0.021, 0.001	0.14
	PC2	0	0.56	-0.007	-0.012, -0.001	0.28
<b>Tarsus sexual size dimorphism</b>	PC1	0	0.30	-0.003	-0.011, 0.006	-0.05
	PC2	0.33	0.25	0.002	-0.007, 0.011	-0.08
	Agility	0.38	0.24	0.001	-0.004, 0.006	-0.08
<b>Agility score</b>	SSD+PC1	0	0.39	SSD: -22.942 PC1: -1.382	SSD: -43.661, -2.223 PC1: -2.258, -0.506	0.47
	SSD	1.07	0.23	-22.059	-47.004, 2.886	0.14
	PC1	1.55	0.18	-1.398	-2.410, -0.386	0.35
<b>Female mass</b>	Agility	0	0.28	-0.074	-0.535, 0.388	-0.08
	PC2	0.08	0.27	0.071	-0.770, 0.912	-0.09
	PC1	0.13	0.27	0.765	-0.228, 1.759	0.10

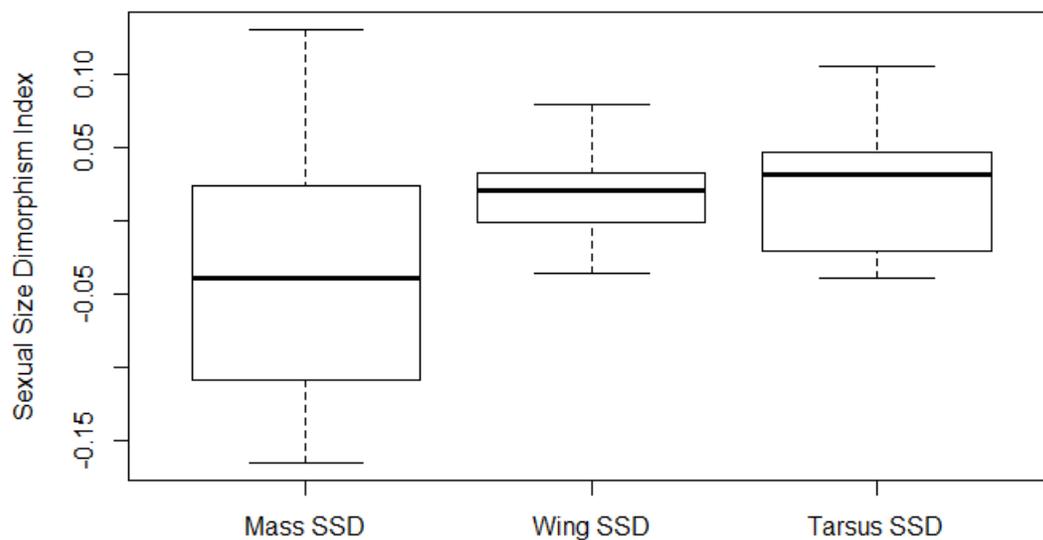
Response variable = variable used as response in model selection; Model = predictor variables of respective model;  $\Delta$ AICc = number of AICc units from top model; weight = relative model weight;  $\beta$  = slope of relationship between response and predictor variable(s); 95% CI = 95% confidence interval of slope;  $R^2$  = adjusted R-squared value. Predictor variables are abbreviated as follows: Agility = agility score, PC1 = principal component 1 (temperature and elevation), PC2 = principal component 2 (precipitation), SSD = mass sexual size dimorphism.

**Table 2.4** Complete model results, with model description,  $\Delta$ AICc value, and model weight

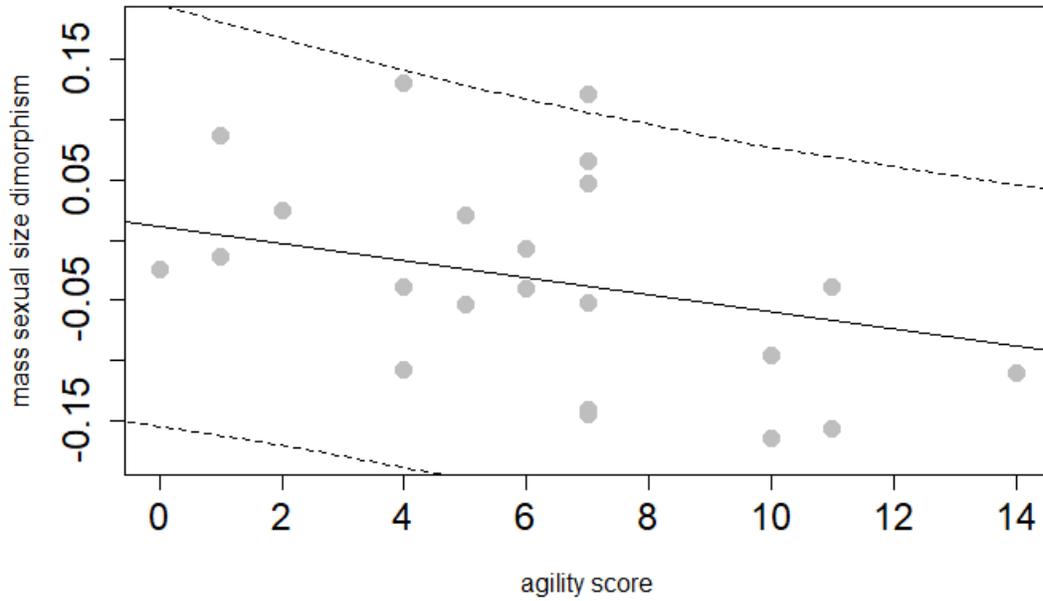
<b>Response Variable</b>	<b>Model</b>	<b><math>\Delta</math>AICc</b>	<b>weight</b>
<b>Mass sexual size dimorphism</b>	Agility	0	0.52
	PC2	3.10	0.11
	PC1	3.11	0.11
	Agility+PC1	3.13	0.11
	Agility+PC2	3.46	0.10
	PC1+PC2	6.56	0.02
	Agility*PC1	6.60	0.02
	PC1*PC2	7.54	0.01
	Agility*PC2	7.79	0.01
<b>Wing sexual size dimorphism</b>	PC2	0	0.56
	PC1+PC2	2.53	0.16
	Agility+PC2	3.45	0.10
	PC1	4.29	0.07
	Agility	4.33	0.06
	PC1*PC2	5.58	0.03
	Agility*PC2	7.43	0.01
	Agility+PC1	7.75	0.01
Agility*PC1	11.45	0.00	
<b>Tarsus sexual size dimorphism</b>	PC1	0	0.30
	PC2	0.33	0.25
	Agility	0.38	0.24
	PC1+PC2	2.62	0.08
	Agility+PC1	3.46	0.05
	Agility+PC2	3.63	0.05
	Agility*PC2	5.31	0.02
	PC1*PC2	6.90	0.01
	Agility*PC1	7.70	0.01
<b>Agility score</b>	SSD+PC1	0	0.39
	SSD	1.07	0.23
	PC1	1.55	0.18
	SSD*PC1	3.91	0.06
	PC2	4.12	0.05
	SSD+PC2	4.48	0.04
	PC1+PC2	4.98	0.03
	SSD*PC2	7.49	0.01
	PC1*PC2	9.30	0.00

<b>Response Variable</b>	<b>Model</b>	<b><math>\Delta AICc</math></b>	<b>weight</b>
<b>Female mass</b>	Agility	0	0.28
	PC2	0.08	0.27
	PC1	0.13	0.27
	Agility+PC1	3.38	0.05
	Agility+PC2	3.45	0.05
	PC1+PC2	3.59	0.05
	PC1*PC2	6.30	0.01
	Agility*PC1	7.42	0.01
	Agility*PC2	7.66	0.01

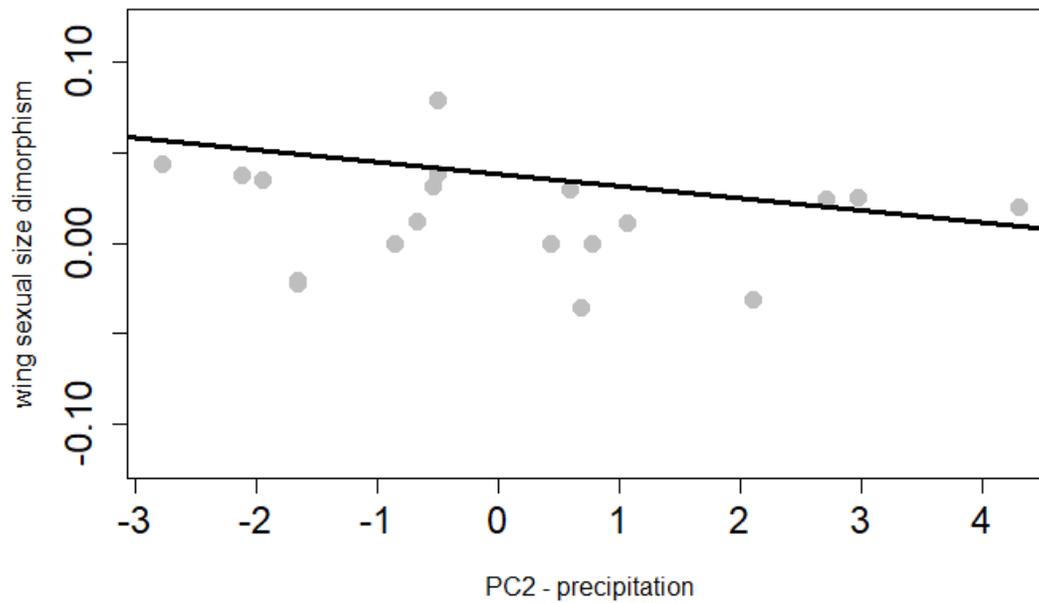
## Figures



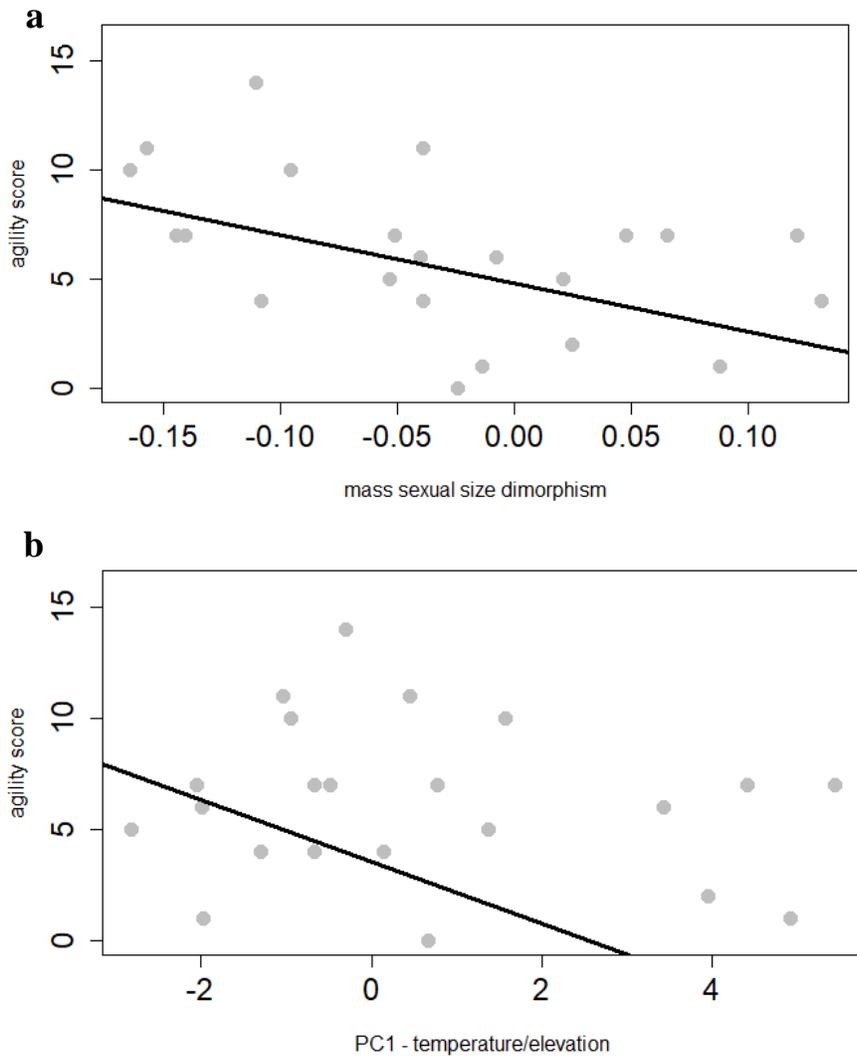
**Figure 2.1** Variation in sexual size dimorphism of three morphological traits. Note that number of species varies for each trait. Mass = 22, Wing = 19, Tarsus = 14. When restricted to only 14 species for which we have all three measurements, the pattern of distribution is qualitatively similar.



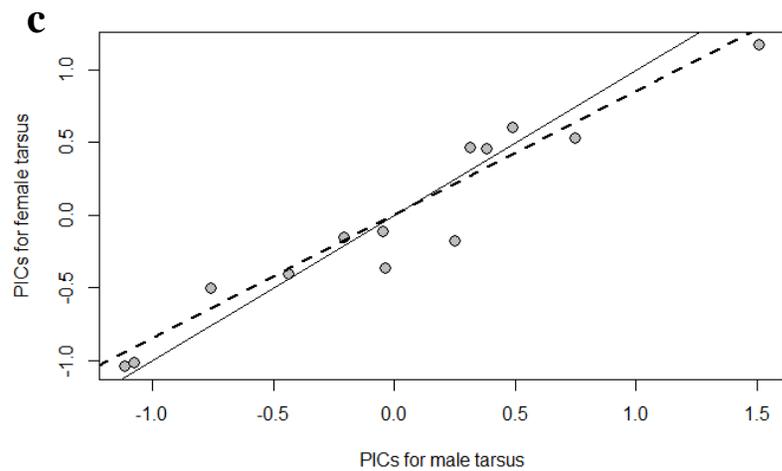
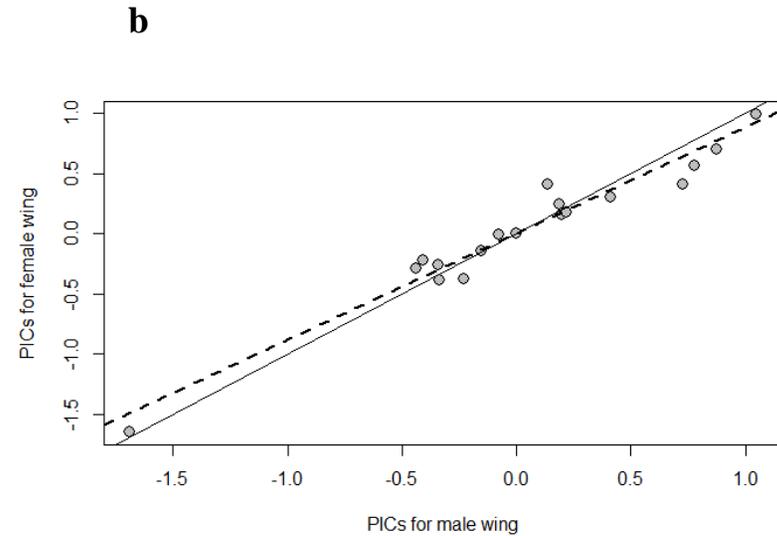
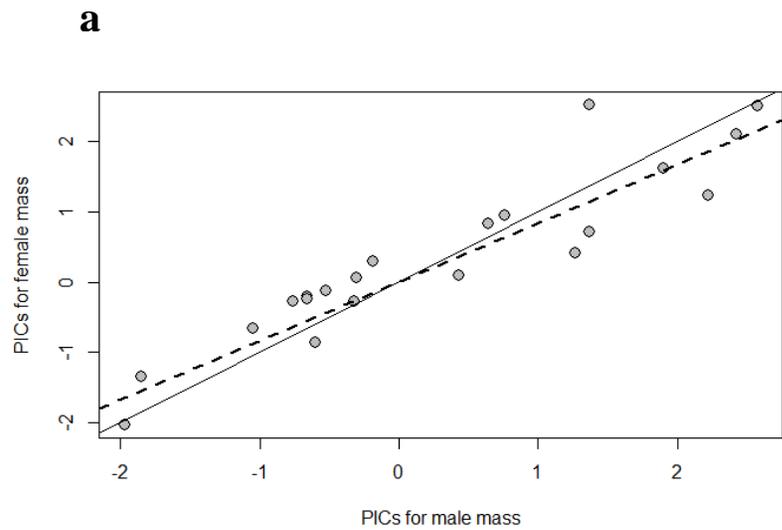
**Figure 2.2** Relationship between mass sexual size dimorphism and agility score. Data points are raw and not phylogenetically corrected, but line is extracted from phylogenetic generalized least squares model, dashed lines represent 95% confidence interval calculated using R package *evomap*



**Figure 2.3** Relationship between wing sexual size dimorphism and principal component 2, which represents variation in precipitation environmental variables. Points are not phylogenetically corrected, but lines are extracted from phylogenetic generalized least squares model.



**Figure 2.4** Relationship between agility score and single effects of (a) sexual size dimorphism and (b) principal component one (representing variation in temperature and elevation environmental variables). Points are not phylogenetically corrected, but lines are extracted from phylogenetic generalized least squares single effect models.



**Figure 2.5** Relationships between the phylogenetic independent contrasts of log(male) and log(female) morphological traits. Dashed line is slope of relationship ( $<1$  follows Rensch's rule), while the solid black line represents a 1:1 ratio (i.e., isometry) mass (a), wing (b), and tarsus (c).

## **Chapter 3 - Apparent survival of tropical birds in a wet, premontane forest in Costa Rica**

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## **Abstract**

Despite the importance of tropical birds in the development of life history theory, we lack information about demographic rates and drivers of population dynamics for most species. We used a seven-year (2007-2013) capture-mark-recapture dataset from an exceptionally wet premontane forest at mid-elevation in Costa Rica to estimate apparent survival for seven species of tropical passerines. For four of these species, we provide the first published demographic parameters. Recapture probabilities ranged from 0.21 to 0.53, and annual estimates of apparent survival varied from 0.23 to 1.00. We also assessed the consequences of inter-annual variation in rainfall on demographic rates. Our results are consistent with interannual rainfall increasing estimates of apparent survival for two species and decreasing estimates for three species. For the three species where we could compare our estimates of apparent survival to estimates from drier regions, our estimates were not consistently higher or lower than those published previously. The temporal and spatial variability in demographic rates we document within and among species highlights the difficulties of generalizing life history characteristics across broad biogeographic gradients. Most importantly, this work emphasizes the context-specific role of precipitation in shaping tropical avian demographic rates and underscores the need for mechanistic studies of environmental drivers of tropical life histories.

## Introduction

Factors shaping population dynamics of tropical birds remain poorly understood. A prevailing view is that tropical species typically have “slow” life history strategies where individuals prioritize future reproductive efforts over success in a given year, have lower fecundity, extensive parental care, and high adult survival (Skutch 1967, Ghalambor and Martin 2001, Lloyd and Martin 2016, Pizzaro Muñoz et al. 2018). However, little demographic data for testing these predictions is available for most tropical taxa (Martin et al. 2011, Martin 2015, Boyle et al. 2016, Boyce and Martin 2017). In particular, estimates of apparent survival of tropical birds vary widely, and are often lower than expected (Karr et al. 1990, Sandercock et al. 2000, Blake and Loiselle 2013). However, variation in methods among studies (e.g., use of color band resighting, sampling effort, and estimation technique) and age distribution and site fidelity of populations may explain some of the differences among studies (Johnston et al. 1997, Martin et al. 2017). Robust estimates from a wide range of species and sites are needed to predict and understand the selective pressures that lead to biogeographic patterns in avian life history traits (Brawn et al. 1995, Pizzaro Muñoz et al. 2018).

Understanding the basis for taxonomic and spatial variation in survival is crucial, not only from the perspective of testing fundamental questions in life history theory, but to better understand the implications of global climate change for tropical animals. A long-standing paradigm for patterns of diversity in tropical bird communities emphasizes the importance of biotic interactions and downplays any potential role for direct abiotic sources of selection (Loiselle and Blake 1992, Stutchbury and Morton 2001). Unlike temperate ecosystems, periods of severe cold are unlikely to be a driver of variation in life history traits of tropical species (Martin and Wiebe 2004). However, precipitation creates seasonality in tropical regions and both

the amount and magnitude of seasonal variation in rainfall impose dramatic constraints on plant productivity and consumer responses (van Schaik et al. 1993, Prada et al. 2017). Variation in rainfall can have indirect effects on tropical animals via reduced food availability (Wright et al. 1999) or access to food via foraging constraints (Boyle et al. 2010). Inter-annual variation in precipitation is recognized as an important driver of population dynamics of some tropical bird species, but the strength and direction of rainfall effects on demographic performance vary widely. For example, recruitment and population growth rates decreased during severe and extended dry seasons in Panama (Brawn et al. 2017), whereas reduced recruitment and apparent survival were associated with wetter years in Costa Rica and Ecuador (Wolfe et al. 2015, Ryder and Sillett 2016). In addition, precipitation can interact with phenotype, yielding different effects on behavior and demography depending on the environmental context and condition of individuals. For example, dispersal by Green-rumped Parrotlets (*Forpus passerinus*) both increased and decreased in years of higher rainfall, depending on natal environment and phenotype (Tarwater and Beissinger 2012, 2013). Most tropical research efforts are not primarily designed to collect long-term data on survival and, except in a few systems (e.g., Wolfe et al. 2017), we currently lack sufficient data to predict how changes in rainfall may influence tropical avian populations or determine the degree to which shifts in demography mediated by abiotic conditions are caused by indirect drivers (e.g., food availability and foraging success) versus direct factors (e.g., mortality).

A mechanistic, bottom-up perspective predicts positive associations between above-average rainfall and demographic rates in drier and more seasonal environments where primary productivity is constrained by soil moisture (Meir and Woodward 2010). Conversely, negative relationships between demographic performance and rain might be predicted for wetter regions

where solar energy is limiting (Esquivel-Hernández et al. 2017). Some evidence suggests that, in wet environments, tropical birds can experience direct negative consequences of heavy rain. For example, storm events are physiological stressors that induce short-term fasting and increase corticosterone levels in White-ruffed Manakins (*Corapipo altera*; Boyle et al. 2010). Birds also respond behaviorally to severe wet-season storms in montane regions by moving to lower elevations during the non-breeding season to escape the heaviest storms (Boyle et al. 2010, Boyle 2011). These results suggest that years with especially high rainfall could impose direct survival costs in wet environments. However, this prediction has not yet been tested. Insight into the nature and magnitude of such costs is important given that tropical rain events are projected to increase in intensity and frequency (Aguilar et al. 2005), and we need a better understanding of how climate change could affect survival of tropical birds.

Relatively few demographic estimates exist for birds in tropical communities. Low population densities of many tropical forest-dwelling bird species make recapturing large numbers of marked birds difficult (Ruiz-Gutiérrez et al. 2012). Additionally, maintaining the long time series and substantial effort necessary to gather adequate data for demographic studies of tropical vertebrates is logistically challenging, and relatively few banding stations are located in the Neotropics (Karr et al. 1990, Sandercock et al. 2000, Parker et al. 2006). We collected mark-recapture data for forest-dwelling passerine birds during the breeding season over seven years in a mid-elevation primary forest on the Caribbean slope of Costa Rica subject to exceptionally wet conditions (i.e., pluvial; Holdridge 1967). We estimated apparent survival for as many species as our dataset allowed, then used our estimates to test relationships between annual survival and precipitation in a high-rainfall environment. We predicted that birds would experience reduced apparent survival in years of especially heavy rain. Rain could act directly by

either increasing mortality due to exposure and short-term fasting during storms, or by increasing permanent emigration from the site. If rain exerts direct negative effects, estimates of apparent survival should be lower in years with more precipitation across all species.

## **Methods**

We captured birds at a single elevation in primary forest owned by Rara Avis Rainforest Lodge and Selvatica Rainforestry (10°17'3"N, 84°02'47"W). Rara Avis and Selvatica are adjacent private reserves on the Caribbean slope of north central Costa Rica, spanning elevations of 500–900 m, and are contiguous with nearly 50,000 ha of primary forest in Parque Nacional Braulio Carrillo. Daily rainfall was collected on site using a manual rain gauge from 1990 through the study period, and averaged ~ 8300 mm of rain per year (Boyle 2010). Mean monthly precipitation ranged from 514–839 mm, and mean monthly temperatures vary negligibly over the year at this latitude (Boyle and Sigel 2015). Bird communities at low and middle elevations along this elevational gradient comprise some of the most diverse avifauna in Costa Rica (Blake and Loiselle 2000).

We captured birds at 16 fixed-net locations in an 11.5-ha plot using 12-m mist-nets with a 38-mm mesh (Ecotone, Gdynia, Poland). We opened nets from 06:00 to 13:00 for 4–6 days in a single week every month for a 2–5 month period spanning the dry season and early wet season (February-July, a period corresponding to peak breeding season of most species) each year from 2007 to 2013. We uniquely marked birds using numbered aluminum leg bands, and aged and sexed individuals by plumage coloration, molt patterns, and the presence of cloacal protuberances in males and brood patches in females (Bailey 1952, Wolfson 1952).

We constructed encounter histories for banded birds where 1 = captured and 0 = not captured in a given year; the interval between capture occasions was one year. We did not assess

within-year recaptures and included only one capture record per year when an individual was captured multiple times in a single year. For each capture history, we included covariates that varied annually, including precipitation of the preceding biological year (March – February) and year-specific capture effort, measured in mist-net hours (one 12-m mist-net open for one hour = 1 mist-net hour). We estimated apparent survival ( $\phi$ ) and recapture probability ( $p$ ) for the seven species in our database with sufficient data for models to converge, fitting Cormack-Jolly-Seber (CJS) models for live-encounter data (Lebreton et al. 1992). Analyses were conducted in Program MARK (White and Burnham 1999) and using the R package RMark (Laake 2013; R Core Team 2018) as an interface to Program MARK. Apparent survival ( $\phi$ ) is the product of true survival and site fidelity (the probability an individual remains in the study area), whereas the probability of recapture ( $p$ ) is the product of site propensity (the probability an individual does not temporarily leave the study area) and true detection (Sandercock 2006).

We constructed a set of seven candidate models to test relationships between apparent survival, recapture probability, and the z-score of annual covariates (precipitation and mist-net hours) for each species (Table 3.1). For all but one species, our datasets were too sparse to test for age or sex effects on apparent survival. Given the focus of our study, we opted to evaluate the influence of rain on estimates of apparent survival and did not include age or sex covariates for any species. We first considered a model where apparent survival and recapture probability were constant across all years, i.e.  $\phi(.) p(.)$ . We tested for a relationship between apparent survival and annual precipitation (precip) using z-transformed rainfall values from the preceding biological year, i.e.,  $\phi(\text{precip}) p(.)$ . We also assessed models that accounted for variation in recapture probability due to differences in annual capture effort, i.e.,  $\phi(.) p(\text{effort})$ , measured as the z-transformed total number of mist-net hours (mnh) per season. Thus, precipitation and effort

varied by year and were associated with each individual capture history. We did not assess models where precipitation influenced detection probability during the breeding season because (a) breeding is seasonal in our study area and occurred during the months we sampled, and (b) downhill altitudinal migration at our study site occurred after our sampling was concluded each year (Boyle 2008). In addition, we evaluated models including an effect of time-since-marking on apparent survival and constant recapture probability, i.e.,  $\phi(\text{TSM}) p(\cdot)$ . The time-since-marking model separately estimates apparent survival for individuals following first capture ( $\phi^1$ ; potential transients or young individuals) and following subsequent capture ( $\phi^{2+}$ ; individuals inferred to be residents; Pradel et al. 1997, Parker et al. 2006) because estimates of apparent survival can be negatively biased by inclusion of transient individuals and the characteristically low survival rates of young birds (Sandercock 2006). We considered models with annual covariates for both apparent survival and recapture probability, i.e.,  $\phi(\text{TSM}) p(\text{effort})$ ,  $\phi(\text{precip}) p(\text{effort})$ . Last, we included a model assessing an effect of time on estimates of apparent survival while holding recapture probability constant, i.e.,  $\phi(\text{time}) p(\cdot)$ . We were unable to evaluate a fully time-dependent model ( $\phi(\text{time}) p(\text{time})$ ) due to sparse capture histories and failure of models to converge. Table 3.1 contains the full set of models evaluated for each species.

We used the analysis of deviance (ANODEV) procedure in Program MARK to estimate the percentage of annual variation in precipitation that explains annual variation in estimates of apparent survival (White and Burnham 1999). We ran the ANODEV procedure using the following models:  $\phi(\text{precip}) p(\cdot)$ ,  $\phi(\text{time}) p(\cdot)$ , and  $\phi(\cdot) p(\cdot)$ . To adjust for possible overdispersion of the data and to test goodness of fit, we estimated the overdispersion parameter  $\hat{c}$  by applying the median  $\hat{c}$  procedure in Program MARK to the global model, ( $\phi(\text{time}) p(\cdot)$ ; White and Burnham 1999). For four species, the median  $\hat{c}$  procedure could not perform logistic regression

with the  $\phi(\text{time}) p(\cdot)$  model. We then performed additional goodness-of-fit tests in Program MARK (Bootstrap Goodness Of Fit, Program Release) to determine an appropriate correction for overdispersion. For two species, we were unable to calculate  $\hat{c}$  using the  $\phi(\text{time}) p(\cdot)$  model and, therefore, used the overdispersion parameter  $\hat{c}$  calculated by the median  $\hat{c}$  procedure run on the less complex model  $\phi(\text{TSM}) p(\cdot)$ . We then ranked models using Akaike weights ( $w_i$ ) and either Akaike's Information Criteria (AICc) or the Quasi-Akaike's Information Criteria (QAICc) corrected using the appropriate  $\hat{c}$  for each species

## Results

Over our seven-year study period, capture effort ranged from 286 – 1598 mist-net hours per year (mean =  $970 \pm 497$  [SD] mnh/year; Figure 3.1). We recorded annual precipitation for the biological year preceding each sampling event (i.e., March to February), which ranged from 6990 to 8981 mm/yr (mean =  $8130 \pm 888$  [SD] mm/yr; Figure 3.2). We recorded a total of 2187 captures of 1674 individuals representing 79 species. Despite our extensive sampling effort, the median number of individuals captured per species was only five (range = 1 – 253). Across all years of sampling, the median number of recaptured individuals for each species was one (range = 0 – 85).

We were able to estimate apparent survival for seven species with a sufficient number of captures and recaptures for model convergence, including Wedge-billed Woodcreepers (*Glyphorynchus spirurus*, Furnariidae), White-ruffed Manakins (*Corapipo altera*, Pipridae), White-breasted Woodwrens (*Henicorhina leucosticta*, Troglodytidae), Tawny-crested Tanagers (*Tachyphonus delatrii*, Thraupidae), Orange-billed Sparrows (*Arremon aurantiirostris*, Passerellidae), Carmiol's Tanagers (*Chlorothraupis carmioli*, Cardinalidae), and Tawny-capped Euphonias (*Euphonia annae*, Fringillidae). All seven species are small-bodied passerines (< 40

g) that inhabit low and mid-levels of forested regions. The manakin and euphonia are primarily frugivorous, whereas the tanagers and sparrow are omnivorous and consume substantial quantities of arthropod prey along with fruit. The wren and woodcreeper are insectivorous and forage exclusively on arthropods. Table 3.2 contains a complete summary of the model selection results for these species.

Estimates of  $\hat{c}$  for all species were  $< 3$ , indicating slight overdispersion of data in capture histories that was addressed by use of QAICc where appropriate. For four species (White-breasted Woodwrens, Tawny-crested Tanagers, Orange-billed Sparrows, and Carmiol's Tanagers), a model with constant probabilities of apparent survival and recapture was the best fit to the capture histories ( $\phi(\cdot) p(\cdot)$ ; Table 3.3). For White-ruffed Manakins, time since marking influenced estimates of apparent survival for the top-ranked model, and an effect of time since marking was the second-ranked model within 2 AICc units for Orange-billed Sparrows. For both species, individuals had greater apparent survival following their second capture than following their initial capture (Table 3.3).

For Wedge-billed Woodcreepers and Tawny-capped Euphonias, the top-ranked model indicated that annual variation in precipitation affected estimates of apparent survival (Table 3.3). Additionally, the ANODEV results for both of these species were significant ( $P < 0.05$ ) and estimated that 84% and 74% of annual variation in apparent survival of Wedge-billed Woodcreepers and Tawny-capped Euphonias, respectively, were explained by precipitation (Table 3.4). However, the nature of the relationship between precipitation and estimates of apparent survival seemed to vary, and the small sample sizes and large confidence intervals limit the strength of our inference. We found a negative effect of increased precipitation for Wedge-billed Woodcreepers ( $\beta = -8.67$ , 95% CI =  $-20.81 - 3.46$ ), and a slightly positive effect for

Tawny-capped Euphonias ( $\beta = 0.70$ , 95% CI =  $-0.15 - 1.55$ ; Tables 2, 3). For an additional three species (Tawny-crested Tanagers, Orange-billed Sparrows, and Carmiol's Tanagers), a model including an effect of precipitation was ranked similarly to the top model ( $\leq 2$  (Q)AICc of the top model; Table 3.3). Orange-billed Sparrows and Carmiol's Tanagers show negative effects of precipitation on estimates of apparent survival, whereas Tawny-crested Tanagers show a positive effect of additional rainfall (Table 3.3). For all three of these species, the ANODEV results indicated that precipitation accounted for  $>50\%$  of annual variation in estimates of apparent survival, but only Carmiol's Tanagers had a significant  $P$  value (Table 3.4).

We also summed the weights of models including rainfall effects for each species (Table 3.1). Although summed Akaike weights ought to be interpreted with caution (Galipaud et al. 2014, 2017), precipitation models accounted for  $>0.25$  of total model weight for four of our seven species (Wedge-billed Woodcreepers, Tawny-crested Tanagers, Carmiol's Tanagers, and Tawny-capped Euphonias).

## Discussion

Using data collected during an intensive field effort spanning seven years, we calculated demographic estimates for seven species of tropical birds, providing some of the first demographic data for four of those species. Across all seven species, annual recapture probabilities were low, as is often the case for systematic mist-netting efforts without additional re-sighting effort (Martin et al. 2017). For White-ruffed Manakins, estimates of apparent survival were lower following initial capture than after subsequent recapture in the top-ranked model. For species where precipitation was the strongest predictor of apparent survival, Wedge-billed Woodcreepers had widely varying estimates, perhaps driven by sparse capture histories, whereas demographic estimates for Tawny-capped Euphonias had not been published previously. For the

remaining four species, estimates of apparent survival were constant across years in the top-ranked model. To our knowledge, estimates of apparent survival for three of these species, including Tawny-crested Tanagers, Orange-billed Sparrows, and Carmiol's Tanagers, had not been published previously. Although our results must be interpreted with caution due to the large confidence intervals surrounding these estimates, they provide difficult-to-obtain demographic data from an under-studied avifauna and habitat type.

Quantitative comparison of demographic estimates is beyond the scope of this study, but, where possible, we compared our results to published point estimates calculated using similar models and age classes. Although differences in estimated apparent survival among populations may be due in part to site differences in field methods or the size of experimental plots, such comparisons provide an opportunity to assess what is known about species across geographic scales and under different environmental conditions. Our estimates of apparent survival were not consistently lower than those of other studies conducted at sites with less rain. Our estimate of apparent survival for Wedge-billed Woodcreepers from the constant model ( $\phi = 0.76$ , 95% CI = 0.42 – 0.93) was at least 14% higher than estimates published from three study sites in the Neotropics ( $\phi = 0.36 \pm 0.06$  [SE], Jullien and Clobert 2000;  $\phi = 0.41 \pm 0.03$  [SE],  $\phi^{2+} = 0.62 \pm 0.02$  [SE], Blake and Loiselle 2013;  $\phi = 0.56 \pm 0.12$  [SE], Wolfe et al. 2014). Conversely, our estimate of apparent survival for White-breasted Woodwrens ( $\phi = 0.71$ , 95% CI = 0.34 – 0.92) was 9% lower than an estimate from Ecuador ( $\phi = 0.80 \pm 0.06$  [SE], Blake and Loiselle 2013). Our estimates of apparent survival for White-ruffed Manakins ( $\phi^1 = 0.39$ , 95% CI = 0.28 – 0.51,  $\phi^{2+} = 0.62$ , 95% CI = 0.50 – 0.72) are similar to those from a lower-elevation site along the same forested gradient as our study site ( $\phi^1 = 0.37 \pm 0.25$  [SE],  $\phi^{2+} = 0.59 \pm 0.18$  [SE], Blake and Loiselle 2002). However, these two estimates of apparent survival for White-ruffed Manakins

were dramatically lower than those reported from the drier Pacific Slope of Costa Rica in a population that does not migrate altitudinally ( $\phi = 0.97 \pm 0.15$  [SE], Ruiz-Gutierrez et al. 2008). Previous work in our population of manakins demonstrated that heavy rainfall causes short-term fasting and energetic stress, driving downhill altitudinal migration during the non-breeding season (Boyle et al. 2010). Thus, although we found no evidence of interannual variation in precipitation influencing apparent survival for this species, variation in rainfall may affect behavior that mitigates survival costs and affect spatial variation in demography among populations.

The results of a growing body of studies suggest that abiotic factors play a greater role in shaping tropical population dynamics than previously appreciated (Whitfield et al. 2007, Wolfe et al. 2015, Ryder and Sillett 2016, Brawn et al. 2017). Our data were collected during a study designed to answer questions about the evolutionary ecology and behavior of a subset of the avifauna rather than a long-term research effort designed to generate survival data. However, we believe our results can provide a starting point for future work and aid in developing novel hypotheses because it is integrated with other data, e.g., diet, behavior, and reproduction. Despite the sparseness of our dataset and low statistical power to detect the effects of covariates, five of seven species models that included rainfall were competitive with top models, and apparent survival was lower in wetter years for three of those species, including the insectivorous Wedge-billed Woodcreepers and omnivorous Orange-billed Sparrows and Carmiol's Tanagers. Conversely, apparent survival was higher in wetter years for two species: Tawny-crested Tanagers, frugivores that vary their diet with a fairly large proportion of arthropod prey, and highly frugivorous Tawny-capped Euphonias.

The differential response of multiple species at a single site to interannual variation in precipitation is intriguing, especially given both positive (Wolfe et al. 2015, Brawn et al. 2017) and negative (Ryder and Sillett 2016) demographic responses of birds during wet years in recent studies. However, our small sample sizes and wide confidence intervals make it difficult to draw conclusions. Additional data would also have permitted us to assess more complex models. In particular, fitting a model that considers the effect of precipitation on the apparent survival of individuals following their second capture would have been especially informative because transients likely limit our ability to discern effects of precipitation on apparent survival. Nevertheless, the ANODEV procedure revealed a strong effect of precipitation that, despite our small sample size, suggests precipitation may be an important driver of tropical bird demography and should be explicitly considered in future studies.

Annual total precipitation is just one way to assess the effect of abiotic conditions on tropical birds. Other metrics can be biologically relevant and influence demography more strongly. For example, Wolfe et al. (2015) and Ryder and Sillett (2016) found that demographic rates were more strongly associated with the El Niño Southern Oscillation (ENSO) than to local variation in precipitation, suggesting that birds may respond more strongly to integrated or interactive consequences of climatic variation (e.g., including the timing and magnitude of rainfall events in combination with temperature) than to total rainfall amounts. Our sampling period of seven years spanned strong, moderate, and weak La Niña years and a moderate El Niño year. Thus, in preliminary analyses, we explored the potential influence of global climatic indices by replacing locally-measured annual variation in rainfall in our models with the ENSO index, but these models did not outperform the results we present here. Other metrics of rainfall, such as the duration of wet or dry seasons, number of extreme storm events, or variability in

daily precipitation may be equally or more important to birds as they breed, migrate, and forage (Boyle et al. 2010). However, making informed choices regarding which of these variables might be most appropriate requires a mechanistic understanding of how precipitation affects fitness, information currently lacking for most species of birds. We encourage investigators in future studies to develop this mechanistic understanding and evaluate associations between demographic rates and different precipitation metrics to help elucidate the direct and indirect links between rainfall and population dynamics in tropical regions.

We know little about what might explain species-level differences in responses to the same environmental conditions in the same community. Inter-annual variation in rainfall does seem to play a role in the survival and life history of a growing number of tropical bird species. This raises the question of how relationships with environmental covariates could affect population dynamics in the context of future changes to rainfall patterns in the Neotropics. Previous studies have demonstrated the complex selective effects that variation in rainfall can have on behavior and fitness (Boyle et al. 2010, Tarwater and Beissinger 2013, Ryder and Sillett 2016). Understanding the role that precipitation plays in the evolution of tropical species is critical because, although predictions of Neotropical rainfall regimes involve complex and locale-specific increases and decreases in mean annual precipitation, the intensity of rainfall events in many regions is predicted to increase and the temporal distribution of those storms is expected to change (Aguilar et al. 2005, Giorgi 2006, Whitfield et al. 2007). Thus, determining the role of environmental drivers of population dynamics will help identify conservation priorities as well as the evolutionary pressures shaping tropical avian life history. Our study helps elucidate fundamental life history characteristics of tropical birds, and highlights both the temporal variability in demographic rates as well as the species-specific responses to

environmental variability even within a single community. Improving our knowledge of demography across tropical environmental gradients is important to understanding the proximate and ultimate causes of variation in life histories within and across species.

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## Tables

**Table 3.1** List of all candidate models evaluated for each species.

<b>Candidate models</b>	<b>Apparent survival (<math>\phi</math>)</b>	<b>Recapture probability (<math>p</math>)</b>
$\phi(.) p(.)$	Constant	Constant
$\phi(\text{precip}) p(.)$	Precipitation	Constant
$\phi(.) p(\text{effort})$	Constant	Effort (mist-net hours)
$\phi(\text{tsm}) p(.)$	Time-since-marking	Constant
$\phi(\text{tsm}) p(\text{effort})$	Time-since-marking	Effort (mist-net hours)
$\phi(\text{precip}) p(\text{effort})$	Precipitation	Effort (mist-net hours)
$\phi(\text{time}) p(.)$	Time	Constant

Includes combinations of parameters and annual covariates assessed to explain variation in apparent survival ( $\phi$ ) and recapture probability ( $p$ )

**Table 3.2** Cormack-Jolly-Seber model selection results for seven Neotropical bird species.

Species	$\hat{c}^a$	Precip $w_i^b$	Model	npar <sup>c</sup>	(Q)AICc <sup>d</sup>	$\Delta(Q)AICc^e$	$w_i^f$	Deviance <sup>g</sup>
Wedge-billed Woodcreeper	1	0.54	$\varphi(\text{precip}) p(.)$	3	79.52	0.00	0.37	28.97
			$\varphi(.) p(.)$	2	80.27	0.75	0.25	32.05
			$\varphi(\text{precip}) p(\text{effort})$	4	81.06	1.54	0.17	28.05
			$\varphi(.) p(\text{effort})$	3	82.26	2.75	0.09	31.72
			$\varphi(\text{TSM}) p(.)$	3	82.58	3.06	0.08	32.03
			$\varphi(\text{TSM}) p(\text{effort})$	4	84.70	5.18	0.03	31.68
			$\varphi(\text{time}) p(.)$	7	89.67	10.15	0.00	28.38
White-ruffed Manakin	1.25	0.10	$\varphi(\text{TSM}) p(.)$	3	388.56	0.00	0.45	52.07
			$\varphi(.) p(.)$	2	390.49	1.93	0.17	56.04
			$\varphi(\text{TSM}) p(\text{effort})$	4	390.49	1.93	0.17	51.95
			$\varphi(.) p(\text{effort})$	3	392.34	3.78	0.07	55.85
			$\varphi(\text{precip}) p(.)$	3	392.37	3.81	0.07	55.88
			$\varphi(\text{time}) p(.)$	7	393.32	4.76	0.04	48.55
			$\varphi(\text{precip}) p(\text{effort})$	4	394.28	5.72	0.03	55.75
White-breasted Woodwren	1.06	0.18	$\varphi(.) p(.)$	2	37.60	0.00	0.53	15.52
			$\varphi(\text{precip}) p(.)$	3	40.11	2.51	0.15	15.18
			$\varphi(.) p(\text{effort})$	3	40.33	2.74	0.13	15.41
			$\varphi(\text{TSM}) p(.)$	3	40.40	2.80	0.13	15.48
			$\varphi(\text{precip}) p(\text{effort})$	4	43.28	5.69	0.03	15.10
			$\varphi(\text{TSM}) p(\text{effort})$	4	43.47	5.87	0.03	15.29
			$\varphi(\text{time}) p(.)$	7	55.05	17.46	0.00	13.55
Tawny-crested Tanager	2.63	0.29	$\varphi(.) p(.)$	2	31.25	0.00	0.40	7.26
			$\varphi(\text{precip}) p(.)$	3	32.51	1.26	0.21	6.24
			$\varphi(.) p(\text{effort})$	3	33.31	2.06	0.14	7.04
			$\varphi(\text{TSM}) p(.)$	3	33.52	2.27	0.13	7.25
			$\varphi(\text{precip}) p(\text{effort})$	4	34.55	3.30	0.08	5.88
			$\varphi(\text{TSM}) p(\text{effort})$	4	35.66	4.41	0.04	6.99
			$\varphi(\text{time}) p(.)$	7	42.12	10.87	0.00	5.54
Orange-billed Sparrow	1.0	0.18	$\varphi(.) p(.)$	2	46.20	0.00	0.34	18.56
			$\varphi(\text{TSM}) p(.)$	3	47.19	0.99	0.21	16.96
			$\varphi(.) p(\text{effort})$	3	47.50	1.30	0.18	17.27
			$\varphi(\text{precip}) p(.)$	3	48.13	1.93	0.13	17.89
			$\varphi(\text{TSM}) p(\text{effort})$	4	48.95	2.75	0.09	15.86
			$\varphi(\text{precip}) p(\text{effort})$	4	50.03	3.83	0.05	16.94
			$\varphi(\text{time}) p(.)$	7	60.88	14.68	0.00	17.20

<sup>a</sup> $\hat{c}$ : estimate of overdispersion; <sup>b</sup>Precip  $w_i$ : sum of weights of models including precipitation; <sup>c</sup>npar: number of parameters; <sup>d</sup>(Q)AICc: Quasi-Akaike value or AICc value where appropriate; <sup>e</sup> $\Delta(Q)AICc$ : delta QAICc or AICc where appropriate; <sup>f</sup> $w_i$ : model weight; <sup>g</sup>Deviance: deviance of the model.

**Table 3.2 continued.**

Species	$\hat{c}^a$	Precip $w_i^b$	Model	npar <sup>c</sup>	(Q)AICc <sup>d</sup>	$\Delta(Q)AICc^e$	$w_i^f$	Deviance <sup>g</sup>
Carmioli's	1	0.38	$\varphi(.) p(.)$	2	92.19	0.00	0.29	22.20
Tanager			$\varphi(\text{precip}) p(.)$	3	92.61	0.42	0.23	20.31
			$\varphi(.) p(\text{effort})$	3	93.50	1.31	0.15	21.20
			$\varphi(\text{precip}) p(\text{effort})$	4	93.51	1.32	0.15	18.79
			$\varphi(\text{TSM}) p(.)$	3	93.84	1.65	0.13	21.54
			$\varphi(\text{TSM}) p(\text{effort})$	4	95.25	3.06	0.06	20.52
			$\varphi(\text{time}) p(.)$	7	103.03	10.84	0.00	20.22
Tawny-capped	1	0.45	$\varphi(\text{precip}) p(.)$	3	94.97	0.00	0.34	33.58
Euphonia			$\varphi(.) p(.)$	2	95.40	0.43	0.28	36.24
			$\varphi(\text{TSM}) p(.)$	3	96.99	2.02	0.12	35.61
			$\varphi(\text{precip}) p(\text{effort})$	4	97.15	2.18	0.11	33.45
			$\varphi(.) p(\text{effort})$	3	97.53	2.56	0.09	36.14
			$\varphi(\text{TSM}) p(\text{effort})$	4	99.11	4.14	0.04	35.41
			$\varphi(\text{time}) p(.)$	7	103.28	8.31	0.01	32.10

<sup>a</sup> $\hat{c}$  = estimate of overdispersion

<sup>b</sup>Precip  $w_i$  = sum of weights of models including precipitation

<sup>c</sup>npar = number of parameters

<sup>d</sup>(Q)AICc = Quasi-Akaike value or AICc value where appropriate

<sup>e</sup> $\Delta(Q)AICc$  = delta QAICc or AICc where appropriate

<sup>f</sup> $w_i$  = model weight

<sup>g</sup>Deviance = deviance of the model.

**Table 3.3** Model selection and parameter estimates for Cormack-Jolly-Seber models for seven Neotropical bird species captured in wet, premontane forest in Costa Rica, 2007-2013.

Species	C/R <sup>a</sup>	$\hat{c}^b$	Model <sup>c</sup>	$\Delta$ (Q)AICc <sup>d</sup>	$w_i^e$	$p$ (95% CI) <sup>f</sup>	$\phi$ (95% CI) <sup>g</sup>	$\phi_1$ (95% CI) <sup>h</sup>	$\phi_{2+}$ (95% CI) <sup>i</sup>	$p \beta$ (95% CI) <sup>j</sup>	$\phi \beta$ (95% CI) <sup>k</sup>
Wedge-billed Woodcreeper	32/13	1.0	$\phi(\text{precip}) p(\cdot)$	0.0	0.37	0.21 (0.11 - 0.37)	0.23 - 1.00				-8.67 (-20.81 - 3.46)
			$\phi(\cdot) p(\cdot)$	0.7	0.25	0.23 (0.09 - 0.46)	0.76 (0.42 - 0.93)				
			$\phi(\text{precip}) p(\text{effort})$	1.5	0.17	0.13 - 0.36	0.21 - 1.00			-0.54 (-1.64 - 0.56)	-10.83 (-27.82 - 6.17)
White-ruffed Manakin	253/8 5	1.25	$\phi(\text{TSM}) p(\cdot)$	0	0.45	0.45 (0.33 - 0.58)		0.39 (0.28 - 0.51)	0.62 (0.50 - 0.72)		
			$\phi(\cdot) p(\cdot)$	1.9	0.17	0.37 (0.27 - 0.48)	0.53 (0.44 - 0.62)				
White-breasted Woodwren	15/6	1.06	$\phi(\cdot) p(\cdot)$	0	0.53	0.27 (0.08 - 0.61)	0.71 (0.34 - 0.92)				
Tawny-crested Tanager	35/14	2.63	$\phi(\cdot) p(\cdot)$	0	0.40	0.49 (0.21 - 0.79)	0.50 (0.28 - 0.71)				
			$\phi(\text{precip}) p(\cdot)$	1.3	0.21	0.56 (0.25 - 0.83)	0.28 - 0.63				0.68 (-0.13 - 1.48)
Orange-billed Sparrow	20/9	1.0	$\phi(\cdot) p(\cdot)$	0	0.34	0.53 (0.18 - 0.85)	0.56 (0.28 - 0.80)				
			$\phi(\text{TSM}) p(\cdot)$	1	0.21	0.66 (0.26 - 0.91)		0.37 (0.15 - 0.66)	0.76 (0.28 - 0.96)		
			$\phi(\cdot) p(\text{effort})$	1.3	0.18	0.30 - 0.92	0.55 (0.28 - 0.80)			-1.36 (-4.23 - 1.51)	
			$\phi(\text{precip}) p(\cdot)$	1.9	0.13	0.51 (0.17 - 0.85)	0.42 - 0.68				-0.48 (-1.61 - 1.71)

**Table 3.3 continued**

Species	C/R <sup>a</sup>	$\hat{c}^b$	Model <sup>c</sup>	$\Delta$ (Q)AICc <sup>d</sup>	$w_i^e$	p (95% CI) <sup>f</sup>	$\phi$ (95% CI) <sup>g</sup>	$\phi_1$ (95% CI) <sup>h</sup>	$\phi_{2+}$ (95% CI) <sup>i</sup>	p $\beta$ (95% CI) <sup>j</sup>	$\phi \beta$ (95% CI) <sup>k</sup>	
Carmiolo's Tanager	34/15	1.0	$\phi(.) p(.)$	0	0.29	0.23 (0.10 – 0.43)	0.78 (0.48 – 0.93)					
			$\phi(\text{precip}) p(.)$	0.4	0.23	0.23 (0.11 – 0.41)	0.49 – 1.00				-2.80 (-14.34 – 8.74)	
			$\phi(.) p(\text{effort})$	1.3	0.15	0.13 – 0.30	0.77 (0.48 – 0.93)				0.42 (-0.44 – 1.28)	
			$\phi(\text{precip})$ $p(\text{effort})$	1.3	0.15	0.11 – 0.34					0.58 (-0.39 – 1.56)	-2.94 (-11.32 – 5.44)
			$\phi(\text{TSM}) p(.)$	1.6	0.13	0.28 (0.11 – 0.53)			0.58 (0.20 – 0.80)	0.85 (0.40 – 0.98)		
Tawny-capped Euphonia	44/16	1.0	$\phi(\text{precip}) p(.)$	0	0.34	0.38 (0.17 – 0.64)	0.32 – 0.69				0.70 (-0.15 – 1.55)	
			$\phi(.) p(.)$	0.4	0.28	0.36 (0.16 – 0.61)	0.56 (0.34 – 0.75)					

<sup>a</sup>C/R = numbers of captures and recaptures for entire species including all years

<sup>b</sup> $\hat{c}$  = value calculated by median c-hat procedure and used to correct for overdispersion with QAICc model selection where  $> 1$

<sup>c</sup>Model = models within 2 AICc or QAICc units

<sup>d</sup>(Q)AICc = difference in QAICc units or AICc units (where appropriate) from top model

<sup>e</sup> $w_i$  = model weights

<sup>f</sup>p (95% CI) = probability of recapture and 95% confidence interval, or range of probabilities for models that vary by year

<sup>g</sup> $\phi$  (95% CI) = estimate of apparent survival and 95% confidence interval, or range of estimates for models that vary by year

<sup>h</sup> $\phi_1$  (95% CI) = estimate of apparent survival and 95% confidence interval in interval following first capture

<sup>i</sup> $\phi_{2+}$  (95% CI) = estimate of apparent survival for intervals following recapture and 95% confidence interval for time since marking models

<sup>j</sup>p  $\beta$  (95% CI) = beta estimates for recapture probability that varies and 95% confidence interval for models that include an effect of effort

<sup>k</sup> $\phi \beta$  (95% CI) = beta estimates and 95% confidence interval for the effect of inter-annual variation in rainfall on apparent survival

**Table 3.4** Results of ANODEV procedure

Species	Total covariate <sup>a</sup>	Corrected total <sup>b</sup>	Percent variation from precipitation <sup>c</sup>	$\phi \beta$ (95% CI) <sup>d</sup>	<i>P</i> value <sup>e</sup>
Wedge-billed Woodcreeper	3.080	3.675	84	-8.67 (-20.81 - 3.46)	0.01
White-ruffed Manakin	0.024	9.288	0.26	—	0.92
White-breasted Woodwren	0.362	2.095	17	—	0.41
Tawny-crested Tanager	2.697	4.537	59	0.68 (-0.13 - 1.48)	0.07
Orange-billed Sparrow	0.691	1.363	51	-0.48 (-1.61 - 1.71)	0.11
Carmioli's Tanager	1.886	1.976	95	-2.80 (-14.34 - 8.74)	< 0.01
Tawny-capped Euphonia	3.049	4.140	74	0.70 (-0.15 - 1.55)	0.02

ANODEV procedure assessed what percent of annual variation in apparent survival can be explained by precipitation, using  $\phi(\cdot) p(\cdot)$ ,  $\phi(\text{time}) p(\cdot)$ , and  $\phi(\text{precip}) p(\cdot)$  models. The nature of the relationship with precipitation from the  $\phi(\text{precip}) p(\cdot)$  model (where competitive) and the significance of the ANODEV procedure are also shown.

<sup>a</sup>Total covariate = the difference between deviance of  $\phi(\cdot)$  and deviance of  $\phi(\text{precip})$

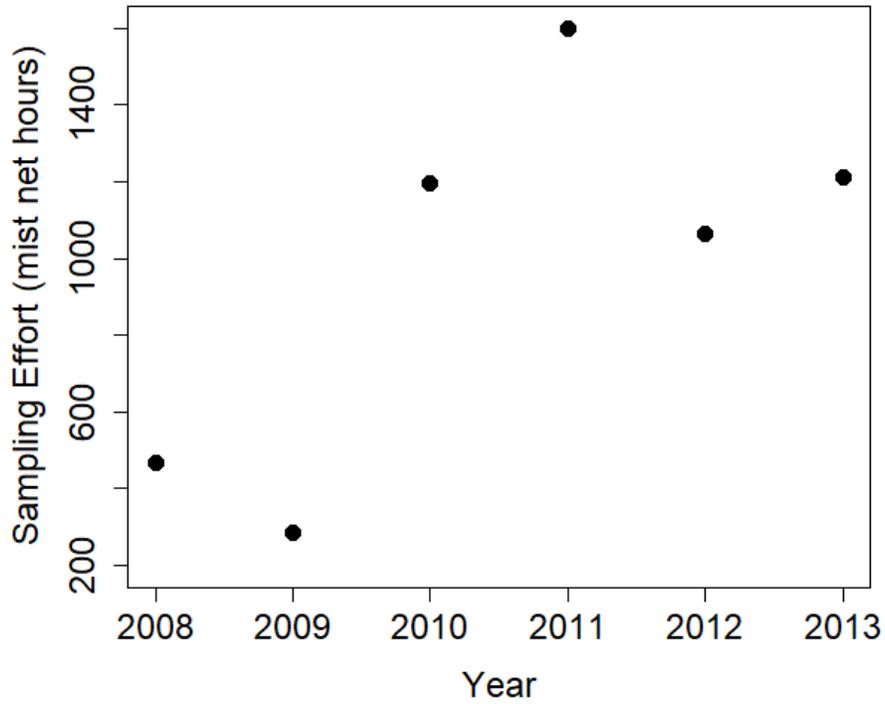
<sup>b</sup>Corrected total = the difference between deviance of  $\phi(\cdot)$  and deviance of  $\phi(\text{time})$

<sup>c</sup>Percent variation from precipitation = the percent of annual variation explained by precipitation, calculated by dividing the total covariate by the corrected total and multiplying by 100

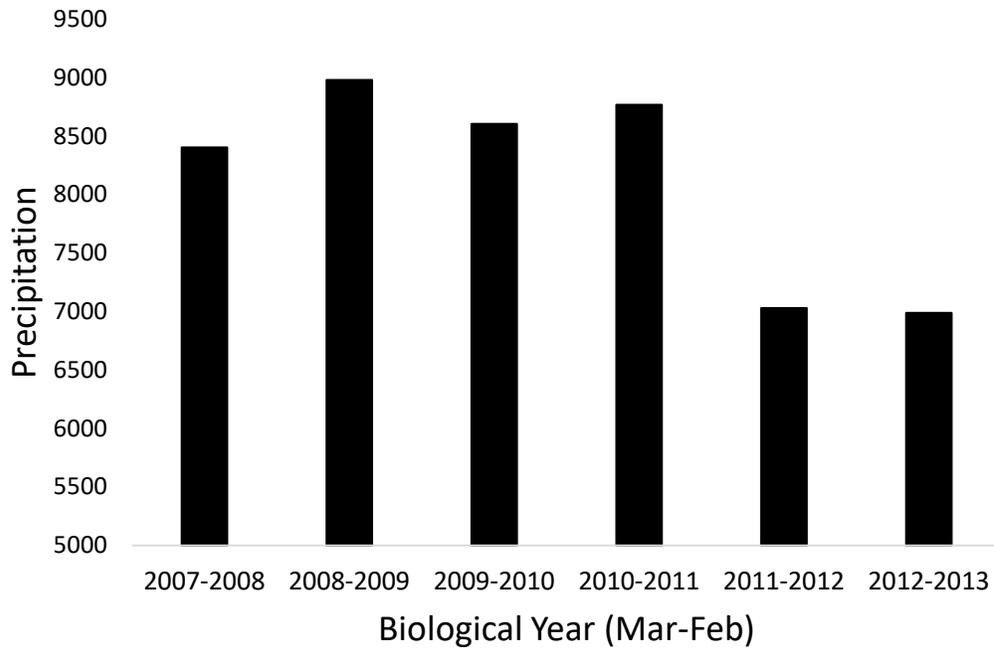
<sup>d</sup>  $\phi \beta$  (95% CI) = the beta estimate and 95% confidence interval from the  $\phi(\text{precip}) p(\cdot)$  models that were competitive with top models in estimating apparent survival

<sup>e</sup>*P* value = the significance of the ANODEV procedure result

## Figures



**Figure 3.1** Variation in sampling effort across years measured in number of hours a 12-m mist-net was open during the sampling event.



**Figure 3.2** Variation in precipitation measured in millimeters during the biological year preceding sampling event (e.g., March 2007 – February 2008).

**Chapter 4 - Genetic evidence of environmental constraints on the strength of sexual selection across populations of a Neotropical bird**

Elsie H. Shogren, W. Alice Boyle

## Abstract

Sexual selection can play a significant role in shaping morphology, behavior, and life history traits, particularly in certain clades. Even within lineages subject to sexual selection, there is considerable variation in behavior and traits, suggesting that the strength of sexual selection varies among species and populations. However, the intensity of sexual selection is difficult to measure and the causes of variation in its strength are not well understood. One possibility is that sexual selection varies due to abiotic constraints resulting in mortality, which in turn affects social dynamics. In the Neotropics, precipitation influences survival and demography of the White-ruffed manakin (*Corapipo altera*), a long-lived species in which males gain mating opportunities through elaborate courtship displays and their position in social hierarchies. Variance in male reproductive success (reproductive skew) is a hallmark of *C. altera*'s lek mating system, but the degree of reproductive skew, and therefore the strength of sexual selection, may be limited by precipitation- or temperature-imposed population-level differences in survival and stability of social hierarchies. To test this prediction, we used a novel genetic approach to measure reproductive skew, quantifying the nucleotide diversity of Z chromosomes relative to autosomes (Z/A) as a proxy for the effective population size of males relative to females in the population. We sampled *C. altera* at seven sites in Costa Rica spanning both Caribbean and Pacific slopes, and subject to a range of environmental conditions, testing relationships between Z/A diversity and temperature, mean annual precipitation, and precipitation seasonality. Z/A diversity declined as precipitation seasonality increased, indicating that reduced reproductive skew, indicative of weaker sexual selection, occurred at sites that were more consistently wet throughout year. To understand what other genetic differences might be associated with this pattern, we also quantified genetic differentiation between and genetic

diversity within sites. ADMIXTURE and  $F_{ST}$  analyses showed clear genetic differentiation between sites on the Caribbean and Pacific slopes of Costa Rica. Inbreeding coefficients and the proportion of heterozygous loci at sites on the Pacific slope were slightly lower than on the Caribbean sites. However, levels of whole-genome nucleotide diversity ( $\pi$ ) were similar across all sites. Taken together, these results suggest that divergent selection or drift in genetically isolated lineages on opposite slopes of Central American mountains may underlie differences in the relative diversity of Z/A among populations. However, further modeling of demographic histories will be required to fully elucidate the relative importance of climate and other evolutionary processes in shaping the genetic diversity of *C. altera*. In summary, using genetic measures in populations subject to a range of environmental conditions provides an elegant way to test predictions arising from ecological and behavioral research, and can advance our knowledge about the ways in which multiple sources of selection interact to shape the diversity of reproductive traits and behaviors.

## Introduction

Animals survive and reproduce across an incredible range of habitats and abiotic conditions. In the process, natural selection generates astonishing diversity of physiological, behavioral, and genetic adaptations (Williams 1966, Boag and Grant 1981, Keller et al. 2013). However, sexually reproducing taxa are subject to another powerful evolutionary driver that interacts with natural selection in multiple ways. Sexual selection has been implicated in the evolution of some of the most distinctive behaviors and traits in animal taxa (Plard et al. 2011, Ligon et al. 2018). High variance in reproductive success due to female choice and male-male competition has led to ritualized courtship behaviors, direct physical competition for mates, and exaggerated traits (Fiske et al. 1998, Lindsay et al. 2019). Although the dual roles of natural and sexual selection have been recognized in the evolution of honest signals of quality (O’Steen et al. 2010, Segura and Mahler 2019), there are many ways these two processes can interact to shape trait evolution, and some of those intersections are not well understood (Cornwallis and Uller 2010, Maan and Seehausen 2011).

Interactions of natural selection and sexual selection in shaping discrete traits and behaviors have been well documented. Sexual selection can operate via the handicap model, where maintenance of a costly trait signals individual quality to prospective mates (Zahavi 1975, Tazzyman et al. 2014). At some point, selection for the trait is limited when costs are elevated due to increased natural selection that limits benefits to reproductive success (Heinen-Kay et al. 2015). In taxa where sexual selection operates in a “run-away” process, the correlation between male traits and female mating preference can lead to reduced male viability (Lande 1980, Kirkpatrick 1982). Again, natural selection is expected to eventually constrain the scope of sexual selection if the fitness benefits of a sexually selected trait or behavior no longer outweigh

the costs incurred by the trait (Koga et al. 1998, Pomiankowski and Iwasa 1998). However, a lingering question remains; why is there apparent variation in the strength of sexual selection even when trait values do not seem to be constrained by natural selection? It is possible that natural and sexual selection are linked indirectly via environmental constraints (Twiss et al. 2007). If natural selection increases mortality through mechanisms that are unrelated to sexually selected traits, this environmental constraint may influence the strength and direction of sexual selection in a population via changes in demography or social interactions. Population-level differences in the strength of natural selection due to environmental variation could therefore be crucial factors in shaping the evolutionary trajectories of sexually selected taxa.

Testing predictions about the drivers of variation in the strength of sexual selection within populations is challenging. Directly quantifying variance in reproductive success (reproductive skew) requires genealogies, tracking survival and monitoring recruitment for large numbers of organisms (Ursprung et al. 2011, Chen et al. 2019). Fortunately, indirectly measuring reproductive skew using genetic estimates and next generation sequencing has become increasingly feasible (Excoffier et al. 2013, Toews et al. 2016, Kraus 2019). Combining novel genetic estimates of reproductive skew with sampling at sites that span environmental gradients make it possible to test predictions for how differences in abiotic constraints can influence the strength of sexual selection. For example, if specific biotic or abiotic factors are known to affect the ecology and life history of a species, measuring the variance in reproductive success of populations distributed along biogeographic gradients can elucidate whether and how natural selection due to environment constrains sexual selection. In particular, environmental variation that can be directly linked to demography and survival allows us to test how mechanisms limiting the strength of sexual selection are modulated.

Variation in rainfall is an often-overlooked potential source of natural selection. Especially in tropical regions, studies of natural and sexual focus heavily on biotic interactions, while abiotic conditions are generalized as mild and therefore less important as a selective force (Dobzhansky 1950). However, as the main axis of tropical climate variability, the role of precipitation in shaping the ecology and evolution of endotherms is beginning to be more broadly appreciated (Boyle et al. 2020, *in press*). Associations between rain and plant productivity makes indirect, food-mediated responses to changing precipitation intuitive (Mendoza et al. 2017). However, rain can also directly affect individual condition with implications for fitness. For example, the metabolic rate of a tropical bat increased two-fold under wet experimental conditions (Voigt et al. 2011). Individual-level effects are expected to scale up to fecundity and survival at the population-level (Dunham et al. 2011, Ryder and Sillett 2016). In addition to total annual precipitation, the distribution of rainfall throughout the year (seasonality) can also be important for demography. Increased rainfall during the dry season was associated with widespread population declines in a community of lowland tropical birds (Blake and Loiselle 2015). Direct and indirect effects of precipitation clearly have the potential to shape behavior and influence reproduction and survival, particularly in wet, tropical forests. Thus, rainfall amounts, the seasonal pattern of rainfall, and interactions between rain and temperature, which affect thermogenic and foraging costs, have the potential to impose constraints on the scope of sexual selection in tropical vertebrates.

Manakins (Pipridae) are a family of Neotropical birds whose morphology and behavior has been strongly shaped by sexual selection. This family is characterized by courtship displays performed by brightly-colored males for females who wield the power of mate choice (Prum 1990). Males do not provide any parental care and mating occurs after females have assessed

males at aggregations of display areas known as leks (Sick 1967). Reproductive skew in male mating success is a defining feature of lek mating systems, as the majority of female matings accrue to only a small proportion of males in the population. Manakins are also long-lived given their small body size, with individuals of some species surviving 10 – 15 years (Snow and Lill 1974, DuVal 2012). In most species males retain age-graded sub-adult plumages for multiple years after hatching (Kirwan and Green 2011); although young males spend time at display sites and practice courtship behaviors, they are rarely seen displaying successfully for females. Instead, they become integrated into complex social hierarchies at display sites (McDonald 2009, Lukianchuk and Doucet 2014), usually characterized by a single dominant male of adult plumage who co-opts the vast majority of mating opportunities at that site. In some species, there are subordinate adult-plumaged males also regularly associated with individual display sites who queue for opportunities to become the dominant male (DuVal 2007). Even among males who have attained dominant status, there is still variability in reproductive success (i.e., reproductive skew), with a relatively few males mating with the majority of females (McDonald 1993, DuVal and Kempenaers 2008). The combination of delayed and highly variable reproductive success of male manakins means that factors that reduce the longevity or disrupt the social stability of such populations would diminish opportunities for sexual selection.

White-ruffed Manakins (*Corapipo altera*) breed in montane primary forests of S. Central America and N. South America (Rosselli et al. 2002). *Corapipo altera* have previously been split into two sub-species based upon slight differences in plumage (Kirwan and Green 2011). In Costa Rica, *C. a. altera* is found on the Caribbean slope while *C. a. heteroleuca* is distributed on the Pacific slope (Rosselli et al. 2002). Due to the importance of rainfall for the species' demography, behavior, and physiology, it is an excellent species in which to test predictions

regarding environmental constraints on reproductive skew. In one of the wettest parts of its range, heavy rainstorms resulted in physiological responses including mobilization of fat stores, evidence of fasting, and elevated corticosterone (Boyle et al. 2010). Individuals facultatively migrate altitudinally in the non-breeding season, to lower elevations where less rain falls. Despite losing social status and female preference during the subsequent breeding season, males are more likely to migrate than females (Boyle et al. 2011). Additionally, in two populations where demographic estimates specifically for males have been calculated, apparent survival differs dramatically. Male *C. altera* subject to more than 8000 mm of rain annually have estimated apparent survival of 0.48 (W.A. Boyle, *unpublished data*). By contrast, estimates of apparent survival range from 0.90 to 0.99 for males in unfragmented forest sites receiving less than 4000 mm of precipitation (Ruiz-Gutiérrez et al. 2008).

We hypothesize that differences in demography related to rainfall should influence the strength of sexual selection and degree of reproductive skew among populations of *C. altera*. Specifically, lower annual apparent survival will decrease the probability a dominant male survives to display the following year, which would increase rates of turnover in the dominant males coopting the majority of copulations. Females in populations with lower apparent survival would then be choosing from a more dynamic pool of candidate males each year, relative to females in populations where males are more likely to survive and maintain dominance to display in subsequent years. The cumulative effect of this relative transience of dominant males in populations with lower survival should be a reduction in reproductive skew. Where populations are subject to more precipitation or other abiotic conditions that could increase mortality (e.g., reduced seasonality in precipitation, lower temperatures), we expect that a larger

proportion of males achieve some reproductive success than do in populations with higher survival and more static social hierarchies.

Alternative patterns could arise in two potential ways. First, the metrics of current environmental variation may not be strong enough or consistent enough over sufficient time to affect skew via demographic processes. Another possibility is that rainfall has affected demography in the ways described, but that differences in demography do not affect reproductive skew as predicted. This could occur if the most successful males survive disproportionately longer than others, remaining dominant for many years, despite low apparent survival throughout the population. If so, females may still choose this very small percentage of potential mates, maintaining high reproductive skew independent of demographic differences imposed by the environment. However, in the population of *C. altera* with low male apparent survival, previous research found 66.5% turnover in alpha status every year, indicating a dynamic social hierarchy (Jones et al. 2014). While these alternatives may bear further investigation, a necessary first step is testing whether reproductive skew varies predictably with environmental conditions known to influence demography.

Measuring reproductive skew directly in the field can be challenging even in a single population as it requires genotyping all males, all mothers, locating nests, and sampling offspring before they fledge. This is infeasible when studying multiple populations, and even in single populations for species such as *C. altera*, where nests are extremely cryptic and located high in trees. Instead, we measured skew indirectly, assessing relative effective population sizes of males and females using genetic methods. Birds have a ZW sex chromosome system males being the homogametic sex; males have two copies of the Z chromosome, females have a Z and a W chromosome, and both sexes have two copies of each autosome (A; Ellegren 2013). This means

there are three copies of the Z chromosome for every four autosomes when a population has a balanced sex ratio and there is no reproductive skew. Thus, the null expectation is that the genetic diversity of Z chromosomes relative to autosomes should be 0.75 (Ellegren 2009). However, reductions in the number of reproducing males relative to females should disproportionately reduce the effective population size and genetic diversity of Z chromosomes in the population (Corl and Ellegren 2012). Under extreme reproductive skew, where a single male monopolizes all reproduction, Z/A diversity can theoretically approach 0.5 (Vicoso and Charlesworth 2009, Wright et al. 2015). Thus, the ratio of genetic diversity on the Z chromosome relative to genetic diversity on the autosomes (Z/A) provides a population-level metric of reproductive skew (Ellegren 2009).

The relative genetic diversity of sex chromosomes and autosomes has recently been used to answer questions about mating patterns, selection history, and speciation in mammals as well as birds (Wilson Sayres 2018). In mammals, measures of X/A diversity have shed light on sex-biased demography and signatures of natural selection in humans (Wilson Sayres et al. 2014, Webster and Wilson Sayres 2016) and positive selection on sexually-selected traits in bighorn sheep (Kardos et al. 2015). In birds, studies of genetic diversity on the Z chromosome have focused on its role in speciation (Borge et al. 2005, Irwin 2018) and inferences about selection and population bottlenecks (Sundström et al. 2004, Balakrishnan and Edwards 2009). In birds, species pairs that differed in mating system also differed in Z/A diversity; polygynous species had lower Z/A, suggesting greater reproductive skew than their monogamous counterparts (Corl and Ellegren 2012). Z/A diversity was unexpectedly lower in monochromatic than dichromatic members of species pairs, suggesting that reproductive skew is in fact greater in monochromatic species (Huang and Rabosky 2015). In two species of lekking sage grouse, Z/A diversity was

consistent with predicted values  $< 0.75$ , ranging from 0.38 to 0.54; values lower than 0.5 may be due to selective sweeps reducing diversity at linked loci (Oyler-McCance et al. 2015).

Reduced diversity on sex chromosomes can be influenced by evolutionary history in ways unrelated to the magnitude of reproductive skew. Population bottlenecks will reduce sex chromosome diversity more rapidly than autosome diversity (although it is also expected to recover that variation more quickly; Pool and Nielsen 2007). Additionally, where there is high variance in male reproductive success, reductions in effective population size will increase the strength of genetic drift in driving evolution on the Z-chromosome (Wright et al. 2015). Disentangling these effects is a challenge but understanding the underlying genetic diversity in sampled populations can help to clarify the context in which environmental variation might be shaping reproductive skew. Assessing population structure and degree of genetic differentiation between sampled sites can provide insight to potential differences in demographic history, as can comparison of measures of inbreeding and overall population genetic diversity.

Although a recent meta-analysis has quantified geographic variation in intensity of sexual selection among populations of barn swallows based on morphology and fitness measures (Romano et al. 2017), to our knowledge, this is the first study to use the Z/A diversity metric to test predictions relating the strength of sexual selection to environmental variation among populations of birds. Because of previously documented adverse consequences of heavy rainfall for physiology, apparent annual survival, and social dominance in *C. altera*, we predicted that the strength of sexual selection and reproductive skew would be lower at sites experiencing higher annual rainfall, precipitation throughout more of the year (i.e., less seasonality) and/or lower temperatures. Consequently, we expected that Z/A genetic diversity would be lower in these populations than in populations at drier, warmer, more seasonal sites. To provide further

context for understanding geographic patterns of Z/A diversity, we also assessed population structure, and quantified genetic diversity, inbreeding, and genetic differentiation.

## Methods

We collected genetic data from *C. altera* at seven sites distributed along replicated precipitation gradients on the Caribbean (three sites) and Pacific slopes (four sites) of Costa Rica spanning the broadest range of climatic variation possible within the breeding elevations of this species (Figure 4.1). On the Caribbean slope, we sampled at Parque Nacional Volcán Tenorio (VT), Rara Avis (RA) biological reserve adjacent to Parque Nacional Braulio Carrillo, and La Reserva Biológica El Copal (EC). On the Pacific slope, we captured birds at Parque Nacional La Cangreja (CG), private reserve La Chaqueta (LQ), private reserve Monte Azul near San Isidro de General (SI), and Organization for Tropical Studies biological station Las Cruces (LC; Table 4.1).

At each site we captured birds by placing 38-mm mesh, 12 m long mist nets (Ecotone) in the understory of intact forest in locations where we detected *C. altera*. Where possible we sexed captured individuals based upon plumage; young male *C. altera* are often indistinguishable from females, and we recorded those individuals as sex unknown. For every sampled individual we collected 50 – 70  $\mu$ l whole blood through brachial venipuncture. We immediately transferred whole blood to Queen's lysis buffer and kept samples at room temperature in the field for 1 – 3 weeks until return to Kansas State University (KSU). We then refrigerated samples at 3 °C prior to DNA extraction. We used DNeasy blood and tissue kit (QIAGEN Inc., USA) to extract DNA from blood, and stored extracted DNA at -80 °C.

We had previously sequenced the genome of a female *C. altera* collected at the VT site (Baldwin et al. *in prep*). This reference genome was sequenced and assembled using 10x linked

read technology and is publicly available at the National Center for Biotechnology Information (ASM394572v1). Following an *in-silico* digest of the reference genome, the next generation sequencing team at the University of Minnesota Genomics Center (UMGC) determined which restriction enzymes were optimal for the project. UMGc prepared libraries and sequenced samples using the following protocols. For each sample, 100 ng of DNA was digested with 10 units each of BtgI and TaqI from New England Biolabs (NEB) and incubated at 37 °C for 2 hours before heat inactivating at 80 °C for 20 minutes. Samples were then ligated with 200 units of T4 ligase (NEB) and phased adaptors with CRYG and CG overhangs at 22 °C for 1 hour before heat killing. The ligated samples were purified with PSRI beads and then amplified for 18 cycles with 2x NEB Taq Master Mix to add unique barcodes to each sample. Libraries were purified, quantified, pooled, and size selected for the 300 – 744 bp library region and diluted to 2 nM prior to sequencing. UMGc sequenced 150-bp single-end reads across four lanes of a NextSeq 550 High-Output FlowCell (Illumina, USA). The resulting fastq files were demultiplexed using Illumina bcl2fastq software and Trimmomatic was used to remove adapter sequences, the first 12 bases, from the 3' ends of reads. The fastq files were then aligned to the *C. altera* reference genome using Burrows-Wheeler Alignment (Li and Durbin 2009). UMGc used FreeBayes to jointly call variants across all samples simultaneously, generating a raw Variant Call Format (VCF) file (Garrison and Marth 2012). The raw VCF file was then filtered using VCFtools to remove variants with minor allele frequency less than 1%, variants with genotype rates less than 95%, and samples with genotype rates less than 50% (Danecek et al. 2011). We then used this filtered VCF file for all subsequent analyses.

To calculate a ratio of Z chromosome nucleotide diversity to autosomal nucleotide diversity, we first obtained a CACTUS alignment of our *C. altera* reference genome to the Zebra Finch Z

chromosome (Armstrong et al. 2019). This allowed us to identify Z-linked scaffolds and separately calculate Z chromosome and autosomal nucleotide diversity. To determine the sex of individuals we could not sex based on plumage or reproductive characters in the field ( $n = 11$ ), we used VCFtools to assess heterozygosity on the largest Z-linked scaffold. We considered individuals that were entirely homozygous with no heterozygosity on Z-linked scaffolds to be females, due to their being heterogametic (only one copy of the Z chromosome). We then restricted subsequent analyses to only males so that measures of Z/A for each site would not be affected by different proportions of females ( $n$  males = 120 diploid individuals, Table 4.1). To assess average variation across the genome we used VCFtools to calculate  $\pi$  in 10 kb pair sliding windows, calculating an average  $\pi$  weighted by the number of variants in each window. For each site we calculated an average  $\pi$  based on all windows on the Z-linked scaffolds ( $Z \pi$ ), and an average  $\pi$  for all windows on autosomes ( $A \pi$ ). We calculated the Z/A metric of reproductive skew for each site as  $Z \pi$  divided by  $A \pi$  based on all males sampled at that site. Because nucleotide diversity varies with the number of individuals sampled (Carreras et al. 2017) and the number of males we captured varied among sites, we used rarefaction to estimate the error associated with our calculations of Z/A (Petit et al. 1998, Xu et al. 2019). That is, for each site we calculated Z/A for every rarefied  $n$ , from the total  $n$  of males sampled at that site down to  $n = 10$ . For example, we calculated a measure of Z/A at site SI for  $n = 12$ , and then randomly subsampled those 12 males to calculate Z/A for  $n = 11$ , and  $n = 10$  (rarefied  $n = 3$ , Table 4.1). We then used the rarefied estimates of Z/A to calculate overall mean and 95% confidence interval for Z/A diversity at each site. At one site (LC) we only captured 6 males. In preliminary analyses, we found that rarefaction to  $n < 10$  individuals biased estimates of Z/A. Therefore, we present only a point estimate of Z/A for LC based on the 6 males sampled at that site.

We assessed relationships between Z/A genetic diversity and climatic conditions using Worldclim data and local precipitation records. Worldclim uses weather station data summarized across three decades (1970 – 2000) to interpolate climatic estimates at approximately 1 km<sup>2</sup> resolution (Fick and Hijmans 2017). We extracted mean annual temperature for all sites, and precipitation data for five of the sites from Worldclim. For two sites, we obtained local precipitation data that was measured on location, assumed to more accurately reflect the conditions experienced by *C. altera* at these sites. Data from RA spanned 1991 – 2009 and data from LC spanned 2009 – 2019 (Organization for Tropical Studies). We regressed Z/A diversity on each of the following environmental variables separately: annual mean temperature, annual mean precipitation, and coefficient of variation for monthly mean precipitation as a metric of rainfall seasonality.

To understand how underlying genetic differentiation between sites might influence measures of Z/A diversity, we converted the VCF file to a binary format using PLINK 1.07 (Purcell et al. 2007) and then analyzed population structure in the ADMIXTURE program using the full dataset (males and females; Alexander and Lange 2011). With the cross-validation error estimation procedure, we evaluated optimal clustering of samples based on ancestry for a hypothetical number of populations ( $K$ ) between 1 and 7. We also visualized probabilities of assigning ancestry of individuals to a given population using structure plots. To further quantify genetic differentiation among sampling sites, we estimated mean pairwise fixation index ( $F_{ST}$ ) across all biallelic loci using ADEGENET and stAMPP packages in R (Weir and Cockerham 1984, Jombart and Ahmed 2011, Pembleton et al. 2013, R Core Team 2018). We calculated 95% confidence intervals for pairwise  $F_{ST}$  using 1000 bootstrap replicates in stAMPP.

Because population bottlenecks or expansions could influence Z chromosome diversity disproportionately, we also assessed more general measures of genetic diversity at each site using the full dataset. We calculated inbreeding coefficient ( $F_{IS}$ ) for all individuals with VCFtools before averaging values to calculate a mean  $F_{IS}$  for each site (Weir and Cockerham 1984). We also calculated the mean proportion of heterozygous biallelic loci for each site. Finally, we calculated mean nucleotide diversity ( $\pi$ ) for each population, averaging and weighting by number of variants in 10 kb pair sliding windows across the whole genome.

## Results

We captured and sampled genetic material from a total of 158 individuals, 15 to 35 individuals per site (mean = 22.6, standard deviation = 9.0; Table 4.1). Mean annual temperature varied between sampling sites relatively little, from 20 – 23 °C, and was associated with ~450 m in elevational differences among sites (Table 4.1, Figure 4.2a). Mean annual precipitation on the Caribbean slope ranged from 3450 mm at EC to 8284 mm at RA (Table 4.1, Figure 4.2b). On the Pacific slope mean annual precipitation varied between 3040 mm at CG to 4115 mm at SI (Table 4.1, Figure 4.2b). Seasonality in precipitation (coefficient of variation of monthly means) was dramatically different between Caribbean and Pacific slopes (Figure 4.2c). Caribbean slope sites received rain throughout much more of the year (CV = 32–44), while precipitation on the Pacific side, was far more seasonal (CV = 66–72, Table 4.1). To put these CV values in perspective, at RA on the Caribbean slope, precipitation seasonality was 44 and mean monthly precipitation ranged from 514 mm to 824 mm. On the Pacific slope at LC, precipitation seasonality was 72 and mean monthly precipitation values ranged from 41 mm to 598 mm.

Initial sequencing of 158 samples resulted in 440,895 markers on 97,470 loci. Following the filtering process, the final dataset consisted of 158 samples and 247,846 markers on 65,277

loci. Ratios of Z chromosome genetic diversity to autosomal diversity ranged from 0.528 to 0.563; all were well below the neutral expectation of equal male and female effective population size (0.75), indicating strong reproductive skew overall (Table 4.1). Although there was clear variation among sites in Z/A, error estimates calculated via rarefaction did overlap for some sites (Figure 4.3). Measures of Z/A did not correlate with annual mean temperature ( $\beta = 0.00033$ , SE = 0.00055,  $p = 0.576$ ) or annual mean precipitation ( $\beta = 2.34 * 10^{-6}$ , SE =  $2.86 * 10^{-6}$ ,  $p = 0.451$ ) among the seven sampling sites (Figures 4.4a, b). However, as precipitation at sites became more seasonal, Z/A decreased ( $\beta = -0.00062$ , SE = 0.0025,  $p = 0.057$ ; Figure 4.4c), indicating that in populations that contend with rainfall distributed relatively evenly throughout the year, there is a larger effective population size of Z chromosomes and reproductive skew is lower. Because sites on the Caribbean and Pacific slopes differed in their degree of seasonality, this meant that measures of Z/A diversity were overall higher for sites on the Caribbean slope (0.548 – 0.563) than for sites on the Pacific slope (0.528 – 0.563; Table 4.1).

Analysis of genetic differentiation and diversity between sites and slopes revealed some evidence of past demographic history on differences in Z/A diversity. We identified strong population structure between the Caribbean slope sites and the Pacific slope sites using the ADMIXTURE program. Genetic similarity of individuals clearly clustered samples by slope origin; cross-validation error was minimized at  $K = 2$  (Figure 4.5), and structure plots distinctly separated Caribbean and Pacific slope individuals (Figure 4.6a). Within slope, gene flow among sites was evident, as some individuals from five of the sites showed mixed ancestry based on Bayesian clustering with ADMIXTURE when  $K$  was set to seven (Figure 4.6b). Pairwise comparison of  $F_{ST}$  between sites echoed this pattern of genetic similarity of sites within slope and greater differentiation of sites on different slopes. Pairwise  $F_{ST}$  values among the Caribbean

slope sites ranged from 0.020 to 0.037, while on the Pacific slope, comparisons ranged from 0.008 to 0.038 (Table 4.2). The pairwise  $F_{ST}$  for any two sites on different slopes ranged from 0.196 to 0.220 (Table 4.2). Site-level inbreeding coefficients ( $F_{IS}$ ) tended to be lower on the Caribbean slope (0.058 – 0.079) than on the Pacific slope (0.080 – 0.091), although there was overlap in the error surrounding these estimates (Figure 4.7, Table 4.3). Caribbean slope sites also had a higher proportion of heterozygous loci overall (0.156 – 0.160) as compared to the Pacific slope sites (0.140 – 0.143; Table 4.3). Despite differences in  $F_{IS}$  and heterozygosity, mean nucleotide diversity ( $\pi$ ) across the whole genome did not differ substantially based on slope. On the Caribbean slope,  $\pi$  ranged from 0.00167 to 0.00194 and on the Pacific slope  $\pi$  ranged from 0.00169 to 0.00192 (Table 4.3).

## Discussion

This study provides the first insight into whether and how the selective pressures of rainfall limits reproductive skew and the strength of sexual selection in a lekking species. Reduced nucleotide diversity on the Z chromosome relative to autosomes is a fundamental genomic prediction of sexual selection; that Z/A diversity should be affected by any constraints on sexual selection imposed by abiotic factors. To our knowledge, this prediction has not previously been tested in populations spanning environmental gradients. Nucleotide diversity on Z chromosomes relative to autosomes was higher in populations subject to rainfall throughout much of the year than in populations with more distinct wet and dry seasons. This result is consistent with environmental constraints – namely precipitation regime – constraining the strength of sexual selection. The lack of trend in the relationship between Z/A and mean annual precipitation potentially elucidates more nuanced effect of rainfall in this system. White-ruffed manakins concentrate their displaying and breeding efforts during the dry season, potentially balancing

energetic output, much as temperate species do when they separate molting, reproduction, and migratory phases of the year (Carlisle et al. 2005, Johnson et al. 2012, Saino et al. 2014). In environments where the “dry” season is in fact quite rainy (i.e., low seasonality in precipitation), separation of two energetic stressors, rainfall and reproduction, is impossible. Thus, how rainfall is distributed throughout the year may be a more important natural selective force than the total amount of precipitation.

Characterizing the overall genetic differentiation and diversity among sites was critical, given the other evolutionary processes that could influence patterns of genetic diversity on Z chromosomes and autosomes. There was clear genetic differentiation between sites sampled on the Caribbean slope and those sampled on the Pacific slope, based on both ADMIXTURE and  $F_{ST}$  analyses. This provides genetic support for previous sub-specific classification of these groups based on morphology and slight plumage differences. Male *C. a. heteroleuca* on the Pacific slope have a shorter “ruff” of white feathers under their bill, and *C. a. altera* has a longer and broader outermost primary wing feather (Kirwan and Green 2011). It is still unclear whether these genetic and morphological differences are simply the result of geographic isolation, or if behavioral changes on the display court have also arisen. To date, extensive field studies of *C. altera* have taken place only on the Caribbean slope, although brief surveys of display behavior of *C. a. heteroleuca* did not uncover any striking differences (Jones 2017), and there seem to be no difference in vocalization between the groups (Kirwan and Green 2011).

It is possible that the association between Z/A diversity and precipitation seasonality is conflated with clade or slope-level genetic differentiation; the limited number of sites and low replication within slopes precludes analytical models that could distinguish the independent role of climate per se from other, slope-level factors. In addition to being genetically isolated and

distinct, populations on the Caribbean and Pacific slopes of Costa Rica experience strikingly different precipitation seasonality. While the range of total annual rainfall is similar at sites on both slopes, seasonality of precipitation is much higher on the Pacific slope. Alternate evolutionary processes could result in a pattern of Z/A diversity that separates sites by slope, however. It is possible that extended geographic isolation and resulting genetic drift could underlie the differences between the sub-species in measures of Z/A. Stronger correlation between alleles within individuals is indicated by overall higher inbreeding coefficients on the Pacific slope than on the Caribbean slope (Holsinger and Weir 2009). Pacific slope sites also had lower heterozygosity when compared to Caribbean slope sites. Despite differences in inbreeding and heterozygosity metrics, whole genome mean nucleotide diversity was similar across all sites, with no emergent pattern based on slope. This suggests that inbreeding and heterozygosity divergence may be due to selection or drift rather than recent population bottlenecks or expansions, because nucleotide diversity should reflect effective population size (Ellegren 2013). To discriminate between potential drivers of genetic patterns, modeling the demographic history of the Caribbean and Pacific groups will allow us to infer the timing, and severity of demographic events (e.g., isolation, gene flow, bottlenecks, or expansions) that are consistent with the single nucleotide polymorphism data we have collected (Gutenkunst et al. 2009). Elucidating the biogeographic history of this species through additional sampling to the north and south on the Caribbean slope and farther south on the Pacific slope could also shed light on whether genetic divergence coincided with the uplift of the central mountains of Costa Rica (Coates and Obando 1996).

Additional sampling could clarify whether the pattern of Z/A diversity is conflated with slope-level differentiation. Here, we present data from seven sites; our analyses are therefore

limited in their power to detect associations with environmental variables and control for confounding factors. It is worth noting that substantially increasing the scope of such a study would require a large collaborative effort to procure research permits, identify and access potential sites, and capture birds, not to mention the effort associated with DNA extraction and sequencing. Given the logistical constraints on sampling, it is notable that despite low power and the small spatial gradients over which we sampled, we detected fairly strong genetic signal in this dataset consistent with key predictions.

Detection of measurable differences in Z/A within species, ranging from 0.527 to 0.563 among sampling sites is itself a key finding that offers exciting prospects for future research. Although closely related taxa have been shown to differ in diversity and selection on Z chromosomes, the implications of these differences have thus far been examined primarily in the context of genetic drivers of speciation or genetic consequences of mating system (Irwin 2018). For example, polygynous shorebird species were found to have slightly lower ratios of Z/A nucleotide diversity (0.45 – 0.57) than monogamous species (0.52 – 0.69; Corl and Ellegren 2012). While the variability in Z/A diversity among populations presented here is low, detectable differences suggest that this approach may have more general applicability in testing predictions related to sexual selection and ecological constraints within species. Manakins in particular are a group that would be amenable to such studies, as they inhabit a range of tropical forest types and exhibit a diversity of putatively sexually-selected behaviors. Generating and testing additional genetic predictions derived from previous research on the ecology, life history, and physiology of this group could substantially enhance our understanding of the mechanisms underlying variation in the strength of sexual selection in lek mating systems.

In lek and other mating systems, integrated study of sexual selection and eco-evolutionary dynamics is critical to better understand how potent evolutionary forces and ecology interact to shape organisms and their environments (Giery and Layman 2019). Most research has focused on how ecology interacts with sexual selection to drive species divergence (Safran et al. 2013). For example, both natural and sexual selection shape behavior and plumage differences between inland and tidal marsh subspecies of the Swamp Sparrow (*Melospiza georgiana*, Olsen et al. 2010). However, studies of temporal variation in sexual selection within populations have also shown that reproductive success and strength of sexual selection can be influenced by environmental conditions (Miller and Svensson 2014). In Collared Flycatchers (*Ficedula albicollis*), mating with highly ornamented males only conferred fitness benefits to females in years with drier breeding seasons (Robinson et al. 2012). Testing for evidence of spatial shifts in sexual selection related to variation in environment is therefore a logical next step in enhancing our understanding of the interactions between natural selection and reproductive skew. Biogeographic gradients provide an excellent framework for testing genetic predictions of variable sexual selection in species that are subject to different environmental conditions throughout their range.

As climate shifts in coming decades, determining how abiotic factors such as rainfall and temperature shape organisms will become increasingly important. In the tropics, precipitation is projected to change in both amount and timing (Feng et al. 2013). Given that the distribution of rainfall throughout the year was the environmental variable that most strongly influenced measures of Z/A diversity, this suggests that the natural selective force of rainfall is likely to increase. Thus, characterizing the genetic diversity and demographic effects of rainfall will be

crucial to understanding the consequences that changing climate poses for evolutionary trajectories of tropical animals.

The genomic patterns that are now visible through next generation sequencing are incredibly valuable in understanding how historic and ongoing sexual and natural selection shape species. Incorporating genetic predictions into behavioral and ecological studies is crucial for advancing our knowledge of the biological world. The complex interactions of organisms with each other and their environment requires an integrative research approach, drawing on multiple fields to comprehensively understand evolutionary processes and patterns. Finally, explicitly considering how rainfall shapes the evolution of tropical organisms is especially relevant, as projections for future change emphasize increased variability and intensity of precipitation.

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## Tables

**Table 4.1** Details and genetic measures for each sampling site.

site	sampling location	latitude	longitude	elev.	temp.	precip (mm)	precip seas.	total n	n males	rarefied n	Z/A	Z/A se
<b>VT</b>	PN Volcán Tenorio	10.70299	-84.99685	792	221	3934	44	35	33	24	0.563	0.00185
<b>RA</b>	Rara Avis	10.28117	-84.04994	810	229	8284	37	16	15	4	0.551	0.00015
<b>EC</b>	RB El Copal	9.78041	-83.75244	1172	200	3450	36	35	29	20	0.548	0.00223
<b>CG</b>	PN La Cangreja	9.71479	-84.36105	1110	217	3040	66	24	11	2	0.533	0.00168
<b>LQ</b>	La Chaqueta	9.50275	-83.91531	807	219	3216	61	18	14	5	0.533	0.00177
<b>SI</b>	San Isidro	9.43836	-83.62223	1121	210	4115	63	15	12	3	0.527	0.00079
<b>LC</b>	Las Cruces	8.78763	-82.97050	1239	206	3432	72	15	6	1	0.540	...

The two-letter code (*site*) and color scheme is maintained throughout tables and figures. *Sampling location* names the sampling site (see text for details). *Latitude*, *longitude* and elevation (*elev.*) provide geographical context. Mean annual temperature (*temp*) is in units of °C\*10 as extracted from Worldclim climate data. Mean annual precipitation (*precip*) is in millimeters. Precipitation seasonality (*precip seas.*) is the coefficient of variation for monthly means of precipitation. Local measured data was used to calculate mean annual precipitation and precipitation seasonality for RA and LC. The total number of individuals captured at each site is listed under *total n* while *n males* shows the number of males that were captured. *rarefied n* provides the number of estimates of Z relative to autosomal nucleotide diversity used to calculate a mean, after rarefying from max n of males sampled at the site, down to n = 10 males. *Z/A* is the mean value of Z chromosome nucleotide diversity relative to autosomal nucleotide diversity, averaged from rarified estimates for Z/A. *Z/A se* provides the standard error for those multiple Z/A estimates.

**Table 4.2** Pairwise  $F_{ST}$  of sites

	VT	RA	EC	CG	LQ	SI	LC
VT	...	0.020 (0.020, 0.021)	0.037 (0.036, 0.037)	0.220 (0.219, 0.222)	0.213 (0.212, 0.215)	0.212 (0.211, 0.214)	0.216 (0.214, 0.217)
RA	...	...	0.024 (0.024, 0.024)	0.217 (0.216, 0.219)	0.209 (0.208, 0.211)	0.208 (0.207, 0.210)	0.212 (0.211, 0.214)
EC	...	...	...	0.204 (0.203, 0.206)	0.197 (0.195, 0.198)	0.196 (0.194, 0.197)	0.198 (0.197, 0.200)
CG	...	...	...	...	0.018 (0.017, 0.018)	0.023 (0.023, 0.024)	0.038 (0.038, 0.039)
LQ	...	...	...	...	...	0.008 (0.008, 0.009)	0.023 (0.023, 0.024)
SI	...	...	...	...	...	...	0.022 (0.021, 0.022)

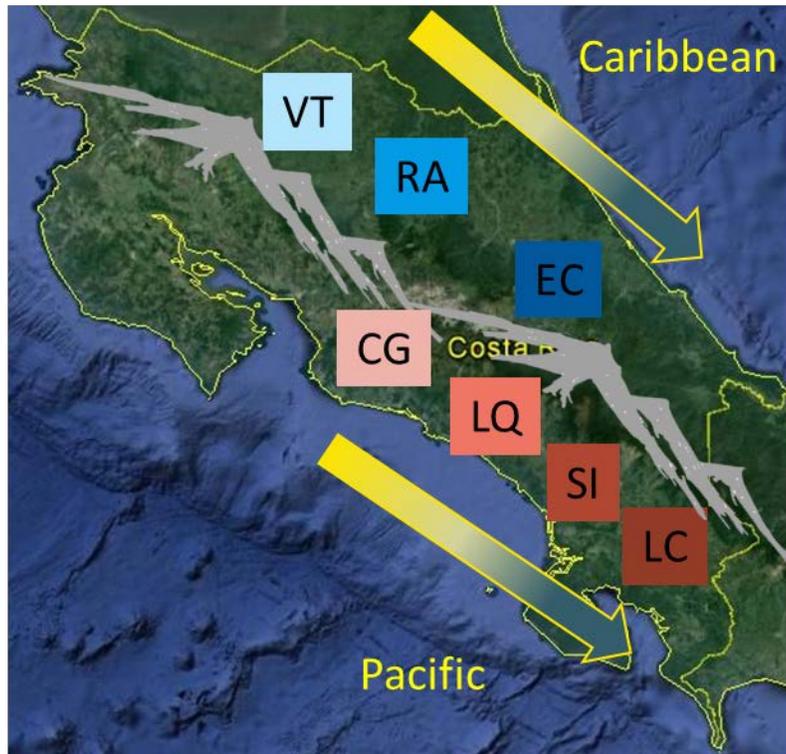
$F_{ST}$  calculated using stAMPP package in R. Values in parentheses are 95% confidence intervals calculated using 1000 bootstrap replications. Bold dashed lines delineate  $F_{ST}$  comparisons of sites on the same or different slopes.

**Table 4.3** Details of genetic diversity for each sampling site.

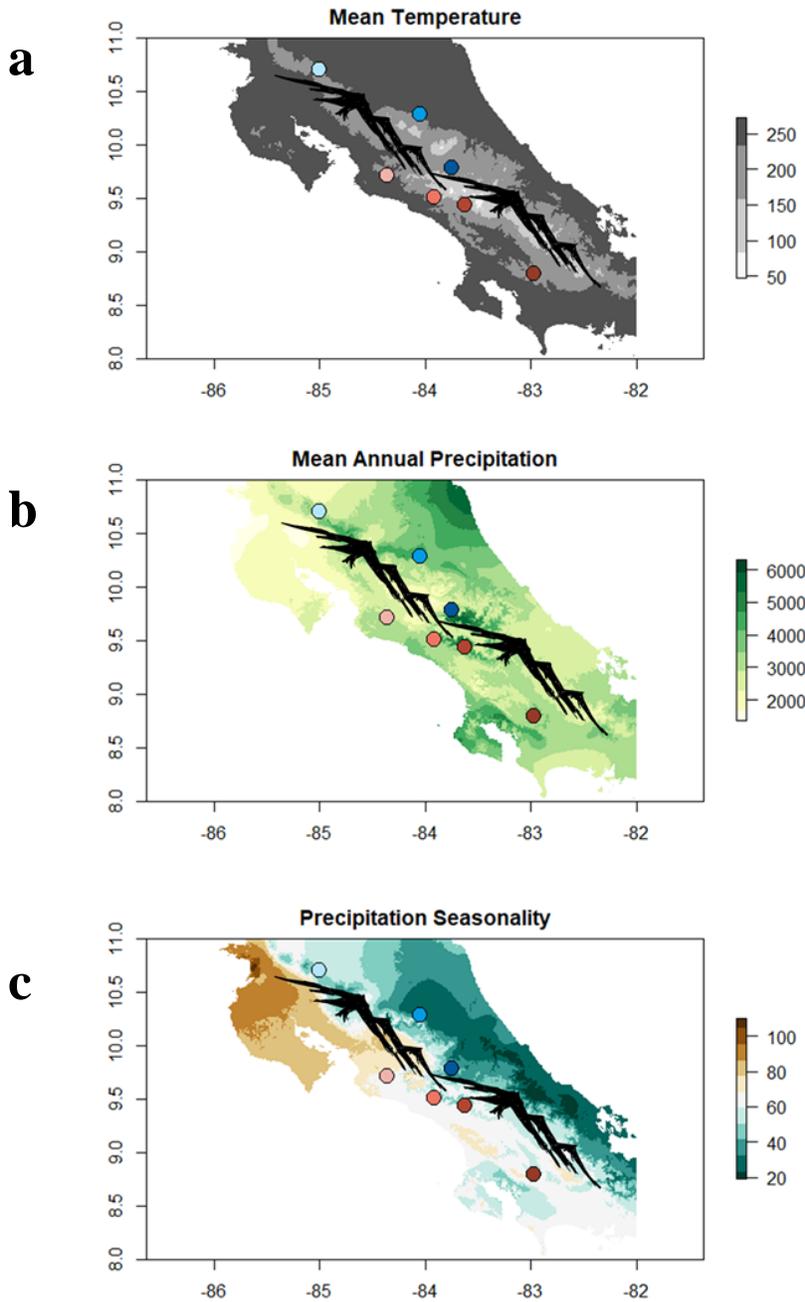
site	proportion heterozygous loci	inbreeding coefficient ( $F_{IS}$ )	$F_{IS}$ se	$\pi$
VT	0.156	0.0577	0.0102	0.00167
RA	0.157	0.0787	0.0068	0.00194
EC	0.160	0.0683	0.0052	0.00178
CG	0.140	0.0802	0.0129	0.00169
LQ	0.143	0.0831	0.0082	0.00184
SI	0.143	0.0844	0.0088	0.00192
LC	0.140	0.0912	0.0067	0.00189

The *proportion heterozygous loci* are averaged across all biallelic polymorphisms. The *inbreeding coefficient ( $F_{IS}$ )* is averaged across calculated  $F_{IS}$  for all individuals at each site, and  $F_{IS}$  se is the standard error of that calculation.  $\pi$  is the overall mean nucleotide diversity across the whole genome, measured in 10 kb pair sliding windows and weighted by number of variants in each window.

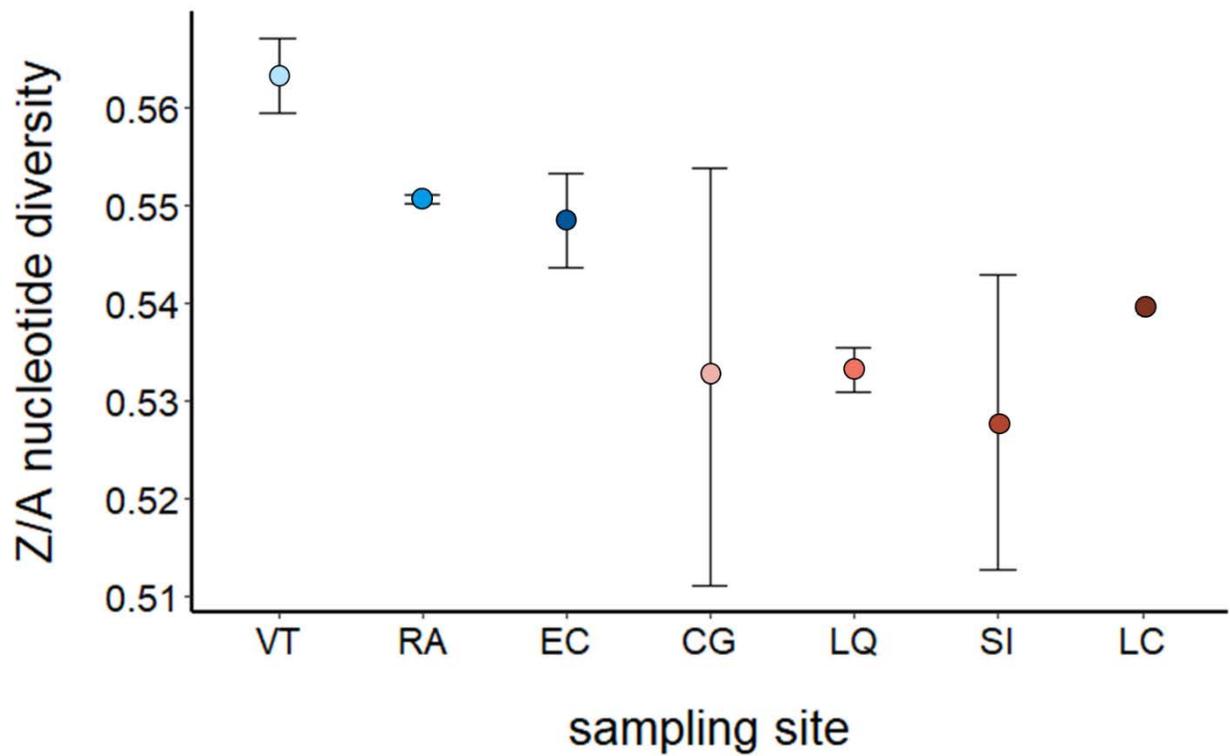
## Figures



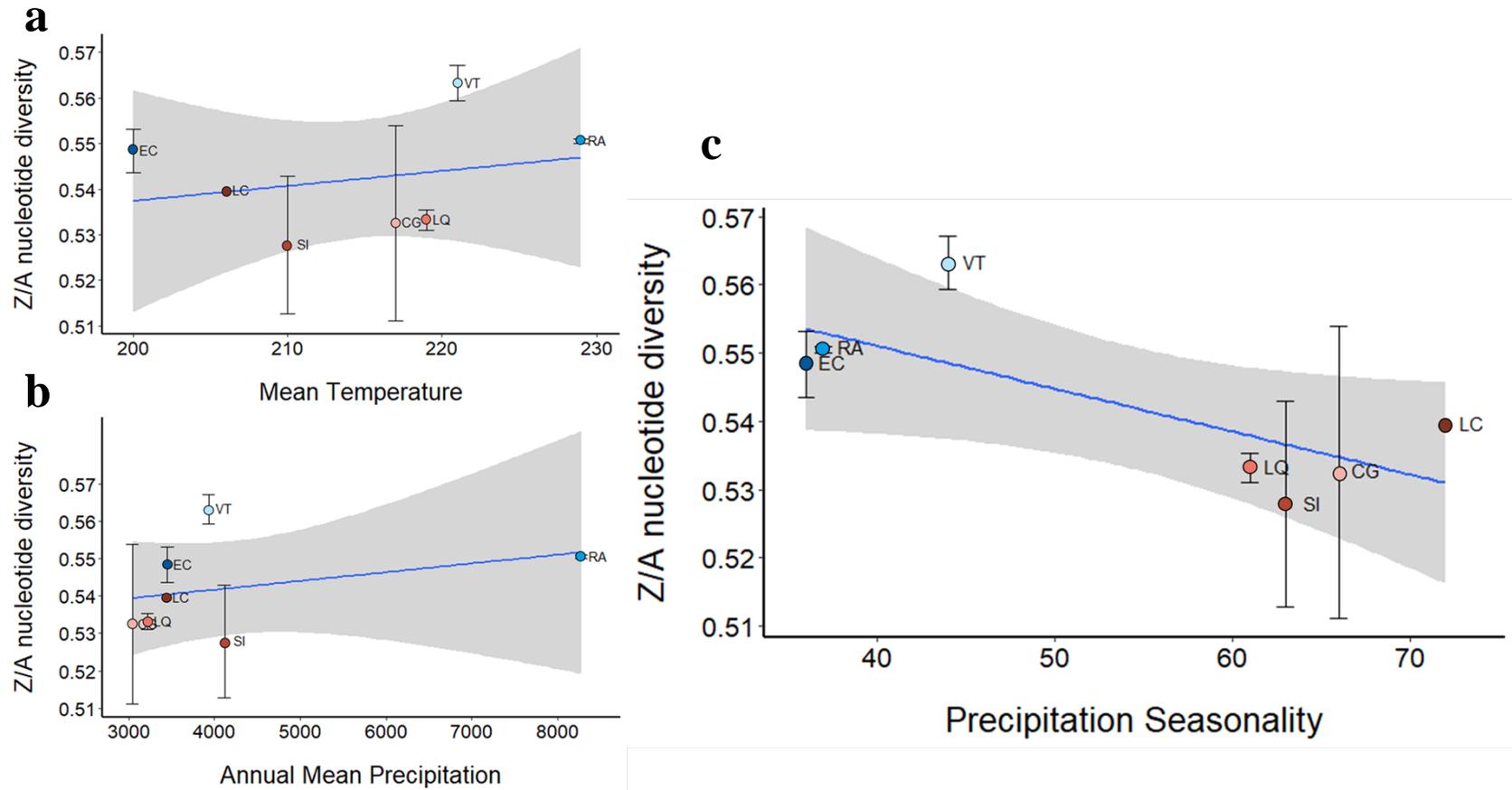
**Figure 4.1** Map of Costa Rica, showing spatial distribution of sampling sites with two letter codes. Grey mountain graphics denote central mountain range separating Caribbean and Pacific slopes of Costa Rica, and arrows show precipitation gradient from relatively drier (yellow base) to wetter environments (teal arrowhead). Color coding of sampling sites maintained throughout figures and tables.



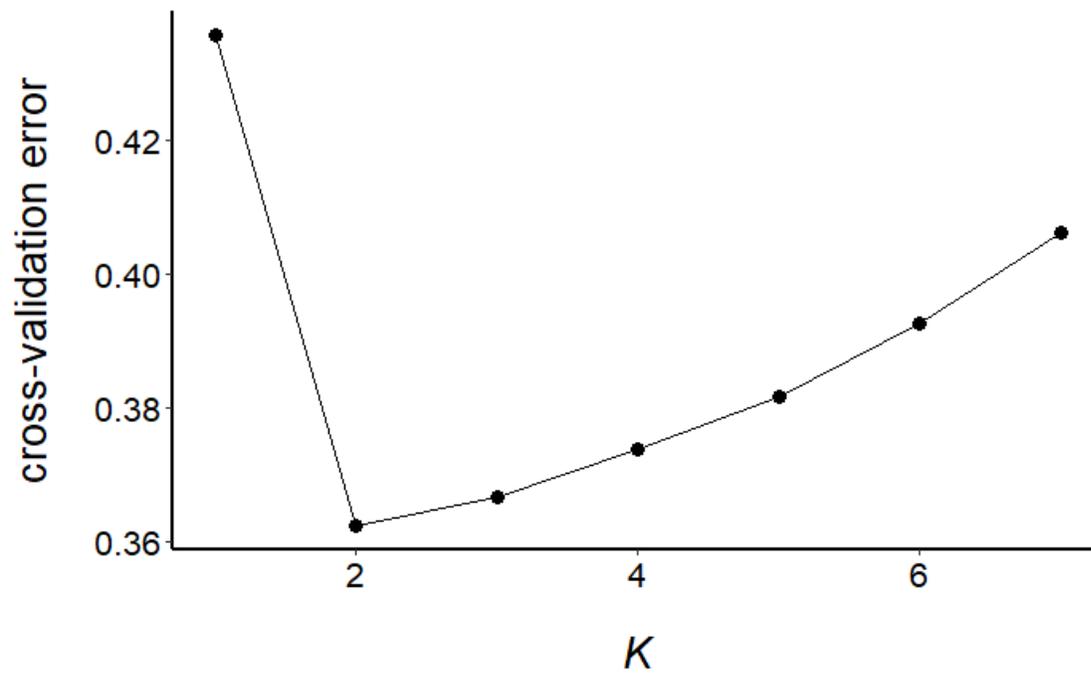
**Figure 4.2** Maps of Costa Rica showing environmental conditions at each sampling site. X axes are longitude values and Y axes are latitude values. Colors denote variation in environmental variables (legends to right of graph). Units of annual mean temperature (a) are  $^{\circ}\text{C} \times 10$  (as extracted from Worldclim), units of mean annual precipitation (b) are millimeters, and precipitation seasonality (c) is coefficient of variation of monthly means. Sites match color coding from other results, and black mountain graphics represent the central mountain range separating Caribbean and Pacific slopes of Costa Rica.



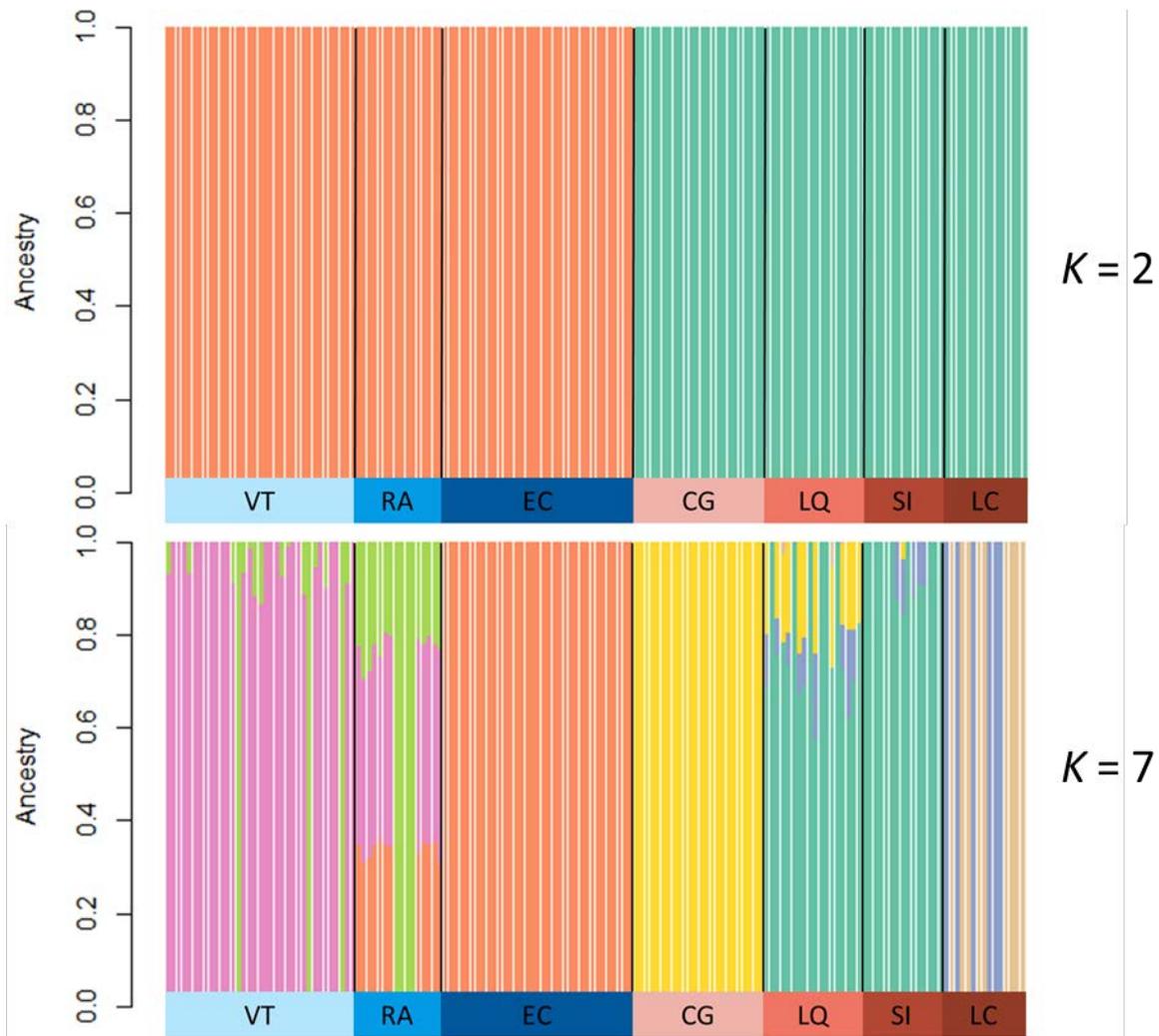
**Figure 4.3** Ratios of Z nucleotide diversity to autosomal nucleotide diversity, a metric for degree of reproductive skew. Higher Z/A nucleotide diversity suggests reduced reproductive skew, while lower Z/A indicates greater reproductive skew and stronger sexual selection. Error bars are 95% confidence intervals generated by rarefaction: calculating Z/A from maximum N to N = 10 for each site. Sample size for site LC = 6, so we did not rarefy or calculate error for that site.



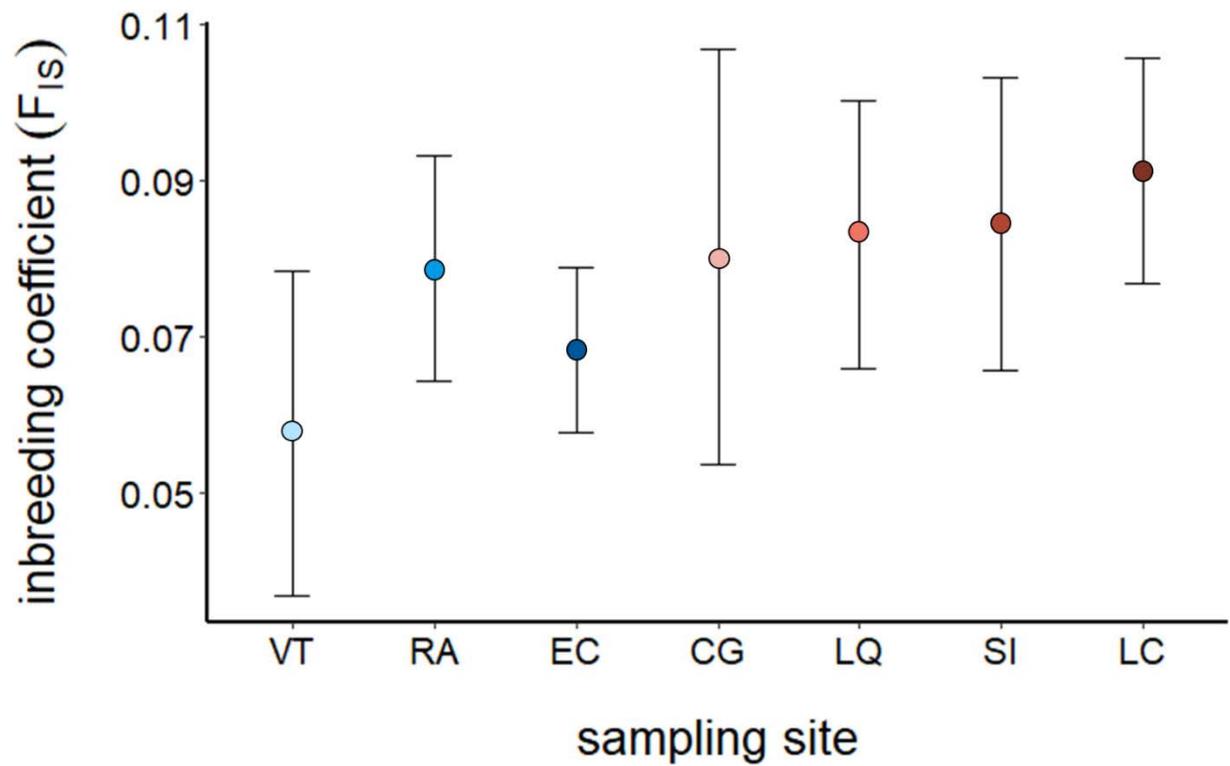
**Figure 4.4** Relationship between Z/A nucleotide diversity and environmental conditions at each sampling site. Units of temperature (a) are °C x 10, precipitation (b) units are millimeters, precipitation seasonality (c) is coefficient of variation of monthly mean values.



**Figure 4.5** Calculated error from five-fold cross-validation procedure in ADMIXTURE analysis. Lowest cross-validation error at  $K = 2$  supports two distinct genetic clusters.



**Figure 4.6** Structure plots from ADMIXTURE analysis. Each colored vertical bar is an individual sample, with colors corresponding to probability of ancestry in specific population. Black bars group individuals by site whether they were sampled. Top plot (a) is analysis with hypothetical population number ( $K$ ) = 2, bottom (b) is  $K$  = 7, the number of sites sampled.



**Figure 4.7** Average inbreeding coefficients ( $F_{IS}$ ) across all individuals (males and females) for each sampling site. Error bars denote 95% confidence intervals.

**Chapter 5 - Spread the word: male manakins cooperate with neighboring competitors to advertise the presence of display sites**

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## Abstract

Reproductive behavior is generally under strong selection, meaning that differences among individuals in how much they invest in mate attraction reveals important trade-offs in the costs and benefits of reproductive activities. Nevertheless, in many taxa with sex-specific displays, there is dramatic individual variability in investment in mate attraction. Male White-ruffed manakins (*Corapipo altera*), a species in the family Pipridae, exhibit dramatic variation in display investment, despite having a mating system shaped by strong sexual selection. We tested three alternative hypotheses that could explain variability in male investment in display: variation in (1) individual quality and condition, (2) competition, or (3) cooperation. We manipulated the social environment of male manakins at their display sites in two ways. First, we increased the acoustic signal around a focal male's display site, broadcasting the sounds of other displaying males to simulate nearby display sites. Second, we temporarily prevented the neighbors of focal males from using their display sites, thereby increasing the competition for display locations. Overall, our results were consistent with cooperation and not competition mediating individual investment in male display. Specifically, males reduced their vocalization rate in response to locally increased acoustic signaling. This suggests that males may cooperate with neighbors to advertise the locations of leks, minimizing their individual effort when possible. When neighbors were prevented from using their display sites, males at focal sites performed more displays for females, suggesting that manipulation focused female assessment on the focal log. However, the constancy in rates of all other display behaviors throughout both manipulations suggests that male quality or condition underlies much of the individual variation in behavior at display logs. These findings emphasize the importance of considering both intrinsic and social drivers shaping reproductive behavior.

## Introduction

Reproductive success hinges on an individual's ability to secure a mate in sexually reproducing animal species. When parental care falls disproportionately on one sex (generally females), there is typically strong selection on the other sex (generally males) to compete for mates (Clutton-Brock 2007). Strong sexual selection in these species can result in ritualized displays performed by males to compete with rivals and/or impress potential mates (Frith and Frith 2004, Girard et al. 2011, Ligon et al. 2018). Thus, theoretical and empirical evidence predicts strong directional selection on males to invest in courtship displays to attract mates (Amorim et al. 2013). Why, then, is dramatic within- and among-individual variation in display effort common in many species (McAuley and Bertram 2016, Ribeiro et al. 2019)? Despite strong selection on reproductive behavior, there are at least three, non-mutually exclusive potential drivers of individual variability in display effort.

First, males may vary in effort due to (1) *male quality and condition*—the intrinsic variation among individuals in their ability to perform displays and the associated costs and benefits they reap from reproducing. Male quality is influenced by genetic or physical traits such as size or ornamentation that remain relatively static throughout an individual's adult life (Brooks and Endler 2001). For example, male cichlids of differing color morphs are restricted to certain alternative mating strategies that incur corresponding consequences for reproductive success (Martin and Taborsky 1997). Additionally, condition-dependent traits which vary within individuals across their lifetime also contribute to variability in display effort. Male European tree frogs subject to experimental food limitation reduced their calling rates in response to energetic constraints (Brepson et al. 2013). The costs and benefits of investing maximally in a

reproductive bout may also change over an individual's lifetime, as residual reproductive value declines with age or condition (Williams 1966, De Moraes et al. 2019).

In addition to intrinsic factors, male frequently adjust their investment in display in response to extrinsic circumstances including at least two important social drivers. Specifically, (2) *competition* (Bretman et al. 2011, Legendre et al. 2012) can lead to elevated rates of display if a female is nearby or there is strong competition from neighboring males. Indeed, such responses appear to be common; in three-spine stickleback fish, males invest more in signaling and courtship behaviors when in the presence of a dummy rival while male sac-winged bats sing more often in colonies with more male rivals (Eckenweber and Knörnschild 2013, Kim and Velando 2014). Finally, some display contexts involve (3) *cooperation*, where males that are competing for reproductive opportunities coordinate their efforts to more effectively attract females and/or reduce their individual effort (Díaz-Muñoz et al. 2014). For example, a higher proportion of male Woodhouse's toads adopt a non-calling satellite role as the density of chorusing males increases (Leary et al. 2008). Similarly, chorusing male tropical katydids adjust the timing of their calls to fill either leader or follower roles while attracting females (Hartbauer et al. 2014).

Social modification of display investment should be especially important in lek mating systems where males aggregate and display consistently in the same locations. Males displaying near each other compete for position in the social hierarchy at the lek site and visiting females often mate with the most dominant male (Kirkpatrick and Ryan 1991, Höglund and Alatalo 1995, Magaña et al. 2011). Although dominant individuals mate more often than subordinates, lower-ranking males may still benefit from cooperating with rivals at the lek (Díaz-Muñoz et al. 2014). Improved reproductive success can derive from displaying in proximity to high quality

individuals or desirable resources (“hot shot” and “hot spot” hypotheses; Beehler and Foster 1988). Delayed fitness benefits could also be conferred to males who “queue” for status, and rise through the dominance hierarchy over the course of their life (Kokko et al. 1998, DuVal 2007a). Regardless of the underlying evolutionary forces, the duality of cooperating and competing at a lek could result in variable effort both within and between individuals, as subordinate or dominant individuals manage tradeoffs differently based on their status.

The ways in which males modify their reproductive effort depends on the nature of species-specific displays. Complex displays involving multiple components and diverse signaling modalities can be adjusted to maximize signal transmission across different spatial scales targeting different receivers. For example, vocalizations can advertise the presence of a potential mate across long distances while visual assessment of ritualized body movements at close range may inform female mating decisions (Gibson 1996). Use of multiple signaling modalities (e.g., visual, acoustic, tactile, seismic) can offer flexibility in male display. Wolf spider (*Rabidosa rabida*) males reduced investment in visual display elements when their ability to transmit visual signals was compromised (Wilgers and Hebets 2011). Similarly, male Green Tree Frogs (*Hyla cinerea*) in poor condition produce unattractive acoustic signals and will switch to silently associating with an actively calling male (Humfeld 2013). When males can differentially invest in multiple display components or signals, individual variability in display behavior may be more likely.

Neotropical Manakins (family Pipridae) are an ideal system for testing these hypotheses. These birds are known for their elaborate mating displays which take place at leks (Prum 1990). Males do not contribute any parental care; their reproductive success derives solely from their ability to attract females willing to mate with them on their lek (Kirwan and Green 2011). Males

queue for dominance at display sites within leks, and often subordinate males immediately take the place of a disappeared higher-ranking male. Given the paramount importance of courtship display for reproductive success of male manakins, we expect substantial and consistent male investment in maintaining display site “ownership” and performing for potential mates.

Surprisingly, White-ruffed manakins (*Corapipo altera*) exhibit dramatic variability in behavior and activity both within and between display sites (Jones et al. 2014). Display sites in this species are fallen mossy logs with a single dominant male; these are typically situated in loosely aggregated leks of 2 – 3 logs, with each log having its own displaying male. Some males are extremely attentive to their logs, leaving infrequently and perching nearby or practicing courtship behaviors throughout the day. Other males rarely attend their log, appearing only occasionally to display for a female or vocalize. In addition, normally attentive males are sometimes absent while “slacker” males sporadically spend extended periods of time practicing displays. Understanding what underlies this variability in White-ruffed manakin behavior will ultimately provide insight into the fitness tradeoffs shaping reproductive and display effort of sexually selected species.

To understand why White-ruffed manakins exhibit such dramatic individual variation display effort and lek attendance, we experimentally manipulated male social environment in two ways. First, we used speakers broadcasting manakin vocalizations and mechanical display sounds to simulate an increase in display activity elsewhere within the lek. Second, we covered all but one display log within a lek to prevent neighboring males from displaying; at the uncovered focal log we then monitored response to this reduction in nearby display activity and the potentially increased competition for display sites. For both experiments, if *male quality or condition* underlies individual variation, we predicted no change in display effort or behavior at

the focal display site. This prediction is indirect but still allows us to distinguish between this hypothesis and the alternatives presented here. If the intensity of *competition* drives variation in male behavior, we predicted that activity at the focal display log would increase following both manipulations as males invest more to maintain dominance and ownership at the focal log. Finally, if males modify display investment *cooperatively* to maximize signal efficiency, we predicted that males would (a) reduce their effort in response to an increase in acoustic signal near their lek, and (b) increase their effort to compensate for declines in activity at the lek as neighboring males are prevented from displaying.

## Methods

### Study species

White-ruffed Manakins (*Corapipo altera*) are small (9 – 13 gram), frugivorous suboscine passerines found in primary montane forest in Central and northern South America. Males resemble green-plumaged females for their first and second year, then gain a black mask and white beard in their third year, and attain definitive black and white plumage in their fourth year of life. Males display on and near fallen logs on the forest floor (Rosselli et al. 2002). Display logs are frequently clustered within auditory range (10 – 30 m) of neighboring display logs (Rosselli et al. 2002, Jones et al. 2014). These clusters, or leks, typically consist of 2 – 3 display logs spaced over 100 m from each other, but in some cases, consist of a single, isolated log (Rosselli et al. 2002, Jones et al. 2014). Each active display log has one dominant or “alpha” male associated with it (Rosselli et al. 2002). Some logs have additional subordinate males that spend time near the log and coordinate their display behavior with the alpha, including during multi-male displays when females are present; displays of multiple males at a single log are considered to be facultatively cooperative (Jones et al. 2014). Alpha males (and to a lesser

extent, subordinate males) often spend much of their time near their display log, perching, foraging, vocalizing, and performing display behaviors (Rosselli et al. 2002, Jones et al. 2014).

Displays of *C. altera* are multi-modal and likely function as signals over different spatial scales (Rosselli et al. 2002, Jones et al. 2014). The majority of display behaviors are *silent displays*, involving ritualized postures and short flights near the display log that are visible only within the immediate vicinity of the log. Such behaviors include: “butterfly flights” (slow, undulating flights with the body held upright around and to/from display log), “throat flag” (exaggerated bowing on display log while inflating white throat feathers), “rapid flight” (quick, short flights between two perches near log), and “log landing”. *Acoustic displays* are potentially perceptible from much longer distances and include sounds incorporated with visual display behaviors and stand-alone vocalizations. “Seew-seew calls” are high, repeated tones emitted while the male performs flight displays above the canopy, while “aerial flaps” are loud mechanical sound made when the male aborts a dive at or below canopy height. “Flap-chee-wah” sounds are produced during a complete dive from above the canopy, in which the male lands in a specific location on display log (the landing pad). This behavior precedes copulation if a receptive female is perched on the landing pad and includes multiple mechanical sounds and a vocalization. Partial “flap-chee-wahs” are dives which end on the display log and include some but not all acoustic elements of the complete flap-chee-wah display. These acoustic display elements and silent displays are performed whether or not a female is present, but the intensity and frequency of both silent and auditory displays increase when females visit. Males also *vocalize* when not performing physical displays. Single “Trills” are emitted at regular intervals by males while perched near the display log, and bursts of “emphatic trills” typically involve groups of males of various ages. Trills and emphatic trills do not accompany physical, visual

displays for females and are putatively a means of male-male or male-female communication within leks (Rosselli et al. 2002).

We studied the behavior of *C. altera* at Parque Nacional Volcán Tenorio (N 10.71554, W 84.98732) on the Caribbean slope in northwestern Costa Rica beginning in 2016. This site is premontane tropical wet forest, receiving approximately 3750 mm of rain annually (Sistema Nacional de Áreas de Conservación de Costa Rica). During the dry season (late February through mid-July) we located display logs using audio and visual cues in old growth forest at elevations between 740 and 870 meters above sea level. Males consistently attended and females visited display sites from early March through June. Over four breeding seasons (2016–2019) we searched for new display logs, monitored all previously-active logs, and collected behavioral data at all active logs. We captured and uniquely color-banded 246 individuals, targeting netting sessions around known display leks to maximize captures of displaying males. We conducted extensive behavioral observations at all active display logs starting in 2017 (range 16 – 26 display logs per field season). During the 2018 field season we manipulated acoustic activity around 10 focal display logs at 8 leks (experiment 1), and during the 2019 field season we manipulated access to display logs near 7 focal logs at 3 different leks (experiment 2).

### **Experiment 1: Increased acoustic signal within leks**

To test the behavioral response of males to an increase in perceived manakin signaling, we broadcast the sounds of male manakins vocalizing and displaying near focal display logs. We used a before-after-control-impact experimental design in which each log served as its own control for assessing treatment effects (Morrison et al. 2008). We compared responses at the focal display log to the manakin broadcast treatment and two controls; (1) no sounds broadcast from speakers (silent control), and (2) songs of a Spotted Antbird (*Hylophylax naevioides*;

heterospecific control). Spotted Antbirds live in similar habitat but are insectivores and therefore are not direct competitors with White-ruffed Manakins. We selected 10 active, focal display logs, all in different leks (i.e., separated by at least 100 m). At each display log, we placed 3 speakers ~2 m high in the forest, each ~20 m away from the log and the nearest speaker (Figure 5.1). Our experimental treatment (manakin playback in fig. 1) was playback of a suite of manakin sounds (trills, excited trills, flap-chee-wah sounds, Macaulay Library Catalog Numbers 190863, 190864, 190866). To avoid influencing behavioral response by playing sounds of known individuals at display logs, we used recordings from other populations of *C. altera*. Each speaker played a different suite of recordings to represent three different individuals. We staggered the timing of both treatment and heterospecific controls, such that one of the three speakers broadcast sounds (in rotation) for ~1 minute every 10 minutes from ~0800 hours to ~1600 hours. We used the same three suites of recordings in each trial, so each focal log was subject to the same set of sounds during corresponding phases of the experiment. We observed the focal display log on two days during each of the three treatments: silent control, heterospecific control, and experimental playback (for a total of 6 days of observation, Fig 1a). During the silent control treatment, we observed the focal log on two consecutive days. We observed the focal log on the first and third day of heterospecific control and experimental treatments to capture initial and lagged responses to treatment. On each observation day we conducted one in-person, 2 hr (mean = 119 min,  $\pm$  SD 6.7 min) observation from a blind positioned 6-8 m from display log. To obtain more data on behavior at focal logs, we also recorded video on the same days that we observed them for an additional ~1.5-hr period (mean = 107 min,  $\pm$  SD 17.2 min) that did not overlap with in-person observations. We used GoPro video cameras (HERO Session and HERO5 models) camouflaged with leaf litter and placed near the end of the display log. This camera placement allowed us to

document behaviors taking place on or near the log accurately (most silent and acoustic display behaviors) but did not permit individual identification of vocalizing individuals. Prior to the experiment we observed no avoidance responses to the camera, and previous studies with this species found no quantitative differences in behavior of alpha males, visiting males, or females between in-person and video observation data (Boyle et al. 2011).

The complete sequence of silent control, heterospecific control, and experimental treatments was typically 8 days long (Figure 5.1a). In a few cases, we delayed observations for a day due to inclement weather, but trials never extended longer than 10 days. On the appropriate days, we switched to the next treatment when turning on speakers at ~0800 hr. We alternated the order of in-person and video observations, starting either in the morning (0800 – 1000 hrs) or afternoon (1200 – 1400 hrs) to capture variation in activity at the display log throughout the day (Rosselli et al. 2002). We recorded start time, duration of observation, and observation type. During in-person and video observations we recorded the number of unique individuals present at the focal log, i.e., either visible or heard vocalizing within approximately 20 m. We also recorded the proportion of observation time each individual spent in the vicinity of the focal log. As video observations focused on the display log itself, determination of individual presence was more dependent on detecting vocalizations, while in-person observers could visually identify individuals farther from the display log (e.g., in the higher canopy). We recorded the number of displays for females occurring at the focal log. Females are cryptic and secretive in this species, often initially approaching and observing displays well concealed in understory vegetation. Thus, we inferred the presence of a female based on a dramatic increase in intensity of male display behavior for ~5% of recorded displays for females. If the female left and the male stopped displaying for more than two minutes, we considered it to be a new display for female when she

returned and he resumed displaying for her. We summed each observed instance of each of the display behaviors listed above, dividing by duration of the observation (in hours) to obtain hourly rates.

## **Experiment 2: Log removal**

In the second experiment, we prevented neighboring males in a lek from using their display logs to test whether presumably increased competition for display logs affects activity at a focal display log. We selected focal display logs that were part of a lek consisting of at least two logs within 100 m and human auditory range of each other. To temporarily “remove” a nearby display log, we placed large palm fronds over the area of the log used by males for their displays, which effectively prevented them from displaying. Leaves and falling vegetation often obstruct the landing areas of the display logs on the forest floor, and males “clean” their dance floor when fallen debris is not too heavy. If they cannot remove the vegetation from their landing pad, males will not display, waiting until the material falls off or eventually shifting displays to a different log (Jones et al. 2014). Our manipulation only affected the log for a short time (8 days) and we observed males resuming displays on their log within a day after removal of the palm fronds. We are therefore confident manipulation did not permanently affect use of the display log. We quantified behavioral responses to removal of all neighboring logs within the same lek at seven focal logs distributed among three different leks. Because baseline display activity varies by log and alpha male, we repeated the treatment, such that each log in the lek was a focal log, and each log in the lek was at some point “removed”. To allow male behavior to return to normal but minimize the effect of seasonal change in display activity, we waited 10 days before returning to the lek to repeat the protocol with a different focal log. As in the increased acoustic signaling experiment, we conducted one in-person observation and one video observation at the focal log

each day, alternating which type of observation started in the morning or afternoon (Figure 5.1b). During each observation, we recorded the same data as described for the increased acoustic signaling experiment. At each log, we conducted control observations on four consecutive days (Figure 5.1b). On the morning following completion of control observations, we “removed” the other log(s) in the lek (i.e. all display logs within auditory range) with palm fronds. Immediately after covering the neighboring logs, we began observations at the focal log. Additional observers also observed the covered logs for a single 2 hr period immediately following manipulation to verify that our treatment was effective in preventing displays on neighboring logs. We conducted 4 days of experimental observations at the focal log (Figure 5.1b), checking that the neighboring logs remained covered by vegetation during all four days. Following completion of the final observation at a focal log, we immediately removed the vegetation from the other log(s) in the lek. After a minimum of 10 days of no manipulation, we returned to the lek and began control observations prior to experimental treatment at a new focal log that had previously been covered.

### **Analytical approach**

We assessed the display effort and number of males at visiting and displaying on focal logs by recording several response variables. For each observation, we recorded the proportion of time the most attentive individual (generally the alpha) was present at the log (arc sine square root transformed) and a minimum estimate of the number of unique individuals observed. This estimate is likely conservative in observations where unbanded individuals were present, as we considered unbanded individuals of the same plumage type observed at different times throughout the observation as a single unbanded bird. We also counted the number of times males displayed for a female during each observation, dividing that number by the duration of the observation to obtain a rate of displays for females. We tallied all behaviors performed at the

display log by any male during an observation (including those performed during displays with and without females present). We then aggregated behaviors into three types based on putative signal function and range: “vocalization” (trills and emphatic trills), “silent display” (butterfly flight, throat flag, rapid flight, log landing), and “acoustic display” (seew-seew calls, aerial flaps, flap-chee-wah, partial flap-chee-wah). For each behavior type, we divided the tallied number of behaviors by the duration of the relevant observation, to calculate a vocalization rate, silent display rate, and acoustic display rate for each observation. We then rounded these values to the nearest whole integer to satisfy assumptions of count-based distributions.

Certain factors unrelated to our experimental manipulations may influence behavior at the display log. Due to our modest sample sizes, including all potential factors in analyses could result in overfitting of models; we therefore used preliminary univariate analyses of data collected prior to experimental manipulation (during control periods) to determine which factors influenced specific response variables. We tested for relationships between response variable and observation type (in-person/video), observation start time (morning/afternoon), and ordinal day of season. Observation type may influence which behaviors are detectable, given video field of view and inability to track individual movements off camera. We tested for associations between both observation type and start time and each response variable using Wilcoxon rank sum tests. To assess seasonal patterns of variation in behavior, we used linear regression and generalized additive model to check for non-linear association between ordinal day and activity. We included any factors that had a strong effect on a given response variable in either the increased acoustic signaling or log removal experiment as fixed effects in final generalized linear models for that response variable in analyses for both experiments (Table 1). For example, if observation type was related to acoustic display rate in control observations during the acoustic signaling

experiment, it was included as a fixed effect in analysis of both experiments. We also included a fixed effect of treatment and random effect of log identity to account for repeated measures at a single log. We analyzed each response variable (time present, number of individuals, displays for females, vocalization, silent display, and acoustic display rates) in separate generalized linear models. In analyses of the log removal experiment, we also included random effects of lek identity and the order in which the log was observed within the cluster (first, second or third focal log). We ran generalized linear mixed models with multiple error distributions using the R package “glmmTMB” (Brooks et al. 2017, R Core Team 2018). We selected the appropriate error distribution for each response variable based on Q-Q plots, goodness of fit tests, and residual plots using a simulation-based approach in the R package “DHARMA” (Dunn and Smyth 1996, Gelman and Hill 2006). Each analyzed behavioral variable can provide a unique insight to how individuals respond to manipulation, therefore it is not necessary to correct for multiple comparisons.

## **Results**

Between 4 April 2018 and 4 June 2018, we simulated increased acoustic signal at 10 focal logs at eight different leks, observing each for ~22 hours (combined in-person and video) over the course of the experiment (mean = 22.5 hrs,  $\pm$  SD 2.8 hrs). Between 28 March 2019 and 22 May 2019 we recorded behavioral responses to removal of nearby logs at seven focal logs in three different leks. We observed each focal log for ~28 hours (combined in-person and video, mean = 28.7,  $\pm$  SD 1 hr). Only one of the focal logs in the removal experiment was also a focal log in the acoustic signal experiment in the previous year; it was attended by the same alpha in both years.

## **Analysis of correlates of behavior during control observations**

During control observations, the proportion of time the most attentive male at a given display log was present ranged from 0.01 to 0.98 in the acoustic signal experiment and 0.06 to 0.92 in the log removal experiment. The maximum proportion of time an individual male spent at the focal display log in the control period was related to observation start time in the increased acoustic signal experiment, and ordinal day in the log removal experiment. On average, the most attentive individual at a given focal log was present 17% longer during control observations that began in the afternoon during the acoustic signal experiment ( $p = 0.030$ , Table 5.1). During control observations for the log removal experiment, the average proportion of time the most attentive individual spent at a given focal display log declined by ~10% per month ( $\beta = -0.004$ , SE = 0.002,  $p = 0.015$ ). The number of individuals recorded at focal logs was ~32% lower during video observations compared to in-person observations during control treatments in both experiments (acoustic signal: 34%,  $p = 0.045$ , log removal: 29%,  $p = 0.075$ , Table 5.1), likely due to reduced ability to identify individuals farther from the display log during video observations. The number of individuals at the focal log during control observations also declined as the season progressed in both experiments., We recorded ~1 fewer individual per month in the acoustic signal experiment ( $\beta = -0.029$ , SE = 0.013,  $p = 0.034$ ) and 1.5 individuals per month in the log removal experiment ( $\beta = -0.052$ , SE = 0.018,  $p = 0.006$ ). The rate of displays for females also declined throughout the field season during control observations, especially during the log removal experiment when ~1 fewer display occurred per month ( $\beta = -0.030$ , SE = 0.008,  $p = 0.001$ ). Vocalization rate of males were 62% higher in observations that started in the afternoon during control observations of the acoustic signal experiment ( $p = 0.037$ , Table 5.1), but males tended to vocalize half as much in observations starting in the afternoon

compared to those that began in the morning in the log removal experiment ( $p = 0.070$ ). Silent display rates declined as the field season advanced in both experiments. During the increased acoustic signal experiment males tended to perform two fewer silent displays per hour each week than they did the previous week ( $\beta = -0.308$ ,  $SE = 0.166$ ,  $p = 0.072$ ), and during the log removal experiment males performed approximately four fewer silent display behaviors per hour than they did the previous week ( $\beta = -0.645$ ,  $SE = 0.195$ ,  $p = 0.002$ ). In the control treatment of the acoustic signal experiment we detected acoustic displays five times more frequently during in-person observations from blinds than from video observations ( $p = 0.008$ , Table 5.1) but did not detect them any more or less frequently during video observations of the log removal experiment control treatment ( $p = 0.291$ ).

### **Experiment 1: Increased acoustic signal within leks**

We constructed generalized linear models, which included fixed effects of experiment treatment and factors related to each response variable as well as a random effect of log identity (Table 5.2). The proportion of time the most attentive individual spent at a focal log, the total number of individuals visiting a focal log, and the number of displays for female did not differ during manakin call playback relative to either silent controls or heterospecific playback controls (Table 5.2). Males vocalized at similar rates during silent control and heterospecific control playback ( $\beta = 0.020$ ,  $SE = 0.148$ ,  $z = 0.137$ ,  $p = 0.891$ ). By contrast, males vocalized less in response to increased manakin acoustic signaling, decreasing the frequency of vocalization by approximately a third ( $\beta = -0.414$ ,  $SE = 0.156$ ,  $z = -2.660$ ,  $p = 0.008$ , Figure 5.2). Silent display rates and acoustic display rates did not change during manakin call playback compared to heterospecific playback and silent controls (Table 5.2).

## Experiment 2: Log removal

We constructed generalized linear mixed models, which included fixed effects of treatment and factors related to the relevant response variable as well as random effects of log identity, lek identity, and order of manipulation (Table 5.3). The proportion of time the most attentive individual spent on average and the total number of individuals observed at the focal display log did not increase or decrease in response to temporary removal of nearby logs (Table 5.3). The frequency of displays for females at the focal log did change, with males at the focal log performing on average 50% more displays for visiting females per hour when their neighbors were temporarily prevented from using their logs ( $\beta = 0.800$ ,  $SE = 0.319$ ,  $z = 2.508$ ,  $p = 0.012$ , Figure 5.3). For male vocalization rate data, the hurdle negative binomial distribution was the best fit based on dispersion and outlier tests and the QQ-normal plot. However, the Kolmogorov-Smirnov test for goodness of fit on model residuals indicated deviation from the expected distribution. With this in mind, the model showed that males did not change their vocalization rate when neighboring logs were removed ( $\beta = -0.140$ ,  $SE = 0.138$ ,  $z = -1.015$ ,  $p = 0.31$ ; Figure 5.4a). There was a tendency for males to perform more silent displays when their neighbors were prevented from displaying ( $\beta = 0.438$   $SE = 0.232$ ,  $z = 1.888$ ,  $p = 0.059$ , Figure 5.4b). However, removal of nearby display logs did not elicit a change in how frequently male manakins performed acoustic displays at the focal log ( $\beta = -0.06$ ,  $SE = 0.309$ ,  $z = -0.198$ ,  $p = 0.843$ , Figure 5.4c).

Because we could not observe the covered logs throughout the treatment due to time and effort limitations, we were not able to analyze the behavior of neighboring males at their respective logs statistically. However, observations immediately following manipulation allowed us to detect initial behavioral responses of neighboring males to the covering of their display logs

anecdotally. In all cases, neighboring males spent time at their manipulated log and vocalized actively throughout the observation. On occasion, these males also performed some display elements that did not require landing on the log, such as butterfly flights and aerial flaps.

## Discussion

To understand why display investment of male *C. altera* varies within and between individuals, we used two experimental manipulations to test predictions of three hypotheses based on intrinsic *male quality or condition*, or the social environment affecting *competition or cooperation*. Manipulating the perceived social environment by broadcasting manakin sounds caused male *C. altera* to vocalize less frequently. Importantly, the frequency of displays for females and other display behaviors did not change when acoustic signaling was increased at the focal log, suggesting that reduced vocalization by the male at the focal log did not affect his potential reproductive success. These results are consistent with the hypothesis that *cooperation* among males within leks underlies some of the variation in male investment in display. When surrounded by loud “neighbors” producing sufficient signal to advertise the presence of a lek, male *C. altera* minimized their vocalization effort. After preventing neighboring males from using their display logs, males at focal logs actually performed more displays for females than during control observations. The time males spent at the log and the number of individuals observed were unchanged throughout the log removal experiment, suggesting that the increase in displays for females was not due to a change in male attentiveness or overall increase in activity at the focal log. Although other rates of male behavior were unaffected, there was a slight trend of males performing more silent displays when neighbors’ logs were covered, likely due to the increase in displays for females, when many silent display behaviors are performed.

With the exception of vocal rates, all other metrics of behavior were unaffected by increasing the acoustic signal within leks. This consistency fits the predictions of the *male quality or condition* hypothesis. Specifically, individual variation in display behavior results from intrinsic differences among males, with changes in social environment not materially changing individuals' investment in display. Contrary to the predictions of the *competition* hypothesis, males did not increase the amount of time they spent attending the logs, nor did the number of visitors to focal logs change during either experimental manipulation. Furthermore, males at the focal logs maintained consistent rates of most display behaviors throughout both experiments. Although we cannot determine whether our manipulations truly increased competition at the focal logs, the collective results of these experiments suggest that perceived increase in local *competition* did not change behavior of males at focal logs.

Both male quality and cooperation hypotheses can operate concurrently in the context of different behaviors within a multi-modal display and the different information they convey. Long-range signals such as vocalizations may function at the level of the lek, with males jointly advertising the presence of their group of display sites. Upon arrival to the lek, females can then assess individual male quality based on performance of other display behaviors. This distinction between advertisement and display could explain why males responded divergently in vocalization rate during the two experiments. During the log removal experiment, we confirmed that neighboring males remained in the vicinity of their log immediately after manipulation and continued to vocalize. Although these neighboring males were prevented from using their preferred logs for display, it is possible that they could perform a subset of display behaviors and use an alternative log in the event a female visited. Neighboring males could then continue to produce long-range acoustic signals continuing to advertise lek presence. With the level of total

signal preserved, the behavior and vocalization effort of the focal male remained consistent throughout the experiment. By contrast, in the playback experiment, when acoustic signaling was experimentally increased, the male at the focal log reduced his vocalization effort without reducing the total level of signal advertising the presence of the lek.

Cooperative alliances among males occupying a single display site are a key feature of the lek mating systems in some manakins. In the genus *Chiroxiphia* some display behaviors can only be performed by two or more individuals, although solo displays for females also lead to successful copulation (Foster 1977, DuVal 2007b, Cárdenas-Posada et al. 2018, Ribeiro et al. 2019). In other species, alliances and coordinated displays are facultative (Ryder et al. 2008, Jones et al. 2014). Because cooperation in manakins frequently occurs within a display site, cooperation between display sites within a lek is discussed less frequently. However, increased or synchronized signaling output possible when males aggregate is one advantage proposed as a driver for evolution of lekking behavior (Wiley 1991, Johnsgard 1994). Our findings suggest that it may be reasonable to think of manakin leks as cooperative “signaling units” advertising the presence of an aggregation of displaying males. Once females arrive to the lek, males are once again competitors, when females can assess their behavior individually at their respective display sites. Jointly producing an advertisement signal could be considered a fundamental characteristic of sound-producing lekking species. This cooperation in signaling effort could then be a foundation of the more unusual long-term male associations of some manakin species in which social partners develop a specialized display repertoire that they perform only with each other.

Complex display and multi-modal signaling may facilitate this duality of cooperation and competition. If information is conveyed to prospective mates through multiple channels (Coleman et al. 2004), some elements of display may evolve to be cooperative while others

remain competitive. For example, there may be fewer fitness costs for males cooperating to attract females to a lek with long-distance signals, while behaviors assessed at close range may be more important to female mate choice (Gibson 1996). Multi-modal signals with different functions can also provide an opportunity for males to respond to changing social environments. When males at our focal log experienced increased acoustic competition, they reduced their vocalization effort, potentially conserving signaling effort rather than attempting to outcompete the “new males” joining their lek.

Previous studies involving playback of manakin sounds reveal diverse behavioral responses. In Long-tailed Manakins (*Chiroxiphia linearis*) broadcasting conspecific vocalizations stimulated songs associated with male cooperation (Trainer and McDonald 1993). Subsequent studies of the same species showed that males time their vocalizations to avoid overlapping with the calls of known neighboring males (Maynard et al. 2012). However, during broadcast of unknown males singing, focal males increased overlapping of their songs with the playback. *C. linearis* males also increased variability of their vocalization timing and called at lower rates during playback (Maynard et al. 2012). Our dataset does not allow for analysis of overlap in vocalizations, but our reduced vocalization rates do parallel the reduction in calling rate and potential for cooperation rather than competition, even though the signals broadcast were unknown to males at focal logs.

The integration of both cooperative and competitive elements in manakin lek-mating systems is intriguing, given the costs and benefits of close associations among rival males. Wire-tailed manakins exhibit plasticity in cooperative behavior, modulated by circulating testosterone levels (Ryder et al. 2020). In *C. altera* social hierarchies within a display site break down if subordinates challenge dominant males (Boyle and Shogren 2019). These and other lines of

evidence make clear that male-male competition is still a strong driver of behavior at display sites in manakins. Despite this, there was no indication that competition with neighboring males influenced display behavior during our experiments. Thus, when there is lower risk of males out-competing each other (i.e. long-range vocal signal) and females have opportunities to assess males individually at close range, adjusting signaling effort and cooperating with rival males may be an efficient signaling strategy.

Individual variation and plasticity in display investment is a potentially a key strategy for males to conserve time and energy. Investing maximally in securing mates at all times is rarely the best use of a male's resources as they balance tradeoffs between current and future reproductive output (Housley et al. 2017). In some species or social contexts, cooperation increases male reproductive success over their lifetime (Díaz-Muñoz et al. 2014). Mating systems in which male coalitions cooperate to gain shared access to females through direct physical competition are an intuitive example (Pope 1990). But even when reproductive success is based on female choice or indirect male-male competition, there are still potential benefits to pooling resources and flexibly adjusting investment in reproductive effort (Stiver et al. 2013). Thus, framing male-male interactions as strictly competitive when disentangling drivers of individual variation may obscure complexities in behavioral response. Although sexual selection undoubtedly hinges on differences in reproductive success, how individuals maximize their fitness is not always obvious. Considering the possibility that animals are balancing benefits of cooperation with competition for mates is key to understanding individual variation in reproductive behavior and the evolution of diverse mating systems.

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## Tables

**Table 5.1** Results of preliminary analyses to determine fixed effects for each response variable.

response variable	observation type	observation time	ordinal day
<i>max proportion time present</i> ( <i>arcsine square root transformed</i> )	$p = 0.178, r = 0.23$	$p = \mathbf{0.030}, r = \mathbf{-0.37}, \uparrow$ afternoon	$\beta = 0.003, SE = 0.003, p = 0.439$
	$p = 0.083, r = 0.24$	$p = 0.229, r = -0.17$	$\beta = \mathbf{-0.004}, SE = \mathbf{0.002}, p = \mathbf{0.015}$
<i>number of individuals observed</i>	$p = \mathbf{0.045}, r = \mathbf{0.34}, \downarrow$ video	$p = 0.552, r = -0.10$	$\beta = \mathbf{-0.029}, SE = \mathbf{0.013}, p = \mathbf{0.034}$
	$p = \mathbf{0.075}, r = \mathbf{0.24}, \downarrow$ video	$p = 0.407, r = -0.11$	$\beta = \mathbf{-0.052}, SE = \mathbf{0.018}, p = \mathbf{0.006}$
<i>number of displays for female</i>	$p = 0.915, r = -0.02$	$p = 0.818, r = -0.04$	$\beta = \mathbf{-0.010}, SE = \mathbf{0.057}, p = \mathbf{0.077}$
	$p = 0.835, r = -0.30$	$p = 0.103, r = -0.22$	$\beta = \mathbf{-0.030}, SE = \mathbf{0.008}, p = \mathbf{0.001}$
<i>vocalization rate</i>	$p = 0.884, r = -0.03$	$p = \mathbf{0.037}, r = \mathbf{-0.35}, \uparrow$ afternoon	$\beta = 0.061, SE = 0.176, p = 0.733$
	$p = 0.788, r = -0.04$	$p = \mathbf{0.070}, r = \mathbf{-0.25}, \downarrow$ afternoon	$\beta = -0.536, SE = 0.929, p = 0.566$
<i>silent display rate</i>	$p = 0.933, r = -0.02$	$p = 0.200, r = -0.22$	$\beta = \mathbf{-0.308}, SE = \mathbf{0.166}, p = \mathbf{0.072}$
	$p = 0.605, r = 0.07$	$p = 0.481, r = 0.10$	$\beta = \mathbf{-0.645}, SE = \mathbf{0.195}, p = \mathbf{0.002}$
<i>acoustic display rate</i>	$p = \mathbf{0.008}, r = \mathbf{0.45}, \downarrow$ video	$p = 0.920, r = -0.02$	$\beta = -0.010, SE = 0.020, p = 0.619$
	$p = 0.291, r = 0.14$	$p = 0.186, r = 0.18$	$\beta = -0.056, SE = 0.043, p = 0.197$

Unshaded rows are results from control data collected during increased acoustic competition experiment. Shaded rows are results from control data collected during temporary log removal experiment. Observation type was analyzed using Wilcoxon rank sum test for difference between video and in person observations, and p-values ( $p$ ) and Wilcoxon rank sum test effect size ( $r$ ) are shown, as well as direction of relationship where significant. Observation start time was analyzed using Wilcoxon rank sum test for difference between observations started in the morning and those started in the afternoon. P-values ( $p$ ) and Wilcoxon rank sum test effect size ( $r$ ) and direction of relationship where significant are shown. Results for ordinal day include  $\beta$  coefficients ( $\beta$ ), standard error (SE) and p-values ( $p$ ) from linear regression. However, we used generalized additive models to check for non-linear relationship between behavior and day of season. Any result that is bolded indicates that we included that variable as a fixed effect in all models of the corresponding response variable. That is, if acoustic display rate varied with observation type during control observations of the acoustic competition experiment (that result is bold), we used observation type as a fixed effect in analyses for both the increased acoustic competition and log removal experiments.

**Table 5.2** Model results from increased acoustic competition experiment.

response variable	distribution	fixed effects	$\beta$	SE	test statistic	$p$
<i>max proportion time present (arcsine square root transformed)</i>	gaussian	heterospecific	-0.009	0.070	-0.129	0.372
		manakin	-0.089	0.071	-1.249	
		observation time	0.129	0.056	2.320	
		ordinal day	-0.005	0.003	-1.460	
<i>number of individuals observed</i>	generalized poisson	heterospecific	0.064	0.125	0.509	0.611
		manakin	-0.165	0.130	-1.265	0.206
		observation type	-0.194	0.109	-1.774	0.076
		ordinal day	-0.011	0.004	-2.760	0.006
<i>number of displays for female</i>	poisson	heterospecific	-0.620	0.507	-1.222	0.222
		manakin	-0.567	0.488	-1.162	0.245
		ordinal day	-0.031	0.019	-1.700	0.089
<i>vocalization rate</i>	zero-inflated generalized poisson	heterospecific	0.020	0.148	0.137	0.891
		manakin	-0.414	0.156	-2.660	0.008
		observation time	0.170	0.122	1.392	0.163
<i>silent display rate</i>	generalized poisson	heterospecific	-0.322	0.321	-1.003	0.316
		manakin	-0.439	0.331	-1.329	0.184
		ordinal day	-0.026	0.012	-2.161	0.031
<i>acoustic display rate</i>	generalized poisson	heterospecific	-0.196	0.296	-0.663	0.507
		manakin	-0.516	0.301	-1.713	0.087
		observation type	-0.538	0.272	-1.977	0.048

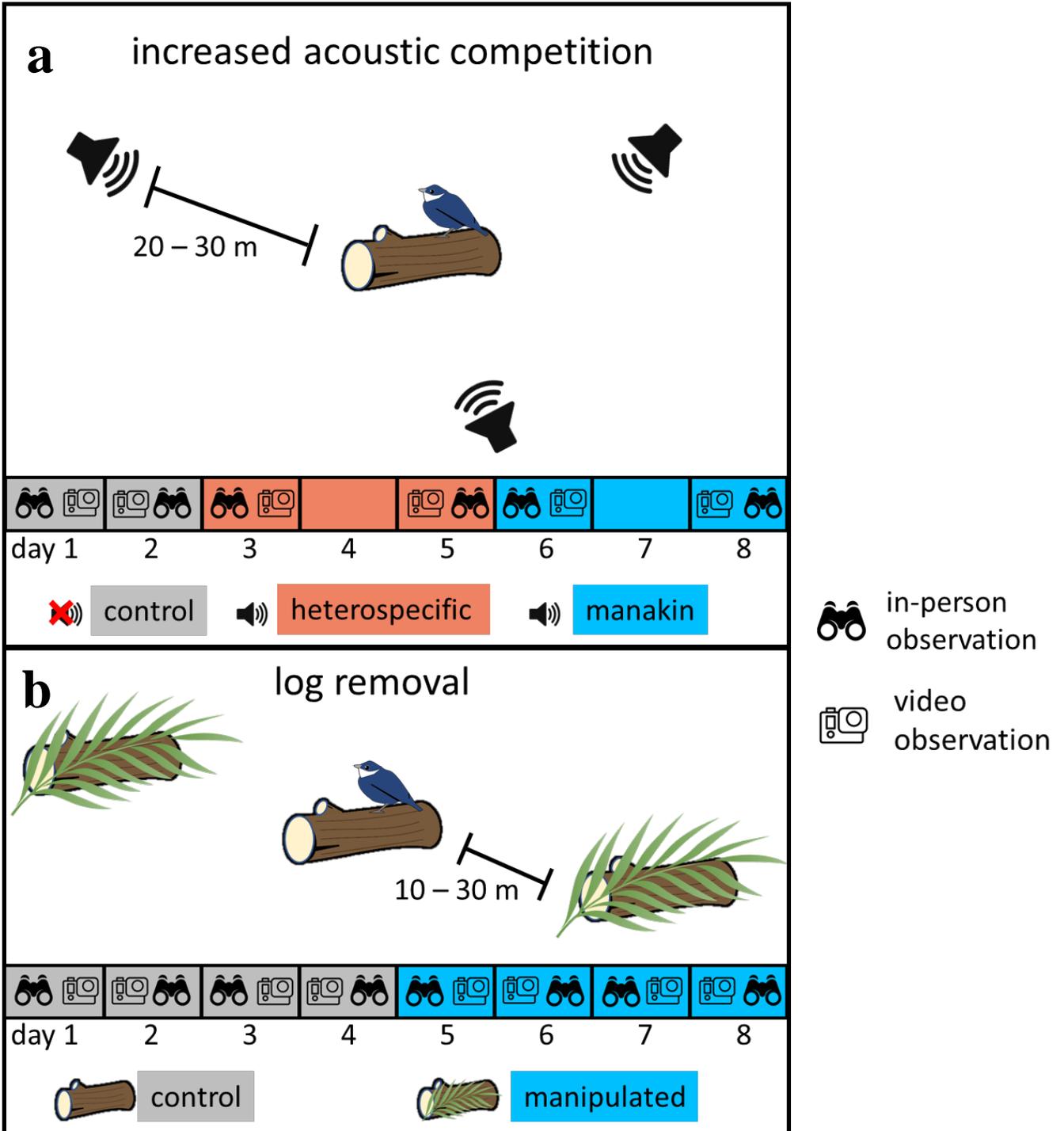
All models included random effect of log identity and fixed effects identified in preliminary analyses (see Table 1). Results are derived from the model having an error distribution (distribution) that best fit the data based upon Q-Q plots and residual distributions (see text for details). We include beta estimates ( $\beta$ ), standard error (SE), test statistic, and p-value ( $p$ ) for treatment (heterospecific control, manakin playback) and other fixed effects in each model.

**Table 5.3** Model results from log removal experiment.

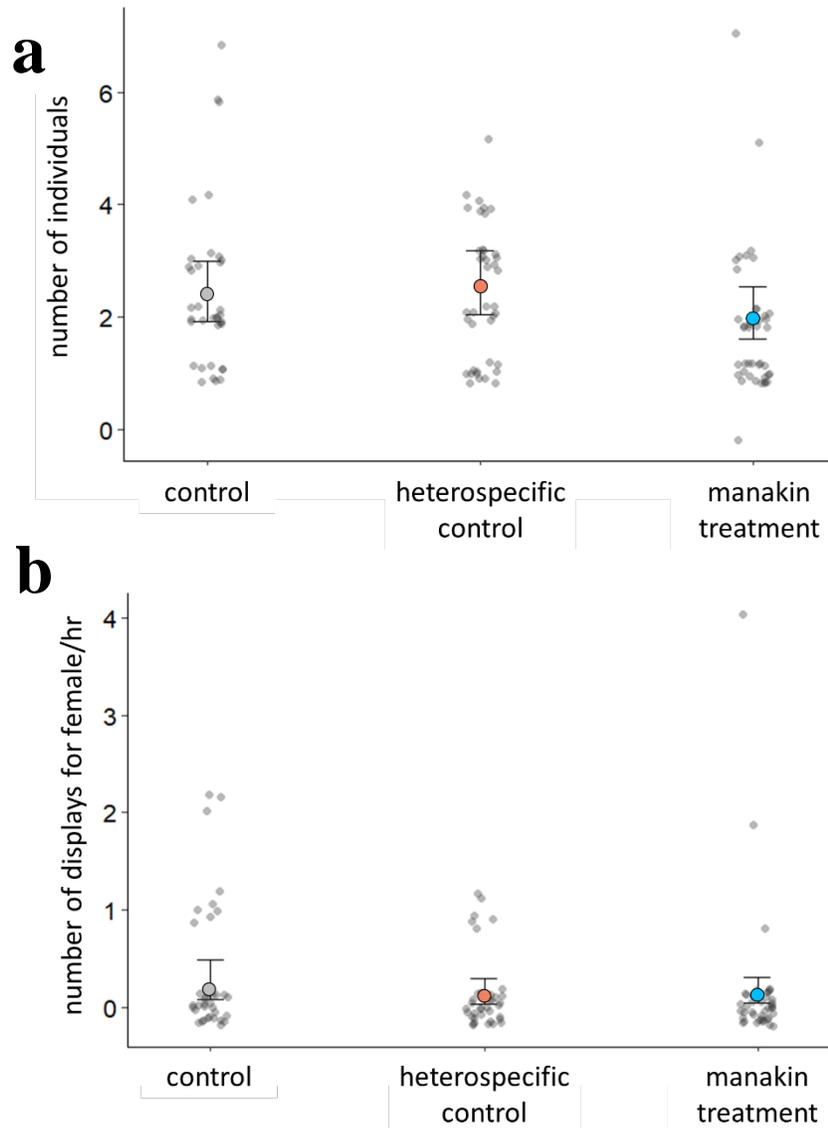
response variable	distribution	fixed effects	$\beta$	SE	test statistic	$p$
<i>max proportion time present (arcsine square root transformed)</i>	gaussian	removal	0.021	0.039	0.524	0.600
		observation time	0.054	0.038	1.412	0.158
		ordinal day	-0.007	0.002	-3.673	< 0.01
<i>number of individuals observed</i>	poisson	removal	0.068	0.109	0.622	0.534
		ordinal day	-0.016	0.008	-2.022	0.043
		observation type	-0.269	0.105	-2.562	0.010
<i>number of displays for female</i>	zero-inflated poisson	removal	0.800	0.319	2.508	0.012
		ordinal day	-0.085	0.036	-2.360	0.018
<i>vocalization rate</i>	hurdle negative binomial	removal	-0.140	0.138	-1.015	0.310
		observation time	0.076	0.146	0.524	0.600
<i>silent display rate</i>	generalized poisson	removal	0.438	0.232	1.888	0.059
		ordinal day	-0.046	0.016	-2.993	0.003
<i>acoustic display rate</i>	zero-inflated negative binomial	removal	-0.061	0.309	-0.198	0.843
		observation type	-0.292	0.315	-0.925	0.355

All models included random effects of log identity, lek identity, and order of removal, as well as fixed effects identified in preliminary analyses (see Table 1). Results are derived from the model having an error distribution (distribution) that best fit the data based upon Q-Q plots and residual distributions (see text for details). We include beta estimates ( $\beta$ ), standard error (SE), test statistic, and p-value ( $p$ ) for treatment (removal) and other fixed effects in each model.

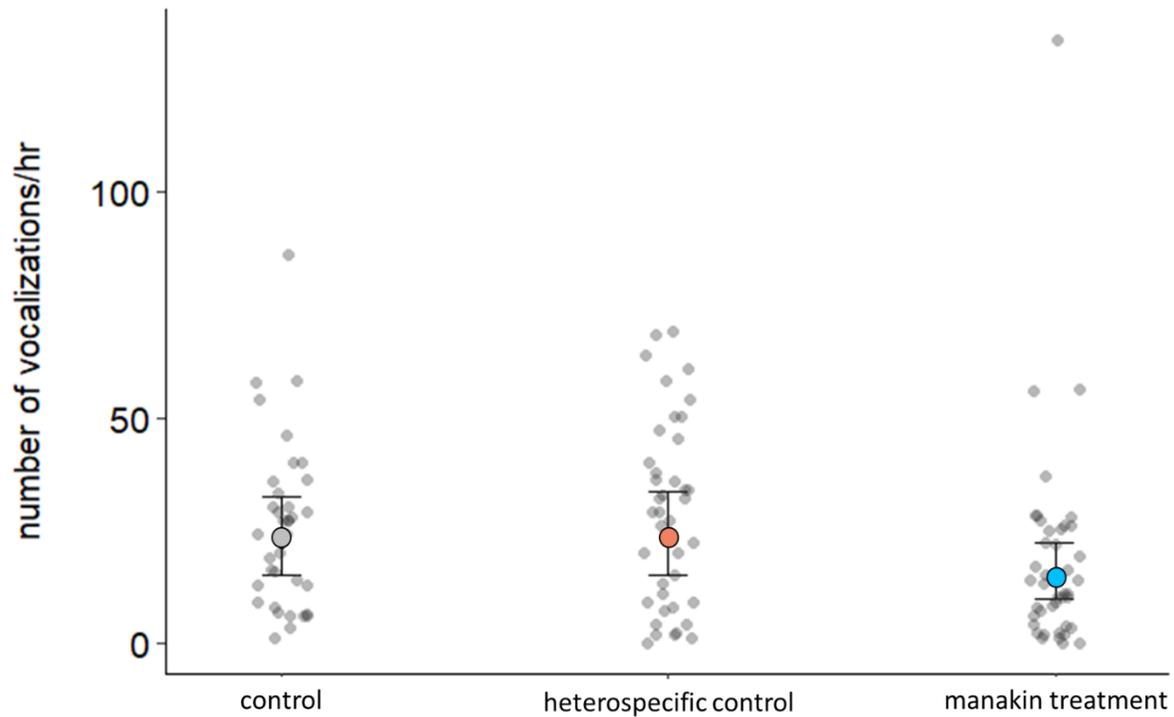
## Figures



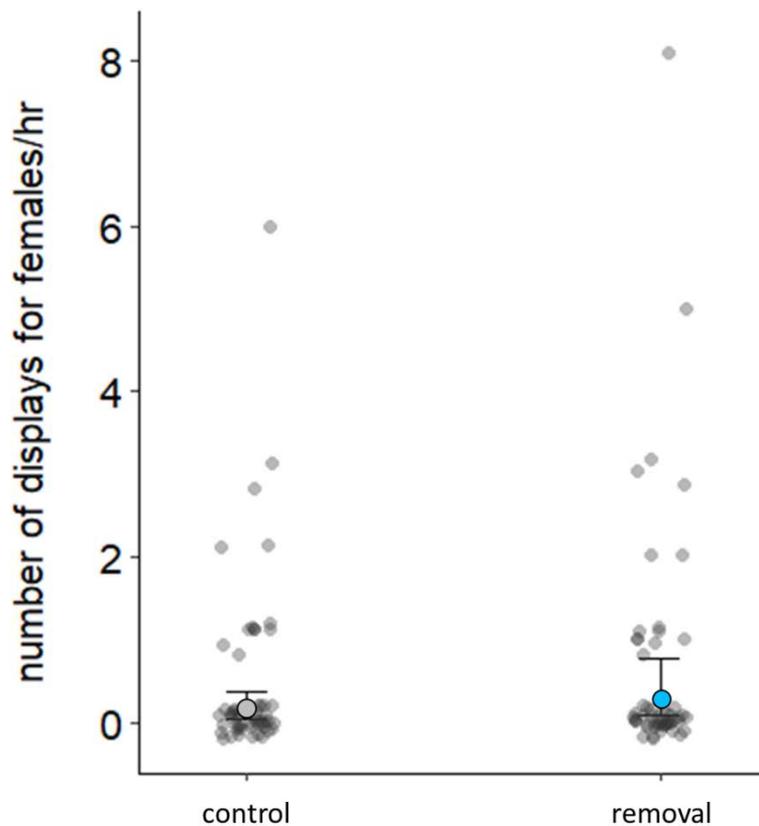
**Figure 5.1** Experimental set up for increased acoustic competition (**a**) and log removal (**b**) experiments. Boxes below diagram represent days of observations, with color corresponding to treatment on that day, and order of icon representing observation type (binoculars = in-person, camera = video) in the morning (left) and afternoon (right).



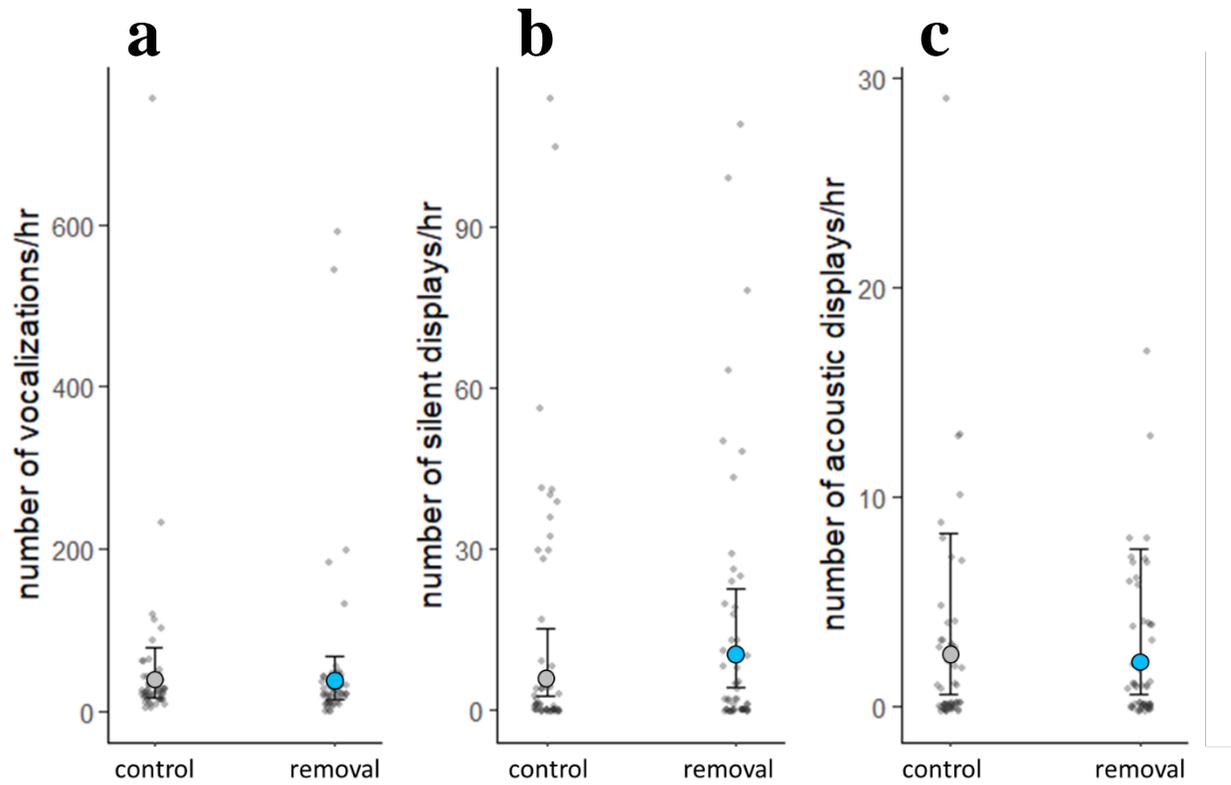
**Figure 5.2** Dot and whisker plot showing model predictions with 95% confidence intervals for (a) number of individuals present in vicinity of display log and (b) hourly rates of displays for females at the focal display log during the acoustic competition experiment. Transparent grey points are raw data collected during the experiment. Large grey point shows vocal rate at focal log when no sounds were broadcast. Orange point shows vocal rate at the focal log when speakers broadcast heterospecific calls. Finally, blue point shows hourly vocalization rate when speakers broadcast manakin acoustic signals.



**Figure 5.3** Dot and whisker plot showing model predictions with 95% confidence intervals for hourly rates for vocalization at the focal display log during the acoustic competition experiment. Transparent grey points are raw data collected during the experiment. Large grey point shows vocal rate at focal log when no sounds were broadcast. Orange point shows vocal rate at the focal log when speakers broadcast heterospecific calls. Finally, blue point shows hourly vocalization rate when speakers broadcast manakin acoustic signals.



**Figure 5.4** Dot and whisker plot showing model predictions with 95% confidence intervals of hourly rates for displays for female at the focal display log during the log removal experiment. Transparent grey points are raw data collected during the experiment. Large grey point shows display for female hourly rate at focal log when neighboring log(s) were not covered. Blue point shows display for female hourly rate at the focal log when other display logs in the lek were covered.



**Figure 5.5** Dot and whisker plots show model predictions with 95% confidence intervals of hourly rates for vocalization (a), silent displays (b), and acoustic displays (c) at the focal log. Raw data from observations are transparent grey points. Hourly rates during control observations when neighboring logs were not manipulated are shown in grey. Hourly rates at the focal log when neighboring logs are covered are shown in blue.

## Chapter 6 - Conclusions and implications

This dissertation contributes to our understanding of the selective forces shaping biodiversity in tropical regions. I addressed the overarching question of how natural and sexual selection interact to drive evolution of morphology, demography, and behavior at multiple levels of biological organization in a strong alternative-hypothesis-testing framework. As the specific questions and predictions tested at each of these levels varied, the overall picture emerging from this body of work is complex. However, this complexity is crucial for gaining a holistic understanding of the forces driving evolution in the tropics.

In some cases, the findings at one level do not align with those at another. Across the manakin clade, sexual size dimorphism in mass was associated with agility and sexual selection for aerial courtship displays. By contrast, a population-level genetic measure of reproductive skew was correlated with a putative source of natural selection, as reduced skew was measured at sites where precipitation fell throughout more of the year. The processes that are important at one level of inquiry may differ from those that are most powerful or detectable at another level. Thus, we cannot draw sweeping conclusions without consideration of the effects that trickle down or up from a particular inference. Much as ecological relationships are a complex web of interactions, disentangling historic and ongoing evolutionary processes requires careful consideration of the multiple selective forces that may act on a single trait or taxonomic unit.

Testing alternative hypotheses and selective drivers is especially important in studies of sexual selection. Although there is a strong tradition of studying evolutionary tradeoffs and constraints on sexually selected traits, there remains a tendency to test hypotheses and interpret findings exclusively in the context of obtaining mating opportunities. However, selection on organisms also occurs outside of the breeding season, with consequences for demography and

behavior that can influence individual fitness and evolution of populations. By not considering explicitly how abiotic or environmental factors could affect sexual selection, there is a risk of ignoring key drivers or making faulty conclusions. Naturally, it is impossible to consider all potential sources of selection in a single study. However, explicit articulation of those sources of selection and the assumptions involved in each study can greatly enhance the clarity of conclusions and expedite the potential for future studies to advance understanding.

This dissertation provides novel biological insights at multiple taxonomic levels and advances our knowledge of how natural and sexual selection interact. I emphasized that assumptions about sexual size dimorphism as a signal of sexual selection should carefully consider the direction of sexual selection and the context in which females are choosing or males are competing for mates. I provided the first published demographic estimates for four species of tropical bird in a wet montane forest. Applying population genetic methods in a novel context, I tested genomic predictions of natural selective and demographic constraints on the degree of reproductive skew and the strength of sexual selection. Finally, I documented behavioral evidence consistent with the hypothesis that cooperation among neighboring males to advertise their presence and location to potential female visitors.

An overarching conclusion of this work is that future research ought to consider explicitly the sometimes-important role of abiotic conditions, especially rainfall, in shaping tropical organisms. Precipitation and seasonality of precipitation were key factors associated with morphological variation, demographic rates, and genetic diversity in various sections of my dissertation. Rainfall plays a critical and historically underappreciated role in driving behavior, adaptation, and distribution of tropical taxa despite being the main axis of climate variability in the tropics. Much remains to be learned about how rain influences tropical organisms (Boyle et

al. 2020 *in press*). We need more research to uncover the mechanisms linking rain and fitness, and to determine the relative importance for tropical taxa of total annual rainfall, severe weather events, global climatic cycles, or seasonal patterns of precipitation.

Climate change is projected to alter the pattern and intensity of rainfall in the tropics in varying and unpredictable ways (Karmalkar et al. 2008, Hidalgo et al. 2013). Testing the mechanistic links between precipitation, selection, and ecology and evolution of tropical organisms is a critical area of future research. An integrative approach to answering key questions that span levels of biological organization, and devising predictions capable of distinguishing amongst alternative sources of selection are foundational to advancing knowledge of how changes in climate will affect the biodiverse tropics. This dissertation offers insights into the ways that such changes in natural selection will interact with sexual selection to shape the future of a charismatic group of birds

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