

**IMPACT OF FRUIT ENVIRONMENT ON DISPLAY COURT DEFENSE
INTENSITY IN WHITE-BEARDED MANAKINS**

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TABLE OF CONTENTS

ACKNOWLEDGEMENTS	ii
TABLE OF CONTENTS.....	iii
<u>1.</u> INTRODUCTION	1
<u>2.</u> METHODS	5
<u>3.</u> RESULTS	11
<u>4.</u> DISCUSSION.....	13
<u>5.</u> APPENDIX.....	17
<u>6.</u> REFERENCES	23

INTRODUCTION

Competition over limited resources is crucial for survival and reproduction. Individuals engage in conflicts with each other to secure exclusive access to shelter, food, and mating opportunities, even when such conflicts entail significant energetic or injury-related costs (Keddy 2012; Lane and Briffa 2017). These competitive interactions shape fitness and evolutionary trajectories via natural selection and sexual selection processes (Andersson and Iwasa 1996; Wade and Kalisz, 1990). Understanding the factors that shape the intensity and outcomes of competitive interactions remains a core goal of the behavioral ecology research agenda.

The strength of sexual selection is thought to be especially pronounced in lek-mating systems, where males congregate in a compact area with clusters of male courtship display sites to compete for visitations by and copulations with females (Shorey 2002; Fiske et al. 1998). Usually, males do not provide parental care, so females visit multiple displaying males at leks to choose the one that provides the most beneficial genes to their offspring (Höglund & Alatalo, 2014). Research on lekking behavior in insects (e.g., *Hetaerina* damselfly, Córdoba-Aguilar et al. 2009), reptiles (e.g., marine iguana, Partecke et al. 2002), amphibians (e.g., bullfrog, Emlen 1976), birds (e.g., sage grouse, Gibson & Bradbury, 1985), and mammals (e.g., blackbuck Isvaran and Jhala, 2000) has revealed high reproductive skew, where only a small proportion of males gain the majority of mating opportunities (Gibson and Bradbury 1985; Beehler and Foster, 1988; Wiley, 1991). In general, lekking species are thought to be characterized by strong female mate choice rather than male-male competition. However, some recent studies have shown that resource defense behaviors are more common than scholars used to assume in lekking insects, birds, and mammals. There is also ample evidence showing that males occupying more central display courts in lek experience higher rates of mating success (Emlen, 1976; Shore 2002; Fiske

et al. 1998), and it is thought that there may also be competition among males for more central courts (Isvaran and Jhala, 2000; Höglund and Robertson, 1990; Beehler and Foster, 1988). These and other studies on resource-defense within leks suggest that we might have been underestimating the role of male-male competition and the influence of ecological factors on male quality and display capacity (Alonso et al., 2012; Anderson et al., 2024; Kajiki et al., 2023).

The manakin family (*Pipridae*) are Neotropical passerines with an exceptional prevalence of lekking behavior among species (McDonald, 2010). Some species have “classical leks,” where males display at locations within acoustic or visual distance of each other, while those with “exploded leks” have more widely dispersed display locations. Covering bigger areas, exploded leks are more likely to contain resources favored by females, such as food and nesting sites. Male-male interactions and social dominance hierarchy have been extensively studied in Long-tailed Manakins (Lukianchuk and Doucet, 2014) and Lance-tailed Manakins (DuVal, 2007a, 2007b). Both species have exploded leks and engage in multi-male coordinated displays where only the dominant male mates with the female attracted to the court. To establish and repeatedly signal their social status, older males would aggressively chase or displace younger subordinate males from display perches (Lukianchuk & Doucet, 2014). Similar displacement behaviors have also been reported in species with a classical lek system. For example, White-bearded manakin (*Manacus manacus*) shows aggression towards the subordinate male by raising its beard and vibrating its wings when two adult males perch closely together (Shorey 2002; Snow 1962; Lill 1974b). White-collared Manakins (*M. candei*) and Golden-collared Manakins (*M. vitellinus*) physically attacked and pecked the mount with conspecific plumage when it was placed 25-50 cm away from the edge of their display arena (McDonald et al. 2001).

Despite the substantial amount of research on male-male interaction in manakins, most studies have focused either on the hormonal mechanism or on its adaptive value in male coordinated displays (Dakin et al., 2021; Day et al., 2007; Ryder et al., 2020), while male-male conflicts in solitarily displaying species like the *Manacus* species mentioned above have received less attention. Moreover, although these species clearly invest in establishing and maintaining ownership over display courts, it remains unclear what specific qualities of a court males value the most. Do they defend a court because it is closer to the lek center and receives more female visitations, or do they value high surrounding fruit abundance that fuels their energetically costly displays? Researchers have found evidence that central courts are richer in fruit, and that fruit abundance increased male display rate, but defense efforts remain unexamined (Anderson et al. 2024). It is also unknown how much effort court-owning males are willing to invest in defense against intruders. To date, none of these questions have been systematically explored or experimentally tested.

Our study aims to investigate the association between food resources in proximity to a display court and the court-owning male's defense intensity in White-bearded Manakins. Males of this Neotropical frugivore display on and around a small area of soil with short sapling sticks on the edges, which is known as a court (Cestari & Pizo 2012a; Snow 1962). Typically, one court is owned by one adult male who would frequently display at the same location during breeding seasons (Shorey 2002; Snow 1962; Lill 1974a, b). We tested the court-owner male's defense intensity by observing its reaction towards an experimentally introduced simulated territorial intrusion (STI) at its court. In addition to fruit abundance, we examined the influence of other court properties, including lek size, distance to lek center, and nearest neighbor distance. We hypothesized that court defense intensifies in leks because fruit adjacent to display courts is

an exceptionally valuable resource sustaining metabolically costly displays (Cestari et al. 2018) while minimizing foraging time away from the lek, which both are factors found to be positively correlated with high mating success in White-bearded manakins (Cestari & Pizo 2012; Anderson et al. 2024). We predicted that the intensity of court defense in response to STI would positively correlate with the abundance of fruit resources within a 10m radius of the court site.

METHODS

We conducted our study at Reserva FCAT (0°22'22.7"N 79°39'53.6"W) (Fundación para la Conservación de los Andes Tropicales), a private reserve in Esmeraldas Province, northwestern Ecuador. The reserve area contained a variety of land types, including restored agricultural fields, primary forests, and secondary forests. Manakins are the most common in early and mid-successional forests. Annual average rainfall ranges from 2 to 3.5m, with the highest amount of precipitation occurring between January and May, and is then followed by dry season lasting from October to December (Carrasco et al., 2013). Monthly rainfall peaked in February (309.1 mm) and March (332.0 mm) in previous years (Anderson et al. 2024).

The studied White-bearded Manakin (*Manacus manacus*) population belongs to the subspecies *leucochlamys* (Höglund and Shorey 2004). White-bearded manakins are small, frugivorous passerines inhabiting lowland Neotropical forests where they forage in the understory (Cestari and Pizo 2013). Males display on a small area (~1m²) of forest floor delimited by several vertical saplings (Snow 1962; Lill 1974b). This display ground is called a court, and a cluster of adjacent courts forms a lek, which may contain 2 to 70 courts in *M. manacus* (Shorey 2002; Olson and McDowell 1983). Each year, the breeding peak lasts 2~4 months when males display at higher rates and females visit courts to select only a small proportion of males to copulate with (Cestari and Pizo 2012a; Lill 1974a; Snow 1962; Olson and McDowell 1983). We monitored 6 leks (**Figure 1**) consisting of 57 active display courts, with individual leks containing 3 ~ 27 courts. The nearest-neighbor distance between courts within a lek ranged from 3.5m to 209.1m, with a mean of 11.43m (S.E. = 3.96). Straight-line distance between lek centers ranged from 131.7m to 1166.5m. We performed simulated territorial intrusion (STI) experiments at all 57 courts and received male responses at 54 courts. If no male responded in the first STI attempt, we retested at the same court at least twice, with each attempt

spaced over a day apart. If there was no male response over these additional attempts, we excluded the court from our analysis. Given that *M. manacus* exhibits a classical lek system with courts densely aggregated, some only a few body lengths apart, we grouped courts within visual or auditory range of each other as part of the same lek (Lill 1974a; DuVal et al. 2018; Cestari et al. 2016). Our grouping was further supported by longitudinal clustering patterns and frequent new court establishment within these pre-defined lek areas (Rathore et al. 2023; Anderson et al. 2024).

M. manacus displays involve elaborate movements such as acrobatic flights, jumps, wing snaps, and wing vibrations, requiring frequent practice since the males' juvenile days. Juvenile males in olive green plumage usually practice in small groups on peripheral courts without established ownership or on vacant courts when the resident adult is away during months outside the breeding peak. (Anderson et al. 2024; Snow 1962). As the juveniles molt into the black-and-white adult plumage in their second year, some secure the ownership of a single court and become "resident males" (Ryder and Durães 2005; Lill 1974b). Resident males spend most of the day at their court, reaching up to 90% during breeding months, asserting ownership through consistent displays and exclusion of intruders.(Cestari and Pizo 2012a; Lill 1974b; Snow 1962). Ownership status persists for several years with an average annual turnover rate of 3.7% over 4 years (Lill 1974b). Joint ownership over the same court is rare and short-lived (Snow 1962). Young males recently molted into adult plumage typically lack consistent court ownership and instead display at multiple peripheral courts in the lek (Cestari and Pizo 2012b). These nonresident males occasionally attempt to oust resident males, leading to aggressive encounters where the resident male approaches the intruder and attempts to displace him while "cheer" calling, often escalating into flight chases (Snow 1962; Shorey 2002; Lill 1974b; Olson and

McDowell 1983). Cestari 2017 has reported an incident of a resident male mounting juveniles while dancing, suggesting that dominance establishment may begin before adulthood during practice displays.

Fruit Survey

White-bearded manakins feed on the fruit of at least 58 understory plant species from 30 different families in Restinga forests in Brazil (Cestari and Pizo 2013). Based on this published diet identified using seeds collected from manakin feces and regurgitation, we identified important plant species based on direct observations of foraging behaviors at our study site in Ecuador (Anderson et al. 2024). We collected approximately 20 ripe berries from each plant species and weighed at least two samples of 5 berries to calculate the average weight for an individual fruit.

To estimate fruit abundance surrounding each display court, we conducted one fruit survey before the experiment day and another after, each within 10 days of the experiment. For each court, we established a circular survey plot centered at the display court with a radius of 10 meters. We visually tallied all ripe fruits, ripeness distinguished based on coloration, from species on manakin diet within the plot using the methods described in Anderson et al. (2024). The total fruit biomass at every court site was calculated by summing the product of fruit count and individual fruit weight by species.

Simulated Territorial Intrusion (STI) Experiment

We conducted 54 simulated territorial intrusion (STI) experiments at distinct display courts in 6 leks to record responses from court-owning males. All trials were executed between 8:00 and 15:00 under good weather conditions without rain. Data collection was completed from

February 12 to March 2, 2025, during the population's annual breeding peak when adult males display at higher rates. All leks were identified in 2022, and 34 courts were monitored by camera traps for at least 6 months before the experiment. In the rest 20 courts, we had at least one field observation of an adult male dancing at each location one week before or during the experimental period.

For each replicate of the experiment, we placed a white-bearded manakin bird mount (black and white adult male plumage) at the center of the display court. The mount was a taxidermized adult male that had previously been collected from the project area. The court center is designated as the midpoint of the cleared ground patch, positioned horizontally closest to the copulation stick. The mount was then covered by a piece of camouflage fabric attached to a string, which the experimenter would later pull to reveal the mount. A SONY SRS-XB100 Compact Bluetooth speaker was placed right next to the mount and camouflaged by leaves at the site. During each trial, two experimenters conducted experimental manipulations and recorded data. One stayed 4–5 meters from the mount and the other 10 meters away. Both experimenters wore full-body camouflage ponchos to minimize human influence on manakins' response towards the experiments.

Each experimental trial lasts 6 minutes, consisting of a 1-minute pre-mount-presentation period followed by a 5-minute mount-presentation period (McDonald et al. 2001; McClelland et al. 2019). In the pre-mount-presentation period, the experimenter broadcast from the Bluetooth speaker a one-minute playback of 10 “cheepo” calls, each spaced 5 seconds apart. The “cheepo” call repeated in the playback was extracted from a recording (<https://xeno-canto.org/169424>) from the same subspecies (*M. manacus leucochlamys*) (Höglund and Shorey 2004) recorded

~146 kilometers away from the studied population to prevent focal males from recognizing the caller's identity.

At the end of the pre-mount-presentation period, we pulled the string to reveal the mount while playing the one-minute playback again. If no adult males were detected visually or acoustically within a 10-meter radius of the court by the end of this playback, the experimenters would terminate this trial. When at least one adult male was detected within the first two minutes, we continued to record behavioral variables for the next four minutes with the taxidermy still present but no additional playbacks. When multiple males responded (11 cases), we used data from the one that remained the longest and responded most actively to the stimulus.

During 5 minutes of mount presentation, the experimenters recorded the focal male's (1) latency (sec) to move in the direction of the taxidermy for the first time, (2) minimum horizontal distance (cm) to the taxidermy, (3) total time (sec) spent inside the court, and (4) total number of vocalizations (cheer, cheepo, and gurgle), mechanical sounds (snap, roll-snap, grunt) and dive-bombs. At the beginning of every minute, the experimenters recorded an estimated distance (m) between the focal male and the taxidermy.

Statistical Analysis

We recorded UTM coordinates of all studied courts in the field with the GPS Tool Box application. We imported the data points and completed all mapping and spatial analyses in QGIS v. 3.42. We used minimum bounding geometry to estimate 6 lek polygons based on the GPS coordinates of all 54 courts. To describe properties relevant to male-male interaction, for each court, we calculated (1) its distance (m) to the centroid of its respective lek polygon, and (2) its distance (m) to its nearest neighboring court.

We performed all statistical analyses and created all figures in R v. 4.4.1 (R Core Team 2023). To reduce dimensionality and summarize behavioral patterns observed in STI trials, we conducted a principal component analysis (PCA) of all 7 behavioral parameters (**Table 1**) after scaling and standardization. Since principal component 1 (PC1) captured the majority of behavioral variation and positively covaried with signals of aggression, we used PC1 as a composite indicator of defense intensity.

To evaluate the relationship between court-owner defense intensity and the court's ecological properties, we employed the *lmer()* function in the *lme4* package to build generalized linear mixed-effect models (GLMMs) (Bates et al. 2015). The models included PC1 as the outcome variable, lek as the random effect predictor, and the courts' fruit biomass, distance to lek center, distance to nearest neighbor, and respective lek size as the fixed effect predictors. We transformed PC1 using $\log(\text{PC1} + 4)$ to improve residual normality. Adding a constant shifted all PC1 values to the positive range, thus avoiding undefined log values while optimizing data normalization. We assessed collinearity between all predictors using variance inflation factors (VIF). To select the best-fitted model, we used *dredge()* from *MuMIn* package (Barton 2017) to rank models based on Akaike information criterion (AIC_c). Since lek explained the main variance in all the best models, we conducted one-way ANOVA and Tukey's post hoc tests to compare defense intensity across leks.

RESULTS

We conducted a total of 54 successful Simulated Territorial Intrusion (STI) experiments at 6 total leks for this experiment (**Figure 1**). Each STI was conducted on a different display court, and each display court was only sampled once in the experiment.

Fruit Biomass

Leks varied substantially in fruit availability, $\chi^2(5) = 26.36, p < .001$, with mean biomass per court ranging from 0g to 947.51g. Notably, 37% of courts had no fruit in both surveys.

Sampled courts had a median fruit biomass of 1.06g (0 – 4.65g) in the first round of survey, and a median of 2.68g (0 – 15.22g) in the second round. *Melastomataceae* dominated fruit biomass in both survey rounds, composing 98.0% and 94.1%, respectively, followed by *Rubiaceae* at 1.9% and 5.9% and *Solanaceae* at 0.1% in the first survey.

Behavioral Response to STI

The first two principal components explained 64.85% of the variance observed in the 7 behavioral variables we recorded. Summarizing 50.12% of the variation, PC1 had high loadings for total time in court defending and total number of vocalizations, thus reflecting sustained defense effort and high acoustic signaling rates towards the intruder (**Figure 2**). Loadings of total dive bombs and distance to the taxidermy on PC1 reflected the court owner's tendency to interact. Overall, 6 out of 7 behavioral variables loaded substantially on PC1. Total number of wing snaps was the sole factor dominating PC2.

GLMM Model Selection

Random effect predictor lek explained 34.1% of the variance in defense intensity in the best fitted model ($\Delta AICc = 0.00, R^2_m = 0.076, R^2_c = 0.417$). With $\Delta AICc$ values smaller than 2,

all the top four models were equally supported given our data (**Table 2**). The best model indicated a marginally significant positive relationship between fruit biomass and defense intensity ($\beta = 0.0005$, $SE = 0.0003$, $t(24.27) = 1.76$, $p = 0.091$). Defense intensity varied significantly across leks, $F(5, 48) = 3.60$, $p = 0.008$ (**Figure 3**).

DISCUSSION

There is currently a lack of understanding about the factors shaping variation in the intensity of lekking males' defense in-lek resources. To address this knowledge gap, our study investigated how food resources and other environmental attributes in proximity to display areas influenced defense intensity in White-bearded Manakins, a solitarily displaying, lekking Neotropical passerine. We expected to see males defending fruit-rich courts, central courts, and courts with closer neighbors significantly more intensely. We also predicted defense intensity to be higher in bigger leks. Our results partially contradicted our predictions and indicated that court-owners who defended more intensely were not always located in fruit-rich courts, despite the weak positive correlation we observed. Instead, we found that males' defensive response to simulated intrusion varied substantially based on the lek to which they belonged, suggesting that other unmeasured properties differentiating lek dynamics (e.g., male density or numbers, habitat composition, female visitation rate) might have played a more dominant role in shaping male defense than fruit abundance.

While previous studies on resource defense by lekking males primarily focused on exploded lek systems, our study is among the first to examine it in a classical lek system. In exploded lek systems such as cichlid fish (Kotrschal and Taborsky, 2010), little bustards (Jiguet et al., 2002), great bustards (Alonso et al., 2012), and helmeted manakins (Kajiki et al., 2023), food resources or optimal habitats defended by males provided direct benefits to females and, in turn, increased female visitation. Compared to exploded leks, classical leks have more closely clustered display areas, and thus are less likely to contain resources other than the court-holding males and their 'good genes' (Emlen and Oring, 1977). Males in classical leks are well known to compete for central courts or higher social status, which conveys a message to females that they are likely the one with the highest attractiveness (Beehler and Foster, 1988; Shorey, 2002).

However, recent work on our manakin population suggested that defending fruit resources could be another competitive strategy males in classical leks employ to directly fuel high display rates and ultimately increase mating success (Anderson et al. 2024). Year-round fruit biomass sampled at the same location suggested our study period as a time with the lowest fruit abundance (Anderson et al., unpublished data). General scarcity of fruit might have limited the amount of variation across courts that we were able to detect, and it might be useful to assess fruit over longer time periods. We found a marginally significant positive correlation between fruit and defense intensity, yet the effective size was too small for us to confidently conclude that fruit shapes male defense intensity. A meaningful increase in fruit biomass (e.g., 20g), which is approximately 10 times of median fruit biomass per court, only resulted in a 0.5 unit increase in PC1. Therefore, our findings highlighted the impact of other environmental attributes and were inconclusive when it comes to the possibility that males in classical leks may have flexibly employed the strategy of resource defense to enhance their mating success.

Moreover, the directionality of causal links between fruit abundance and strong males was unclear. Although resource defense may offer reproductive advantages, the decision to engage in it likely involves complex trade-offs. Energy investment in court defense can benefit males by ensuring consistent ownership and uninterrupted display activity, but it also imposes costs (Cestari & Pizo, 2012b; Fiske et al., 1998; Théry, 1992). For example, allocating more energy towards defense may reduce display quality due to fatigue or limit time and spatial range for effective foraging (Ciuti et al., 2011; Ord, 2021; Cestari et al. 2018). In our study, 11 out of 54 males (20.4%) responded within 10s of playback initiation, and 33 (61.1%) responded within 30s. Such short reaction times correspond with previous findings that manakin males spend up to 80% of their daytime near their court in breeding season (Cestari and Pizo, 2012a). Benefits

outweigh costs for males at fruit-rich courts who can effectively refuel themselves to sustain both defense and display. Another possibility is that genetically superior males are capable of intense defense regardless of surrounding food availability. Males in our study likely represent a mixture of these two possibilities, with individuals in Lek C and Lek 6 evidencing the first one, and individuals in Lek 7E evidencing the second (**Figure 4**). When genetic factors interact with environmental factors, individual differences in defense behavior are likely reinforced via a feedback loop. If an innately stronger male happens to claim a fruit-rich court, the environment will further promote his ability to defend. However, further investigation of the genetic material is needed to confirm these causal links.

Environmental metrics such as lek centrality, nearest neighbor distance, and lek size only represented a small proportion of the key properties underlying the prominent lek-level differences in defense. We were surprised to find no correlation between fruit biomass and court centrality within the lek, contrasting with previous studies that reported a positive association between the two (Anderson et al. 2024). Neither nearest neighbor distance nor lek size significantly predicted defense intensity, but both were responsible for explaining a small amount of variance in defense, which presumably represented mediated effects from the influence of male density per lek. Similar to exploded leks, males in our study also defended more intensely when having closer neighbors (Alonso et al., 2012; DuVal et al., 2018) or when belonging to a bigger but intermediate-sized lek (Cestari et al., 2016; Emlen, 1976; Widemo & Owensi, 1995).

Some limitations of our study point to important directions for future research. First, many male individuals in our study have never been color-banded or measured for morphological traits, making it impossible to determine whether male quality or fruit abundance

better explains variation in defense intensity. Moreover, a single male can display on multiple courts (Cestari & Pizo, 2012b); making it possible we might have some pseudo-replications in our data; however, we consider it unlikely that this was widespread. Continuous tracking of court owners will not only help reveal relationships between response intensity with male age, physiology, and longer-term fruit trends, but will also eliminate the possibility of pseudo-replication. Second, leks differ in a wide array of characteristics and are an important random effect factor to account for. Future studies can include male density at every lek as a main predictor and further examine the habitat composition of each lek. Another predictor that might differ across leks is their location relative to female home range or foraging hotspots (Sheehy et al., 2025; Théry, 1992). Third, little is known about the temporal variation in male defense as ownership establishment and turnover occur. Our pilot data indicated suppressed adult male defense during non-breeding periods like May and June, when court owners allowed juvenile males to use their courts for practicing courtship dances in small groups of 3 to 7. Only 11% of STI experiments during our pilot work at such times received responses from a single adult male. Most trials were responded to by juveniles arriving in groups and doing frequent wing snaps. Repeating the experiment while monitoring court ownership dynamics will further inform the interpretation of resource defense in classical leks.

In summary, our study adds to the growing body of research suggesting that males in classical leks may flexibly adopt resource defense as a strategy to enhance mating success. But because this relationship was weak, we highlight the need for future research to better understand these relationships. We also highlight the need to refine our understanding of how fruit abundance may be related to other factors like the number of males at a lek, court centrality, and individual-level attributes that we were unable to adequately account for in the current study.

APPENDIX

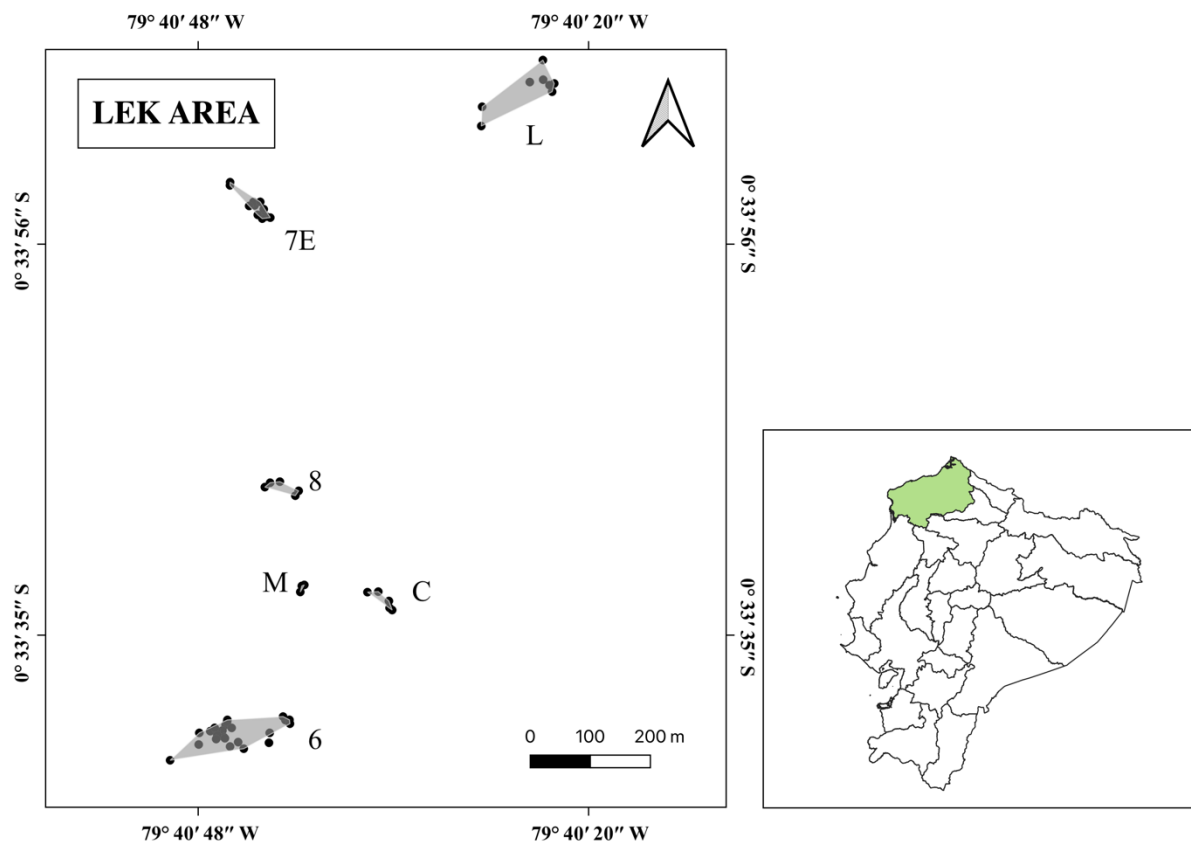


Figure 1. Study area map of six lek sites located in northwestern Ecuador, Esmeraldas province (highlighted in green). Each black dot represents an active display court ($n = 57$), grey polygons are lek areas estimated by convex hull, with names of the lek labeled nearby.

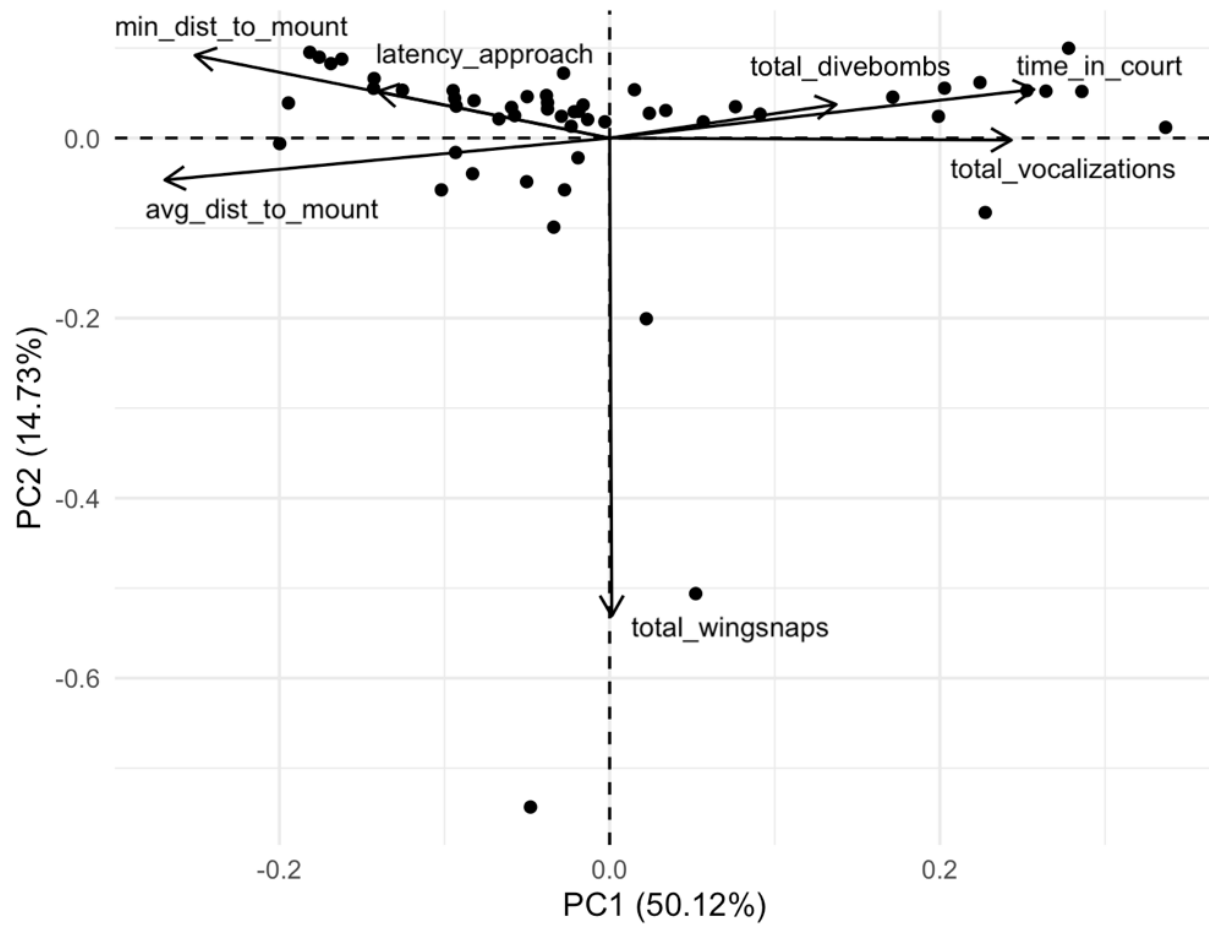


Figure 2. PCA biplot showing male owners of different display courts varying in their behavioral reactions to STI. Arrows represent loadings of the 7 directly measured original behavioral variables, indicating their contribution to the first two principal components (n = 54).

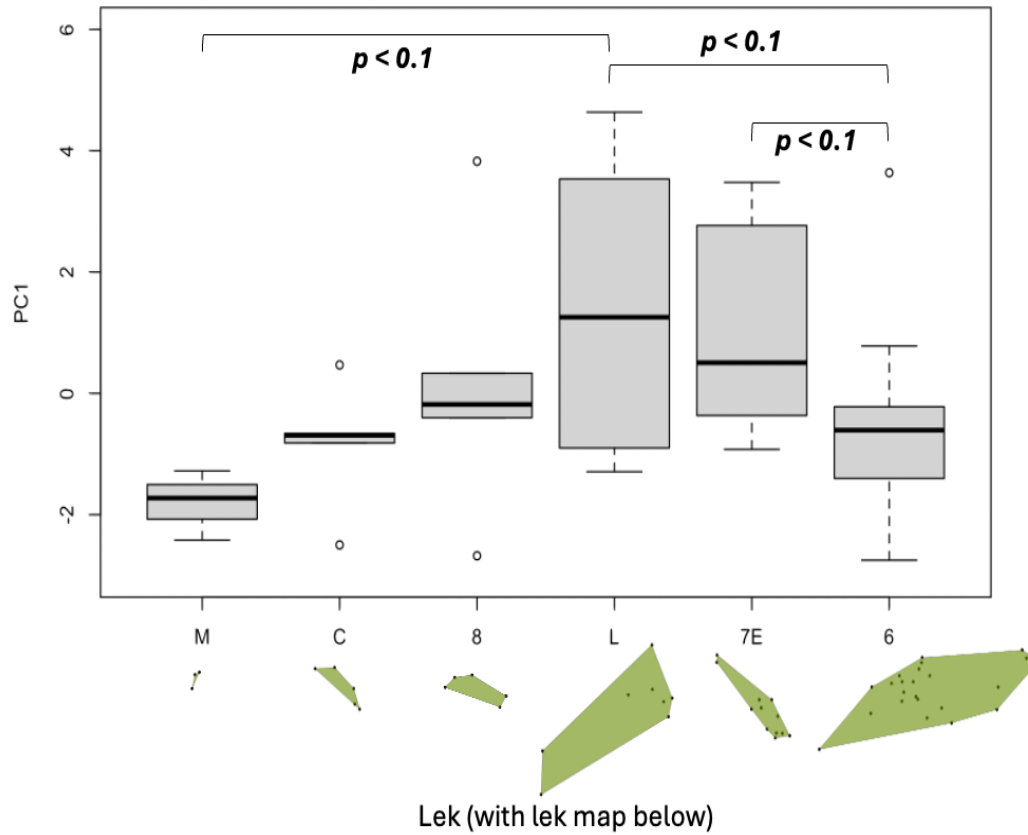


Figure 3. Boxplots showing variation in defense intensity by lek ($n = 54$). Lek maps are proportional to lek size, with the total number of courts increasing from 3 to 24 along the horizontal axis. Results of Tukey's tests indicate marginally significant differences in PC1 between leks ($ps < .1$).

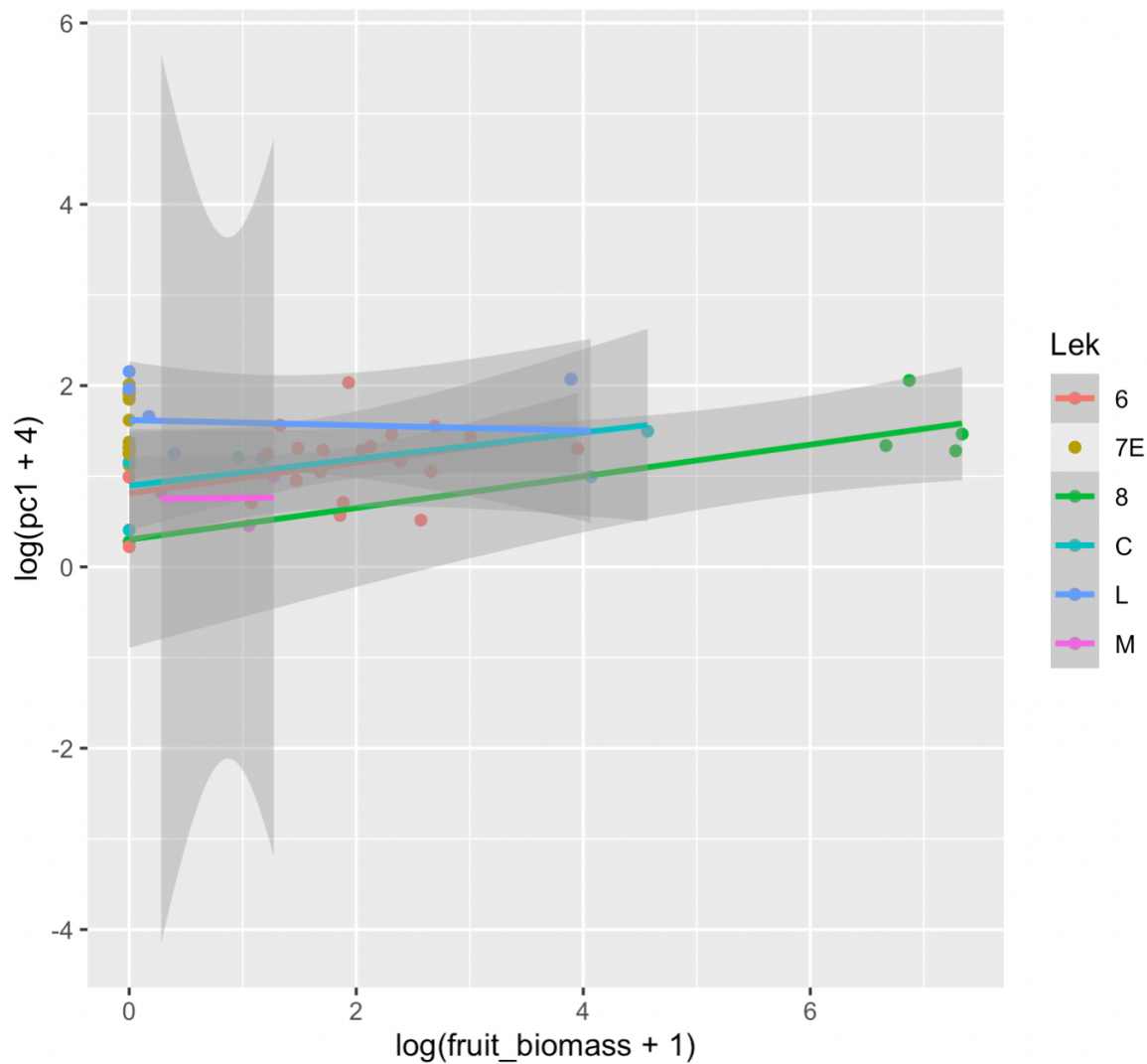


Figure 4. Scatterplot with linear regression lines (with SE) showing the correlation between fruit biomass and male defense intensity by lek. PC1 was log-transformed to normalize model residuals, and fruit biomass was zero-inflated, so we log-transformed it for better visual display. Altogether, the dataset exhibits a weak, positive linear correlation.

Table 1. PCA loadings of owner males' behavioral variables measured during STI on the first two principal components. Total vocalizations combined counts of cheepo, cheer, and gurgle calls, and total wing snaps combined counts of roll-snap, snap, and grunt.

Behavior Variables	PC1	PC2
Average distance to taxidermy	-0.49	-0.09
Total time in court	0.47	0.10
Minimum distance to taxidermy	-0.46	0.17
Total number of vocalizations	0.44	0.00
Latency to approach taxidermy	-0.26	0.09
Total number of divebombs	0.25	0.07
Total number of wingsnaps	0.00	-0.97
<i>Variance Explained</i>	<i>50.12%</i>	<i>14.73%</i>

Table 2. The top 5 best-fitted GLMMs predicting defense intensity based on AICc automated model selection. *Lek* is the random effect predictor, while **Fruit**, NND (nearest neighbor distance), and LS (*lek* size) are all fixed effect predictors. Bolded predictors are marginally significant ($p < .1$).

Rank	Model	df	logLik	AICc	Δ AICc	Weight	R^2_m	R^2_c
1	<i>Lek</i> + Fruit	4	-32.530	73.9	0.00	0.207	0.076	0.417
2	<i>Lek</i>	3	-33.736	74.0	0.08	0.199	0.000	0.240
3	<i>Lek</i> + Fruit + NND	5	-32.266	75.8	1.91	0.080	0.081	0.435
4	<i>Lek</i> + NND	4	-33.527	75.9	1.99	0.076	0.007	0.263
5	<i>Lek</i> + Fruit + LS	5	-32.364	76.0	2.10	0.072	0.087	0.498

REFERENCES

- Alonso, Juan C., Marina Magaña, and Jose M. Álvarez-Martínez. 2012. “Male Display Areas in Exploded Leks: The Importance of Food Resources for Male Mating Success.” *Behavioral Ecology* 23 (6): 1296–1307. <https://doi.org/10.1093/beheco/ars121>.
- Anderson, H. Luke, Jairo Cabo, and Jordan Karubian. 2024. “Fruit Resources Shape Sexual Selection Processes in a Lek Mating System.” *Biology Letters* 20 (9): 20240284. <https://doi.org/10.1098/rsbl.2024.0284>.
- Andersson, Malte, and Yoh Iwasa. 1996. “Sexual Selection.” *Trends in Ecology & Evolution* 11 (2): 53–58.
- Barton, B.K. 2017. MuMIn: Multi-Model Inference. R package version 1.40.0.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Carrasco, Luis, Karl Berg, Jennifer Litz, Andrew Cook, and Jordan Karubian. 2013. “Avifauna of the Mache Chindul Ecological Reserve, Northwest Ecuador.” *Ornitología Neotropical*, January. https://scholarworks.utrgv.edu/bio_fac/296.
- Cestari, C., and M.A. Pizo. 2012. “Lek Phenology of the White-Bearded Manakin (*Manacus Manacus*, Aves: Passeriformes: Pipridae) in a Subtropical Region.” *Journal of Natural History* 46 (47–48): 2999–3009. <https://doi.org/10.1080/00222933.2012.727485>.
- Cestari, César. 2017. “Same-Sex Mounting Behavior between Juveniles and Adult Males of the White-Bearded Manakin (*Manacus Manacus*).” *Ornitología Neotropical* 28:277–80.
- Cestari, César, Bette A. Loiselle, and Marco Aurélio Pizo. 2016. “Trade-Offs in Male Display Activity with Lek Size.” *PLOS ONE* 11 (9): e0162943. <https://doi.org/10.1371/journal.pone.0162943>.
- Cestari, César, and Marco Aurélio Pizo. 2012. “The Use of Auxiliary Courts by the Lek-Forming White-Bearded Manakin *Manacus Manacus* (Aves, Pipridae).” *Acta Ethologica* 15 (1): 73–79. <https://doi.org/10.1007/s10211-011-0110-0>.
- — —. 2013. “Frugivory by the White-Bearded Manakin (*Manacus Manacus*, Pipridae) in *Restinga* Forest, an Ecosystem Associated to the Atlantic Forest.” *Biota Neotropica* 13 (June):345–50. <https://doi.org/10.1590/S1676-06032013000200038>.

- Cestari, César, Marco Aurélio Pizo, and Bette A. Loiselle. 2018. “Display Activity and Foraging Costs of a Frugivorous Lekking Bird.” *The Wilson Journal of Ornithology* 130 (4): 869–73.
- Chase, Jonathan M., Peter A. Abrams, James P. Grover, Sebastian Diehl, Peter Chesson, Robert D. Holt, Shane A. Richards, Roger M. Nisbet, and Ted J. Case. 2002. “The Interaction between Predation and Competition: A Review and Synthesis.” *Ecology Letters* 5 (2): 302–15. <https://doi.org/10.1046/j.1461-0248.2002.00315.x>.
- Ciuti, Simone, Fabio De Cena, Paolo Bongio, and Marco Apollonio. 2011. “Benefits of a Risky Life for Fallow Deer Bucks (*Dama dama*) Aspiring to Patrol a Lek Territory.” *Behaviour* 148 (4): 435–60.
- Córdoba-Aguilar, A., G. Raihani, M. A. Serrano-Meneses, and J. Contreras-Garduño. 2009. “The Lek Mating System of *Hetaerina* Damselflies (Insecta: Calopterygidae).” *Behaviour*, 189–207.
- Dakin, Roslyn, Ignacio T. Moore, Brent M. Horton, Ben J. Vernasco, and T. Brandt Ryder. 2021. “Testosterone-mediated Behaviour Shapes the Emergent Properties of Social Networks.” Edited by Damien Farine. *Journal of Animal Ecology* 90 (1): 131–42. <https://doi.org/10.1111/1365-2656.13305>.
- Day, Lainy B., Leonida Fusani, Estefanía Hernández, Timothy J. Billo, Kimberly S. Sheldon, Petra M. Wise, and Barney A. Schlinger. 2007. “Testosterone and Its Effects on Courtship in Golden-Collared Manakins (*Manacus vitellinus*): Seasonal, Sex, and Age Differences.” *Hormones and Behavior* 51 (1): 69–76.
- DuVal, Emily H. 2007a. “Social Organization and Variation in Cooperative Alliances among Male Lance-Tailed Manakins.” *Animal Behaviour* 73 (3): 391–401.
- DuVal, Emily H., Carla C. Vanderbilt, and Leithen K. M’Gonigle. 2018. “The Spatial Dynamics of Female Choice in an Exploded Lek Generate Benefits of Aggregation for Experienced Males.” *Animal Behaviour* 143 (September): 215–25. <https://doi.org/10.1016/j.anbehav.2018.01.009>.
- DuVal, Emily H. 2007b. “Adaptive Advantages of Cooperative Courtship for Subordinate Male Lance-Tailed Manakins.” *The American Naturalist* 169 (4): 423–32. <https://doi.org/10.1086/512137>.

- Emlen, Stephen T. 1976. "Lek Organization and Mating Strategies in the Bullfrog." *Behavioral Ecology and Sociobiology* 1 (3): 283–313. <https://doi.org/10.1007/BF00300069>.
- Emlen, Stephen T., and Lewis W. Oring. 1977. "Ecology, Sexual Selection, and the Evolution of Mating Systems." *Science* 197 (4300): 215–23. <https://doi.org/10.1126/science.327542>.
- Fiske, Peder, Pekka T. Rintamäki, and Eevi Karvonen. 1998. "Mating Success in Lekking Males: A Meta-Analysis." *Behavioral Ecology* 9 (4): 328–38.
- Gibson, R. M., and J. W. Bradbury. 1985. "Sexual Selection in Lekking Sage Grouse: Phenotypic Correlates of Male Mating Success." *Behavioral Ecology and Sociobiology* 18 (2): 117–23. <https://doi.org/10.1007/BF00299040>.
- Höglund, Jacob, and Rauno V. Alatalo. 2014. "Leks." In *Leks*. Princeton University Press. <https://www.degruyterbrill.com/document/doi/10.1515/9781400864157/html>.
- Höglund, Jacob, and Jeremy G. M. Robertson. 1990. "Female Preferences, Male Decision Rules and the Evolution of Leks in the Great Snipe *Gallinago Media*." *Animal Behaviour* 40 (1): 15–22. [https://doi.org/10.1016/S0003-3472\(05\)80661-X](https://doi.org/10.1016/S0003-3472(05)80661-X).
- Höglund, Jacob, and Lisa Shorey. 2004. "Genetic Divergence in the Superspecies Manacus." *Biological Journal of the Linnean Society* 81 (3): 439–47.
- Isvaran, Kavita, and Yadavendradev Jhala. 2000. "Variation in Lekking Costs in Blackbuck (Antelope Cervicapra): Relationship to Lek-Territory Location and Female Mating Patterns." *Behaviour* 137 (5): 547–63.
- Jiguet, Frédéric, Stéphane Jaulin, and Beatriz Arroyo. 2002. "Resource Defence on Exploded Leks: Do Male Little Bustards, *T. Tetrix*, Control Resources for Females?" *Animal Behaviour* 63 (5): 899–905. <https://doi.org/10.1006/anbe.2001.1970>.
- Kajiki, Lia Nahomi, de-Carvalho, Mariana, Resende Dos Santos, Paulo Victor, Teixeira, Samara de Albuquerque, and Regina H. and Macedo. 2023. "Individual Territoriality in Lekking Species: The Case of the Helmeted Manakin." *Emu - Austral Ornithology* 123 (1): 35–48. <https://doi.org/10.1080/01584197.2022.2160358>.
- Keddy, Paul A. 2012. *Competition*. Vol. 26. Springer Science & Business Media. <https://books.google.com/books?hl=en&lr=&id=l5nnCAAQBAJ&oi=fnd&pg=PR3&dq=competition+animal&ots=NKrF-KoIfP&sig=vmBQaL0M51Y0iR4vg9GvctiWoy8>.

- Kotrschal, Alexander, and Barbara Taborsky. 2010. "Resource Defence or Exploded Lek? – A Question of Perspective." *Ethology* 116 (12): 1189–98. <https://doi.org/10.1111/j.1439-0310.2010.01831.x>.
- Lane, Sarah M., and Mark Briffa. 2017. "The Price of Attack: Rethinking Damage Costs in Animal Contests." *Animal Behaviour* 126:23–29.
- Lill, Alan. 1974a. "Sexual Behavior of the Lek-Forming White-Bearded Manakin (Manacus Manacus Trinitatis Hartert)." *Zeitschrift Für Tierpsychologie* 36 (1–5): 1–36. <https://doi.org/10.1111/j.1439-0310.1974.tb02126.x>.
- . 1974b. "Social Organization and Space Utilization in the Lek-Forming White-Bearded Manakin, *M. Manacus Trinitatis* Hartert." *Zeitschrift Für Tierpsychologie* 36 (1–5): 513–30. <https://doi.org/10.1111/j.1439-0310.1974.tb02136.x>.
- Lukianchuk, Katrina C., and Stéphanie M. Doucet. 2014. "A Young Manakin Knows His Place: Evidence for an Age-Graded Dominance Hierarchy Among Long-Tailed Manakins." *Ethology* 120 (7): 693–701. <https://doi.org/10.1111/eth.12240>.
- McClelland, Stephanie C., Renata Durães Ribeiro, Howard W. Mielke, Myra E. Finkelstein, Christopher R. Gonzales, John Anthony Jones, Jan Komdeur, Elizabeth Derryberry, Emma B. Saltzberg, and Jordan Karubian. 2019. "Sub-Lethal Exposure to Lead Is Associated with Heightened Aggression in an Urban Songbird." *Science of The Total Environment* 654 (March):593–603. <https://doi.org/10.1016/j.scitotenv.2018.11.145>.
- McDonald, David B. 2010. "A Spatial Dance to the Music of Time in the Leks of Long-Tailed Manakins." In *Advances in the Study of Behavior*, edited by Regina Macedo, 42:55–81. Behavioral Ecology of Tropical Animals. Academic Press. [https://doi.org/10.1016/S0065-3454\(10\)42002-1](https://doi.org/10.1016/S0065-3454(10)42002-1).
- McDonald, David B., Robert P. Clay, Robb T. Brumfield, and Michael J. Braun. 2001. "Sexual Selection on Plumage and Behavior in an Avian Hybrid Zone: Experimental Tests of Male-Male Interactions." *Evolution* 55 (7): 1443–51.
- Olson, Deanna H., and Michael K. McDowell. 1983. "A Comparison of White-Bearded Manakin (Manacus Manacus) Populations and Lek Systems in Suriname and Trinidad." *The Auk*, 739–42.
- Ord, Terry J. 2021. "Costs of Territoriality: A Review of Hypotheses, Meta-Analysis, and Field Study." *Oecologia* 197 (3): 615–31. <https://doi.org/10.1007/s00442-021-05068-6>.

- Partecke, Jesko, Arndt Von Haeseler, and Martin Wikelski. 2002. "Territory Establishment in Lekking Marine Iguanas, *Amblyrhynchus Cristatus*: Support for the Hotshot Mechanism." *Behavioral Ecology and Sociobiology* 51 (6): 579–87. <https://doi.org/10.1007/s00265-002-0469-z>.
- R Core Team. 2023 R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. See <http://www.R-project.org/>.
- Rathore, Akanksha, Kavita Isvaran, and Vishwesh Guttal. 2023. "Lekking as Collective Behaviour." *Philosophical Transactions of the Royal Society B: Biological Sciences* 378 (1874): 20220066. <https://doi.org/10.1098/rstb.2022.0066>.
- Ryder, T. Brandt, Roslyn Dakin, Ben J. Vernasco, Brian S. Evans, Brent M. Horton, and Ignacio T. Moore. 2020. "Testosterone Modulates Status-Specific Patterns of Cooperation in a Social Network." *The American Naturalist* 195 (1): 82–94. <https://doi.org/10.1086/706236>.
- Ryder, Thomas B., and Renata Durães. 2005. "It's Not Easy Being Green: Using Molt and Morphological Criteria to Age and Sex Green-Plumage Manakins (Aves: Pipridae)." *Ornitologia Neotropical* 16:481–91.
- Sheehy, Erin, H. Luke Anderson, Luis Carrasco, Jorge Olivo, Domingo Cabrera, Nelson Gonzalez, Renata Ribeiro, and Jordan Karubian. 2025. "Lek Habitat Selection by Sympatric Manakin Species in Northwestern Ecuador." *Ecology and Evolution* 15 (3): e70860. <https://doi.org/10.1002/ece3.70860>.
- Shorey, Lisa. 2002. "Mating Success on White-Bearded Manakin (*Manacus Manacus*) Leks: Male Characteristics and Relatedness." *Behavioral Ecology and Sociobiology* 52 (6): 451–57. <https://doi.org/10.1007/s00265-002-0540-9>.
- Snow. 1962. *A Field Study of the Black and White Manakin, Manacus Manacus, in Trinidad*. <http://archive.org/details/biostor-194060>.
- Théry, Marc. 1992. "The Evolution of Leks through Female Choice: Differential Clustering and Space Utilization in Six Sympatric Manakins." *Behavioral Ecology and Sociobiology* 30 (3): 227–37. <https://doi.org/10.1007/BF00166707>.
- Wade, Michael J., and Susan Kalisz. 1990. "The Causes of Natural Selection." *Evolution* 44 (8): 1947–55.

Wiley, R. Haven. 1991. "Lekking in Birds and Mammals: Behavioral and Evolutionary Issues."
In *Advances in the Study of Behavior*, edited by Peter J. B. Slater, Jay S. Rosenblatt,
Colin Beer, and Manfred Milinski, 20:201–91. Academic Press.
[https://doi.org/10.1016/S0065-3454\(08\)60322-8](https://doi.org/10.1016/S0065-3454(08)60322-8).

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