

BEHAVIORAL ECOLOGY OF COLONIALITY
IN THE HISPANIOLAN WOODPECKER

A Dissertation

Presented to the Faculty of the Graduate School
of Cornell University

In Partial Fulfillment of the Requirements for the Degree of
Doctor of Philosophy

by

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December 2018

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Cornell University 2018

Explaining intra- and interspecific variation in sociality requires understanding the underlying ecological factors that promote or preclude grouping and the fitness consequences of group living. Colonial nesting, the dense concentration of individuals during breeding, offers an excellent opportunity for testing hypotheses to explain sociality and its variation. I studied the Hispaniolan Woodpecker (*Melanerpes striatus*), a facultative colonial breeder, in the Dominican Republic with the following goals, corresponding to the three chapters of this dissertation: (1) identify the ecological resources that explain colony size variation; (2) test for the effects of colony size on reproductive success with the goal of distinguishing the hypotheses of grouping for socially derived benefits from aggregations that form due to the spatiotemporal clustering of resources; and (3) determine whether coloniality impacts the genetic mating system by increasing the incidence of conspecific brood parasitism and extra-pair paternity. In Chapter 1, I show that Hispaniolan Woodpecker colony size is explained in part by the number of cavities on a tree and a nesting tree's status: dead *Roystonea* palms hosted larger colonies than live palms. Dead palms were relatively rare on the landscape but were potentially higher quality because they were easier to excavate and immune to nest loss via cavity flooding. In Chapter 2, I show that, per nesting attempt, clutch size, hatching success, partial brood loss, and the number of fledglings produced were unrelated to colony size. However, nesting success, fledging one or

more young vs. complete failure, was positively associated with colony size. Additionally, annual nesting success and annual fledging success were not associated with colony size. In Chapter 3, I show that Hispaniolan Woodpeckers were socially and genetically monogamous. Conspecific brood parasitism, though not detected genetically, was suspected in three nests based on aberrant changes in clutch size. Together, these chapters suggest that resource availability (dead trees and old cavities) likely promotes coloniality while there are minimal costs and very modest (if any) benefits of sociality for the Hispaniolan Woodpecker.

BIOGRAPHICAL SKETCH

I hail from Haddon Heights, NJ, a borough of Camden County once considered one of the safest towns in the U.S. Much of my life could accurately be described as a tug-of-war between my two passions: zoology and music. For many years, I maintained numerous vivaria and aquaria and brought home nearly every manner of creature suburban New Jersey or the local pet store offered (I will spare you a detailed list for brevity's sake). I became distracted from zoology, though, when in high school I began playing guitar, singing, and writing songs for a ska-punk band called Dirty Larry and became involved in the local music scene, a pastime that consumed the better part of eight years (including all my undergraduate career). A year after I finished my bachelor's degree, though, I forsook my dreams of rock and roll stardom and returned to my first love of zoology.

My academic journey into biology began at the University of Maryland (College Park) with the initial goal of becoming a nature show host. After two years in College Park, I transferred to Rowan University where I earned a B.S. in Biological Sciences with an Environmental Studies concentration (emphasis in Zoology). The original motivation for moving to Rowan and closer to home was to facilitate a dual focus on my studies and my music. Fortunately, the research bug bit me hard at Rowan. First, I worked with Dr. Gerald Hough for a year and a half, conducting an independent laboratory investigation on the navigational behavior of pigeons. Next, I worked for a summer as Dr. Michael Grove's research assistant studying an invasive plant's impact on fiddler crab behavior in the salt marshes of southern New Jersey. Lastly, I worked as Dr. Luke Holbook's research assistant for two years on the phylogenetics and systematics of early perissodactyl mammals. Partly as result of those research experiences and the enthusiastic encouragement of the aforementioned professors and Drs. Courtney Richmond

and Andrew Prieto, I decided to attend graduate school in biology. It is largely a result of my interactions with those wonderful Rowan professors that I landed at Villanova University with a desire to dive deeper into the world of biological research.

While pursuing a Master of Science in Biology at Villanova, I cultivated an intense passion for Neotropical ornithology and behavioral ecology. For my thesis work, I undertook the first intensive behavioral ecological study of the Black Catbird (*Melanoptila glabrirostris*), a species endemic to the Yucatán Peninsula. My thesis advisor, Dr. Robert (Bob) Curry, of chickadee and mockingbird fame, nurtured my growing love and appreciation for the New World tropics and its poorly known denizens. In August 2010, I commenced studies for a Ph.D. in Behavioral Biology at Cornell University under the co-direction of Drs. Walter Koenig and Paul Sherman. Continuing the interests I developed at Villanova, I am presently developing a dissertation on colonial, cooperative breeding and sexual selection in Hispaniolan Woodpeckers (*Melanerpes striatus*) in the Dominican Republic. All the mosquito bites, wasp and ant stings, sun burn, drenching downpours, and intense tropical heat endured could not dissuade me from pursuing my childhood dream.

Along my Ph.D. quest, I also got engaged and then married, published a few papers, made new friends, lost some old ones and some family, gained some new family, very nearly lost my own life, and helped bring a beautiful little boy into the world. My wonderful wife (Concetta LaPergola), hilarious and energetic son (Michele Giuseppe LaPergola), hapless cat (Margaret Morse Mice), and all our books recently moved to Lawrenceville, NJ. Upon completion of my dissertation requirements, I will start work as a postdoctoral research associate in the lab of Dr. Christie Riehl at Princeton University, working on her long-term research project on the Greater Ani (*Crotophaga major*), yet another Neotropical bird.

For Concetta LaPergola, whose unflagging love and support
sustained me through my quest for knowledge;

For Michele Giuseppe LaPergola, who brings me endless joy and
taught me the meaning of unconditional love;

And

For my parents, Linda Sullivan and Kevin LaPergola, who encouraged
the intellectual curiosities of a young naturalist in suburban New Jersey.

ACKNOWLEDGMENTS

Without the help of dedicated and patient volunteers, this dissertation would surely have never come to fruition. I gratefully acknowledge the following individuals (alphabetically) for providing their invaluable assistance in the field: Michelle Angelucci Eshleman, Haley Boyle, Cecilia Cerrilla, Will Coleman, Aracely Diaz, Lauren Emerson, Neil Gilbert, Amy Janik, Kiera Kauffman, Thomas (“Major Tom”) Lacerda, Alex Lascher-Posner, Mia Larrieu, Kai Larsen, Cedar Mathers-Winn, Kaylee Nelsen, Alyssa Occhialini, Spencer Schubert, Hannah Stapleton, Mitch Walters, Allegra Waterman-Snow, Paris Werner, and Amber Wichtendahl.

I am indebted to my committee for their patience and guidance over the past 8.5 years. Many thanks are owed to Walt Koenig for giving ample independence and freedom to pursue a crazy project. Paul Sherman, until mid-2016, was my co-advisor and provided much critical feedback and cheerleading in the early stages of my dissertation research efforts. After my accident, Paul stepped down, and Mike Webster took up the reins as my co-advisor. I owe Mike much gratitude for “adopting” me as one of his advisees and helping steer me towards the end. Janis Dickinson provided much critical and incisive feedback and always pushed me to think more clearly about my research. Kern Reeve helped me appreciate the world of modeling and to recognize the importance of clarifying the assumptions of a research hypothesis. Irby Lovette allowed me to work in the Fuller Lab and provided tough but fair comments on early drafts of my chapters.

I am very grateful to Bronwyn Butcher, who patiently guided me through the molecular methods necessary for the ddRADseq work in my dissertation. Attendees of Lunch Bunch group, members of the Dickinson/Koenig and Webster (Weblab) lab groups, and participants of the joint lab meetings of the Bird Population Studies and Citizen Science programs at the Lab of

Ornithology provided valuable feedback at various stages of this dissertation. I owe special thanks to the regular and semi-regular attendees of the behavioral “jam sessions,” especially Julie Miller, Julian Kapoor, Kristin Hook, and Jay Falk, for valuable feedback and encouragement along the way. The following current and former grad students are also owed special thanks for their feedback, advice, and various practical assistance: Jenélle Dowling, Mickey Pardo, Esther Niemasick, McKenna Kelly, Maria Modanu, David Peck, Geoff Broadhead, Derrick Thrasher, Taza Schaming, Justin Proctor, Sahas Barve, Jim Goetz, Caitlin Stern, Jessie Barker, Becky Cramer, Kevin Loope, Hailey Scofield. I also thank Concetta LaPergola, Amanda Savagian, Maria Smith, and Meghan Strong for providing independent counts for the satellite imagery analysis in Chapter 1.

The following funding sources supported my research efforts: Cornell Lab of Ornithology Athena Fund, Department of Neurobiology Animal Behavior Research Grant, Society for the Study of Evolution Rosemary Grant Award, and Sigma Xi Grant in Aid of Research. I was also supported by the following fellowships during fieldwork: Charles Walcott Graduate Fellowship, Linda and Samuel Graduate Student Fellowship, Eleanore Stuart Graduate Fellowship, Andrew '78 and Margaret Paul Graduate Fellowship, Kramer Graduate Fellowship, Halberstadt Graduate Fellowship, Anne Marie Brown Summer Graduate Fellowship, and Lab of Ornithology Summer Graduate Fellowship.

All research activities described here were approved by the Dominican Republic's Ministerio de Medio Ambiente y Recursos Naturales and conducted in accordance with IACUC protocol 2008-0185 at Cornell University.

TABLE OF CONTENTS

Biographical Sketch	iii
Acknowledgments	vi
Table of contents	viii
Chapter 1: Habitat-mediated aggregation and colony size variation in the Neotropical Hispaniolan Woodpecker (<i>Melanerpes striatus</i>)	1
Abstract.....	1
Introduction.....	2
Materials and Methods.....	5
Results.....	14
Discussion.....	21
Acknowledgments.....	25
References.....	26
Chapter 2: Reproductive success and colonial nesting in the Hispaniolan Woodpecker	31
Abstract.....	31
Introduction.....	32
Materials and Methods.....	34
Results.....	40
Discussion.....	46
Acknowledgements.....	49
References.....	50
Chapter 3: Genetic monogamy and absence of brood parasitism in the colonial Hispaniolan Woodpecker	56
Abstract.....	56
Introduction.....	57
Materials and Methods.....	60
Results.....	68
Discussion.....	73
Acknowledgements.....	79
References.....	80

CHAPTER 1: HABITAT-MEDIATED AGGREGATION AND COLONY SIZE VARIATION
IN THE NEOTROPICAL HISPANIOLAN WOODPECKER (*MELANERPES STRIATUS*)

Abstract

Explaining variation in sociality within and across species requires not only an understanding of the fitness consequences of group living but also the underlying ecological factors that influence group size. Here I test the hypothesis that colony size of the Hispaniolan Woodpecker (*Melanerpes striatus*) is driven by a shortage of suitable nesting sites, which I call the “habitat-mediated aggregation” hypothesis. I demonstrate that royal palms (*Roystonea hispaniolana*), a key nest substrate, are themselves not limiting, but dead palms, which host larger colonies than live palms, are relatively rare. The number of cavities on a palm was also positively associated with colony size, but this relationship exhibited a steeper slope for colonies on dead palms than colonies on live palms due to a greater incidence of flooded cavities and, to a lesser extent, heterospecific use in live palms. New cavities were more frequently built in dead palms, and colony size consistently increased on palms after the trees died. Cavities in dead palms took less time to excavate and were immune to flooding, which caused nearly half of all nest failures on live palms. First nests in a season had earlier first egg dates when in old cavities than in newly constructed cavities, but first nests did not differ significantly in first egg date between live and dead palms. These results suggest that availability of both dead palms, which are a superior nesting substrate, and old cavities, which accumulate on palms, influence variation in Hispaniolan Woodpecker colony size, supporting the habitat-mediated aggregation hypothesis.

Introduction

Colonial nesting, the dense concentration of individuals during breeding (Wittenberger and Hunt 1985, Danchin et al. 2008), poses a challenge for behavioral ecologists. Because group living represents a balance between the costs and benefits of sociality (Alexander 1974), species should exhibit optimum colony sizes or some type of correlation (positive or negative) between colony size and fitness (Brown and Brown 2001). Despite the effects of colony size on fitness, most colonially nesting species exhibit extensive intraspecific variation in colony sizes, sometimes spanning several orders of magnitude (Brown et al. 2013). Understanding the factors that influence colony size is crucial because the persistence of such variation in the face of natural selection is paradoxical (Brown et al. 1990, Safran et al. 2007, Brown 2016).

One key hypothesis for colony size variation is that grouping is forced by a shortage of available habitat or nesting sites (Alexander 1974, Brown et al. 1990, Sachs et al. 2007). This hypothesis is potentially related to the ideal free distribution model (Fretwell and Lucas 1969), which posits that individuals settle among habitat patches in such a way as to maximize fitness, and the abundance of resources in a habitat, or habitat quality, determines the number of individuals that can optimally exploit that patch. Danchin and Wagner (1997), applying this logic to coloniality, suggested that colonies resulting from this process are “habitat-mediated” aggregations. Although this idea is appealing because of its simplicity, it has little empirical support (Gibbs et al. 1987, Kaiser and Forbes 1992, Nuechterlein et al. 2003, Sachs et al. 2007). One argument against this hypothesis is that many seemingly suitable habitats go unused (Brown and Bomberger Brown 1996). Two first steps towards testing predictions of this hypothesis are assessing variation in aggregation size and determining what constitutes a suitable nest site, regardless of the presence or absence of other pairs.

Coloniality is estimated to occur in 13% (Lack 1968) to 30% of bird species (Rolland et al. 1998), but it is especially rare in the woodpecker family (Picidae), having been identified in only 3 (1.2%) of 254 species (Winkler and Christie 2018). The island endemic Hispaniolan Woodpecker (*Melanerpes striatus*) is one of these species and exhibits facultative coloniality: pairs occasionally nest singularly but also frequently aggregate, having up to 26 pairs on the same tree (Short 1974). Previous work on this species has focused mostly on foraging ecology and sexual size dimorphism (Selander 1966, Wallace 1974), with observations on breeding and nesting restricted to anecdotes of unmarked individuals (Short 1974, Wallace 1974). The factors driving Hispaniolan Woodpecker colony size variation have not previously been explored.

Woodpeckers are notable for their ability to create their own cavities for nesting and roosting, but coloniality is not strongly associated with tree-cavity nesting in birds (Eberhard 2002). However, the habitat-mediated aggregation hypothesis could explain variation in colony size in a cavity-nesting species if appropriate nest trees or cavities are clustered (Davis and Brown 1999). Here I test three main predictions from the habitat-mediated aggregation hypothesis as applied to the Hispaniolan Woodpecker.

First, the habitat-mediated aggregation hypothesis predicts that high-quality nest sites are limiting or otherwise difficult to acquire. For Hispaniolan Woodpeckers, this prediction might apply if breeding pairs are more numerous than suitable nest trees. Earlier researchers suggested that native royal palms (*Roystonea hispaniolana*) were the “favorite nesting tree” of Hispaniolan Woodpeckers (Wetmore and Swales 1931:292). If royal palms themselves are limiting, the habitat-mediated aggregation hypothesis predicts that all palms should have one or more cavities. The presence of royal palms lacking cavities would falsify this prediction.

It is also possible that a nest tree species is not itself limiting but that trees of a particular

condition or status (i.e., particularly suitable for nesting) are limited in availability. Short (1974) noted that Hispaniolan Woodpecker colonies frequently occurred in dead trees and suggested that dead tree “availability...must limit severely the degree of social nesting.” Thus, a more specific prediction of the habitat-mediated aggregation hypothesis is that dead palms are (a) a limited resource, and (b) better for nesting than are live palms. If dead palms are limiting, they should be less abundant than live palms, colonies in dead palms should be larger than those in live palms, and colony size on a palm should increase after it dies. Nesting in dead palms should also offer one or more advantages over nesting in live palms. These advantages should make dead palms sufficiently superior to live palms to overcompensate whatever automatic costs might result from aggregating (Alexander 1974).

Dead palms might constitute intrinsically superior nesting sites for Hispaniolan Woodpeckers for at least two reasons. First, a cavity in a dead tree provides a different microenvironment for nesting compared to a cavity in a live tree (Wiebe 2001), and a cavity in a dead palm might therefore provide a better microenvironment for nesting. Second, cavities in dead palms might be easier to construct in that they likely require less time and energy to excavate than those in live palms. If good cavities are unavailable and investment in cavity excavation trades off with higher parental investment (Wiebe et al. 2007), choosing to construct a new cavity in a dead palm would lead to higher fitness compared to excavating in a live palm.

A third prediction of the habitat-mediated aggregation hypothesis is that clustering of cavities themselves predicts the clustering of nesting pairs. In other words, variation in the number of old (i.e., constructed in previous breeding seasons) cavities on trees could explain colony size variation. Such a relationship could exist if environmental conditions promoted the accumulation or clustering of cavities on individual palms. Although cavity persistence in

tropical ecosystems is poorly studied, cavities in temperate ecosystems can persist for many years (Wesołowski 2011a, Edworthy et al. 2012), and individuals of some woodpecker species regularly use old cavities (Wiebe et al. 2007). Building new cavities If the costs of aggregating are negligible or counterbalanced by the benefits of using pre-existing cavities, clustering of Hispaniolan Woodpecker nests could mirror the clustering of available cavities. Colony size should therefore be positively related to the number of old cavities on a tree.

Here I test the habitat-mediated aggregation hypothesis for colony size variation via nest tree limitation, dead tree limitation, and cavity availability. I compare nesting attempts on dead and live trees to determine whether dead trees provide superior nesting sites for Hispaniolan Woodpeckers. Specific advantages I consider include faster construction of cavities, reduced risk of nest loss due to microenvironment differences, and earlier nesting.

Materials and Methods

Study site

I studied Hispaniolan Woodpeckers in the community of Piedra Blanca, 3 km east of Jarabacoa (19°07'09.5"N, 70°34'54.8"W; 550–700 m above sea level), La Vega, Dominican Republic, between April 2012 and July 2017. The site (~84 ha) consists of several private properties in a landscape of pine (*Pinus occidentalis* and *P. caribaea*) and broadleaf wet forest fragments immersed in a matrix of cattle pastures with isolated or clustered royal palms, small fragments of secondary vegetation, and “living tree” (predominantly *Gliricidia sepium*) fences. This region experiences a mild, dry winter season (January - March), followed by a short, wet spring wet season (April - May), a long, dry summer season (June - September), and a short, wet fall season (October - December) coinciding with the latter half of the Atlantic hurricane season (Casey

2010).

Tree monitoring, surveying for cavities, and nest monitoring

Exhaustive palm survey: In 2014, we searched for and visually inspected all the palms in a ~9.4 ha patch of land comprising a subset of the field site. We noted whether each palm was alive, dying, or dead and counted the number of cavity entrances on each tree. Dead palms were easily distinguished from live palms by the absence of the green crownshaft on the former. Dying palms could be identified by the yellowing of leaves and thinning of the crownshaft, and palm death was confirmed in the following year. Although this survey yielded a relatively small number of palms ($N = 37$), it provides a conservative test of the first prediction that royal palms are themselves limiting if many of the live palms lack cavities. Furthermore, while most Hispaniolan Woodpecker cavities consist of one entrance leading to a chamber with an intact floor that supports the nest, some cavities can have two or more entrances (up to nine in a live tree). The presence of cavity entrances on palms in the patch thus overestimates current woodpecker use if the number of entrances is greater than the number of chambers and not all cavities are being used for nests because they are unavailable (see below).

Tree availability: Sampling efforts outside of the exhaustive survey patch were likely biased in favor of nest trees (see below), so I used historical satellite imagery in Google Earth to estimate relative abundance of live and dead royal palms. Individual live royal palms were detected from their characteristic asterisk-like crownshaft, with fronds radiating outward, and the shadows created by their crownshaft and trunk (Fig. 1.1). Dead palms were detected from a long shadow combined with a leaf-less trunk (Fig. 1.1). Compared to dead palms, live palms might have been more likely to be detected in the satellite imagery due to the presence of their

conspicuous crownshafts and larger shadows. To determine palm detectability and compare detectability of live and dead palms, I searched Google Earth satellite imagery from 27 Sep 2013 for 103 palms (85 live and 18 dead) marked with a GPS on site in 2013 and 2014. I used this same satellite imagery to estimate the percentage of live and dead palms more broadly at the field site by searching an area (~84 ha) comprising all actively monitored patches. If I was uncertain of the presence/absence of a palm or palm status (live vs. dead), I used additional historical imagery to confirm whether a crownshaft, shadow, and/or trunk was visible in the same spot before or after 27 Sep 2013 (Fig. 1.1). I compared the numbers of live and dead palms I estimated with those estimated by four naïve observers in 10 different subsections (~6 ha) of the field site to assess the method's repeatability. To calculate the confidence interval (C.I.) for the proportion of palms that were live, I used the formula $95\% \text{ C.I.} = P \pm 1.96 \times \text{S.E.}$, where, P is the proportion of palms that were alive and S.E. is the standard error of the true proportion, calculated as $\text{S.E.} = \sqrt{(P \times (1 - P)/N)}$, where N is the total number of palms counted.

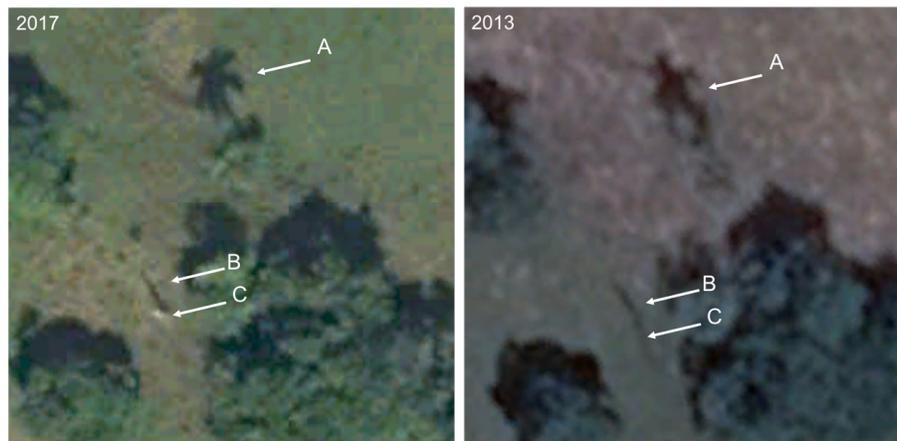


Figure 1.1. Google Earth imagery from 28 Feb 2017 (left) and 27 Sep 2013 (right) showing one live (A) and one dead (B,C) royal palm (*Roystonea hispaniolana*). The live royal palm has a distinctive shadow (A) created by the asterisk-like crown. The long shadow (B) of a dead palm emanates from a leafless snag (C).

Cavity and nest monitoring: Inspection and monitoring of trees and nest cavities were conducted between 2012 and 2017. My field assistants and I mostly selected live and dead palms to monitor nesting attempts based on the presence of cavities or detectable activity of woodpeckers. We also inspected any cavities found opportunistically in non-palms to estimate the relative use of different nest substrates. I do not compare the proportion of nests in live and dead palms because the search effort might have been non-random. We inspected cavities using a penlight and small inspection mirror (1-2" diameter) while climbing trees or with a wireless camera attached to a 15.2 m telescoping pole that broadcasted images to a portable digital television (Huebner and Hurteau 2007, Waldstein 2012). Because palms become unsafe to climb 2-3 years after they have died, the telescoping pole method was used to check cavities whenever possible.

Monitored cavities were either incomplete/in construction or fully complete and large enough to host a Hispaniolan Woodpecker nest. Because individual Hispaniolan Woodpeckers will reuse cavities built by other conspecifics, we considered a cavity to be complete if it was known to have hosted a nest previously or if it appeared greater than or equal to the size of the smallest cavity known to be used for nesting. In total, we monitored 244 complete cavities across 54 unique palms. We monitored each cavity for an average of 2.0 ± 0.1 breeding seasons (range = 1–6), and we inspected each cavity for an average of 10.5 ± 0.5 times per breeding season (range = 1–61), resulting in a total of 5,295 cavity checks. We also monitored 99 cavities in 41 palms that remained incomplete throughout the duration of the study.

Whenever we inspected a cavity, we noted its status, including whether the cavity was currently being used by Hispaniolan Woodpeckers, contained water, or was used by heterospecifics. Complete cavities could be dry (no water), partially inundated (~1 in of standing

water), or fully inundated with multiple inches of standing water. Heterospecific use of cavities was determined by direct and/or trace evidence. Direct evidence included observation of one or more heterospecific animals or, in the case of birds, their eggs in a cavity (see Results). Trace evidence included any signs of cavity occupancy by heterospecifics, including varying levels of bat guano and feathers from bird species other than Hispaniolan Woodpeckers.

We checked cavities containing water or bat guano approximately two or three times per month unless we observed woodpeckers occupying them or if the cavities occurred on trees with other active nests. We checked dry and empty cavities and those being actively excavated more frequently, typically once or more per week, until the first signs of nesting (i.e., first detection of eggs in the cavity). Once we detected a nesting attempt, we checked the clutch every 3-5 days, or daily (when possible) if we did not know the clutch completion date, to determine nest fate and hatch date.

Because incubation typically last 11 days (range = 9–14 days, unpubl. data) and birds lay only 1 egg per day, I back-calculated first egg dates from known or estimated hatch date when nests were found after clutch completion. To determine the length of time required to construct a cavity, we recorded the date when a new excavation was first detected and considered the cavity complete on the day of clutch initiation. This approach does not account for lapses in excavation effort and likely underestimates the duration of actual cavity construction, especially in live palms. Three cavities built in live palms were excluded from analysis because they were started in one year, finished after the breeding season ended, and used for breeding the following year. However, this estimate adequately captures the impact of cavity construction because birds that built new cavities never concurrently nested in already existing cavities (pers. obs.), so time until cavity completion typically translated into time and energy not invested in breeding.

Colony size and nesting observations: I define colony size as the maximum number of pairs nesting (i.e., actively constructing a cavity, incubating eggs, or tending a nest with young) on a given tree in a year. In order to better estimate colony size, we implemented a free-standing mist-net tower system (max height of top trammel line was 15.2 m) to capture and uniquely color-band individuals starting in May 2013. The percentage of individuals color-banded in a colony varied from 0–100% (mean \pm S.E. = $59 \pm 5\%$, N = 41 colony years). We confirmed the identity and presence of breeding pairs via observation of breeding activities, including cavity maintenance, incubation, nestling provisioning, and affiliative behavior at cavity entrances. Observations were made during 2–3 hr nest watches using a spotting scope while seated in the open 15–20 m from the nest or in a blind <10 m from the nest. Affiliative behaviors included perching side-by-side, head swinging or bowing displays in conjunction with “waa” (or “churr”) calls (pers. obs.; Short 1974), and “bill kissing”, in which birds lightly interlocked their bills (pers. obs.).

Analysis

All summary statistics are presented as mean \pm standard error unless otherwise noted. I performed all linear mixed models (LMMs) using the *lmer* function in R v. 3.4.3 (R Core Team 2017) with RStudio v. 1.1.414 with the package *lmerTest*. I performed all generalized linear mixed models (GLMMs) using the *glmer* function in R package *lme4*.

I used an LMM to test the prediction that colony sizes differed between live and dead palms. The response variable was colony size on a tree in a given breeding season (year). For analysis, I included royal palm nest trees where I was confident of colony size and cavity usage because cavities were checked several times each month of the breeding season. Fixed effects in

the model included tree status (live vs. dead), the total number of complete cavities on a tree, and their interaction. I centered the model by subtracting the mean number of complete cavities from the total number of complete cavities for each colony in each year it was observed, and included year and tree ID as random effects. Residuals of the model were normally distributed and not over-dispersed.

To determine if the proportion of cavities used differed between live and dead palms, I used a GLMM with a binomial distribution and logit link. The response variable was the proportion of complete cavities on a tree that were used for nests in a year. I restricted analysis to those nest trees used in the colony size analysis (above). The fixed effect was tree status (live vs. dead), and proportions were weighted by the total number of complete cavities on a tree. Random effects included year and tree ID.

For a separate analysis of cavity availability, I expanded the sample size to include additional trees that had cavities but were either not sampled adequately to determine colony size or were not known to have a nest during monitoring. This sample included an additional 10 live royal palms. For each cavity, I assigned it a summary status for each year it was monitored using a hierarchically exclusive method. A cavity was assigned “nest” status if woodpeckers were known to use the cavity for nesting. A cavity was assigned “flooded” status if it never hosted a woodpecker nest and it contained any water on one or more cavity check. A cavity was assigned to “heterospecific” status if it never had a woodpecker nest, was never flooded, and contained heterospecifics or trace evidence of heterospecifics on one or more cavity check. All remaining cavities were assigned to “unused” status because they were empty but not known to ever contain a nest, be flooded, or be occupied by heterospecifics. Incomplete/unfinished cavities were not included in this analysis.

For testing the prediction that live and dead palms differed in the total number of complete cavities per tree, I used an LMM that included tree status as a fixed effect. The response variable was the total number of complete cavities on a tree in a year. Random effects included year and tree ID.

An LMM was used to test if colony size change was related to tree status. The analysis included tree status change, the total number of complete cavities in the previous year, and their interaction as fixed effects. The response variable, colony size change, was the difference between the colony size on a tree in a year and the colony size on a tree in the previous year. Tree status change included three categories: palms that remained alive between years, palms that died between years, and palms that were dead in both years. Random effects included year and tree ID.

I tested the prediction that the number of new complete cavities excavated on a tree differed between live and dead palms using a GLMM with a Poisson distribution and log link that included tree status as a fixed effect. The response variable was the total number of complete cavities excavated on a tree in a year. Random effects included year and tree ID.

I used a GLMM test the prediction that the proportion of nests in new vs. old cavities differed between live and dead palms. The response variable was cavity age (new vs. old), and the fixed effect was tree status (live vs. dead). Cavities were considered new if they were built in the same year of a focal nesting attempt. Cavities were considered old if they were pre-existing, i.e., built one or more years before a focal nesting attempt. The model had a binomial distribution and logit link. Random effects included tree ID, cavity ID nested within tree ID, and year. Because we never observed pairs changing trees or cavity ages within breeding seasons, I included only the earliest known nesting attempt for each pair in a breeding season.

To determine if first egg dates of first nesting attempts within a season differed between live and dead palms, I used an LMM with tree status, cavity age (new vs. old), and the interaction of tree status and cavity age included as fixed effects. The response variable, first egg dates of the first nesting attempt in a cavity within a season, was \log_{10} transformed. Random effects included year and cavity ID nested in tree ID.

Table 1.1. Results of linear mixed effects models (LMM) or generalized linear mixed models (GLMM) for (a) colony size, (b) proportion of complete cavities used on live and dead palms, (c) number of complete cavities on palms, (d) colony size change, (e) number of new complete cavities built on a tree, (f) proportion of first nesting attempts in new vs old cavities, and (g) log-transformed first egg date (FED).

	<i>N</i>	Estimate \pm S.E.	<i>d.f.</i>	<i>t or z</i>	<i>P</i>
(a) Colony size – LMM †					
<i>Tree status (live)</i>	103 tree-years	-2.50 \pm 0.36	52.4	-7.00	< 0.001
<i>Number of complete cavities</i>		0.77 \pm 0.07	93.4	10.89	< 0.001
<i>Number of complete cavities * tree status</i>		-0.61 \pm 0.10	97.5	-6.33	< 0.001
(b) Proportion of complete cavities used – GLMM (Binomial) †**					
<i>Tree status (live)</i>	103 tree-years	-1.63 \pm 0.24		-6.66	<0.001
(c) Number of cavities – LMM †					
<i>Tree status (live)</i>	103 tree-years	-2.47 \pm 0.72	75.0	-3.41	0.001
(d) Colony size change – LMM †					
<i>Tree status change (dead)</i>	55	3.37 \pm 0.99	44.8	3.40	0.001
<i>Tree status change (died)</i>		2.77 \pm 0.79	48.8	3.53	< 0.001
Number of complete cavities in previous year		-0.16 \pm 0.11	46.3	-1.44	0.16
<i>Tree status change (dead): number of complete cavities in previous year</i>		-0.42 \pm 0.15	45.6	-2.79	0.008
<i>Tree status change (died): number of complete cavities in previous year</i>		0.74 \pm 0.18	46.4	4.23	< 0.001
(e) Number of new complete cavities built on a tree – GLMM (Poisson) †					
<i>Tree status (live)</i>	78 tree years	-2.35 \pm 0.28		-8.43	<0.001
(f) New complete cavities used – GLMM (Binomial) ††					
<i>Tree status (live)</i>	151 nests	-1.49 \pm 0.87		-1.72	0.085
(g) \log_{10} transformed FED – LMM ††					
<i>Tree status (dead)</i>	120 nests	-0.09 \pm 0.05	52.3	-1.97	0.054
<i>Cavity age (old)</i>		-0.15 \pm 0.04	87.0	-3.63	< 0.001
<i>Tree status * cavity age</i>		0.03 \pm 0.05	101.8	0.73	0.466

** model weighted by the total number of cavities on a tree in a given year; † random effects included tree ID and year; †† random effects included tree ID, cavity ID nested in tree ID, and year.

Results

Nest tree availability

In the 2014 exhaustive palm survey, 38% of royal palms ($N = 37$ trees) had one or more cavity entrances. We found 36 live palms and one dead palm in the survey, and of those live palms, 13 (36%) had cavity entrances. The only dead palm found in the exhaustive survey had nine visible cavity entrances. A total of 22 dead palms were found opportunistically, all of which had one or more visible cavity entrances. The total number of complete cavities was determined for 15 of these dead palms, and the mean number of cavities was 6.4 ± 1.1 .

Overall, detectability of known royal palms was 89% ($N = 103$ palms) based on historical satellite imagery (27 September 2013). Live royal palms did not differ from dead royal palms in the percentage of trees detected from satellite imagery (live royal palms: 89%, $N = 85$ palms; dead royal palms: 89%, $N = 18$ palms; Fisher's exact test, $P = 0.71$). Over the entire ~84 ha study area, I estimated a total of 252 royal palms (236 live and 16 dead trees) from satellite imagery. I tested this procedure with four naïve observers on ~6 ha subsections of the field site and found high concordance among the estimates of live and dead palms ($R = 0.90$, $P < 0.001$). Live trees accounted for $94 \pm 3\%$ ($\pm 95\%$ C.I.) of royal palms at the study site.

Tree status and colony size

Nearly all (98%, $N = 343$ nests) nesting attempts documented at the study site occurred in royal palms. Of all nests, 141 (41%) were in 10 dead royal palms, and 194 (57%) were in 35 live royal palms. Only 8 nests (2%) were in five non-royal palms. These non-royal palm nests were omitted from the following analyses.

Results of a LMM showed that tree status (live versus dead), total number of complete

cavities on a palm centered by the mean (4.35 ± 0.26 cavities, $N = 103$), and their interaction significantly predicted colony size (Fig. 1.2, Table 1.1a). Dead palms had larger colonies (mean colony size = 5.0 ± 0.8 pairs, range = 1–12 pairs, $N = 21$ tree years) than live palms (mean colony size = 1.3 ± 0.1 pairs, range = 0–4 pairs, $N = 82$ tree years). The relationship between the number of complete cavities and colony size exhibited a steeper slope for dead palms than for live palms (Fig. 1.2), indicating that Hispaniolan Woodpeckers occupied a higher proportion of cavities on dead palms. Results of a separate LMM showed that the proportion of cavities occupied was significantly associated with tree status (Table 1.1b). The mean proportion occupied on dead palms was higher (0.78 ± 0.05 , $N = 21$ tree years) than that on live palms (0.41 ± 0.03 , $N = 82$ tree years). Tree status also significantly predicted the total number of cavities on palms (Table 1.1c). Dead palms hosted significantly more cavities (6.5 ± 0.8 cavities, range = 1–13, $N = 21$ tree years) than did live palms (mean = 3.8 ± 0.2 cavities, range = 1–10, $N = 82$ tree years).

Tree status change and its interaction with the number of cavities on a tree in the previous year were significantly associated with colony size change between years (Table 1.1d, Fig. 1.3). Colonies on trees that remained alive tended to remain the same size between years (mean colony size change = -0.2 ± 0.1 pairs, $N = 40$) regardless of the number of cavities on the tree in the previous year. Colonies on trees that were dead in both years tended to decrease in size (mean colony size change = -0.6 ± 1.1 pairs, $N = 9$), but showed a negative relationship between colony size change and the number of cavities in the previous year such that these colonies increased in size when the number of cavities was low and decreased when the number of cavities was high.

Colonies on trees that died between years consistently increased in size (mean colony

size change = 4.8 ± 1.1 , $N = 6$), and colony size in the second year increased with the total number of cavities in the previous year. Four trees died containing no cavities but were colonized the year after they died. Two trees that died each had eight cavities prior to death; one of these had three flooded cavities while the other had four flooded cavities and three cavities occupied by bats. The water-filled cavities on these trees drained after palm death and all were used for nesting.

The relationship between tree status change and colony size change was mirrored by cavity construction efforts. Significantly more new cavities were built on dead palms (mean = 3.0 ± 0.5 , range = 0–5, $N = 15$ tree years) than on live palms (mean = 0.3 ± 0.1 , range = 0–1, $N = 63$ tree years; Table 1.1e). New cavities were constructed in live palms in only 18 (29%) of 63 tree years, but new cavities were constructed in dead palms in 13 (87%) of 15 tree years.

Although cavity construction occurred more frequently on dead palms, results of a GLMM showed that live and dead palms did not differ in the relative use of old and new cavities for nests (Table 1f). Pooling across years and live and dead palms, 103 (68%) of 151 of first nesting attempts in a year occurred in old cavities (i.e., reuse of cavities built in previous years). First nesting attempts in live palms tended to occur at a higher frequency in old cavities (80% of 75 nests) compared with nests in dead palms (55% of 76 nests), but this difference was not statistically significant.

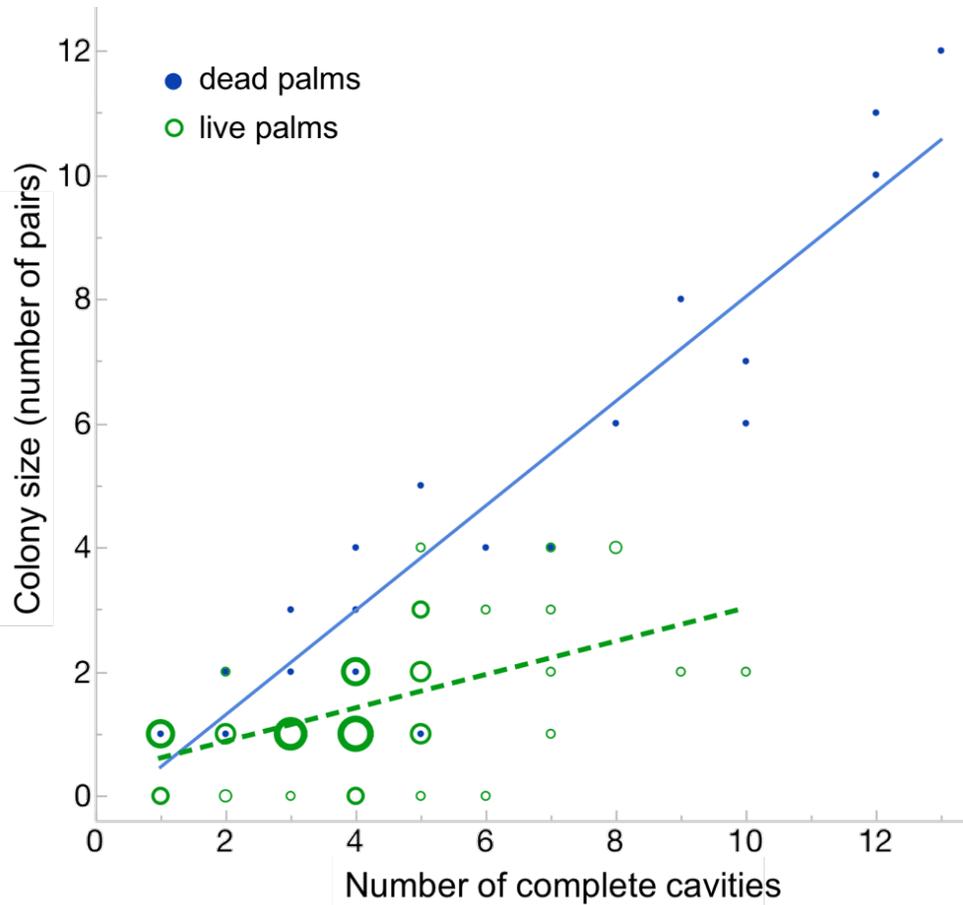


Figure 1.2. Hispaniolan Woodpecker colony size as a function of the total number of complete cavities on a royal palm in a year. Colonies on dead palms are represented by blue points and colonies on live palms are represented by green circles. The size of markers represents the number of tree years (range = 1-14). Lines indicated predicted relationship based on a linear mixed effect model. The blue solid line represents the predicted linear relationship for dead palms and the green dotted line represents the predicted relationship for live palms.

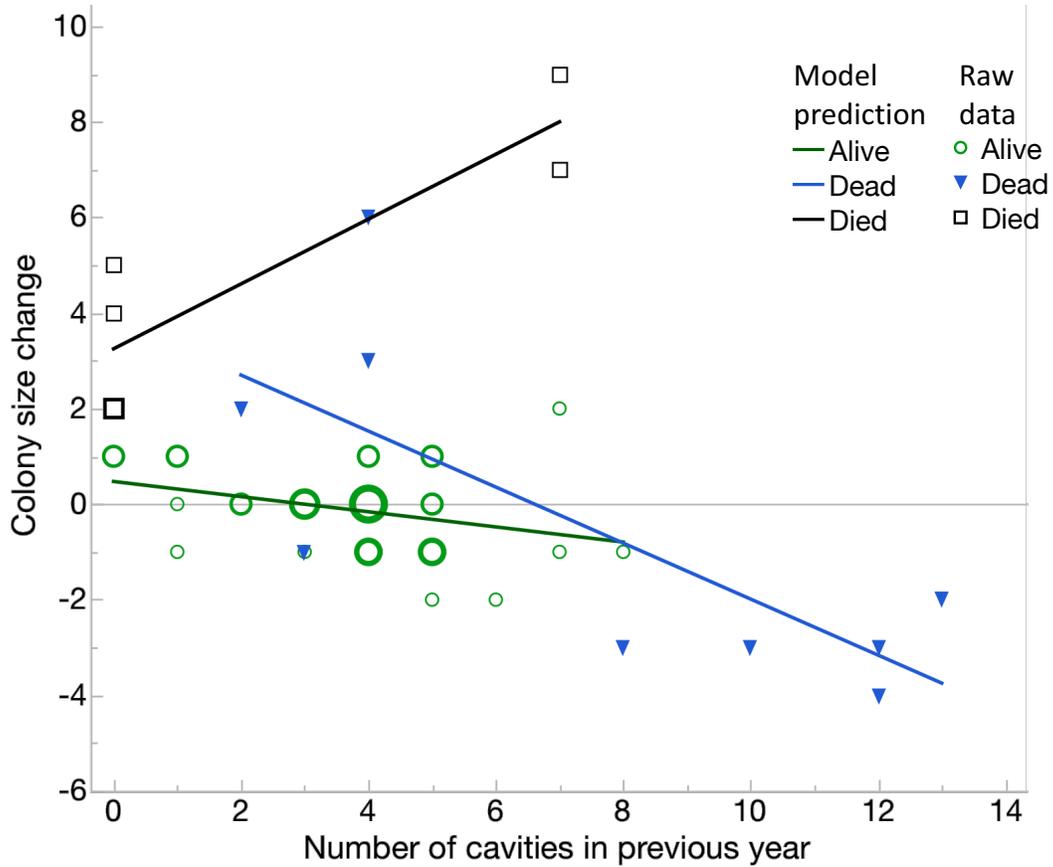


Figure 1.3. The change in Hispaniolan Woodpecker colony size (the difference between colony size in one year and the preceding year) as a function of the total number of complete cavities on the tree in the previous year and tree status change between years. Raw data are shown as points: colonies on trees that were alive in both years are represented by green circles, colonies on trees that were dead in both years are represented by blue inverted triangles, and colonies on trees that died between years are represented by black squares. Marker size represents sample size (range = 1–8 observations). Solid lines in the respective colors represent the relationships predicted by a linear mixed model.

Tree status, cavity quality, and cavity availability

Nest construction in live palms took 60 ± 6 days ($N = 6$ cavities), about one month longer than construction in dead palms (32 ± 3 days, $N = 14$ cavities; Wilcoxon Rank-Sum test: $Z = 3.27$, $P = 0.001$).

In live palms, 121 (32%) of 379 complete cavity-years hosted woodpecker nests whereas in dead palms, 107 (84%) of 127 complete cavity-years hosted woodpecker nests. Complete cavities in live palms were less likely to be available for nesting for all or part of the breeding season than were complete cavities in dead palms. In live palms, 44% of cavity-years were flooded, 22% were occupied by heterospecifics, and 1% were unused. In dead palms, 0% of cavity-years were flooded, 7% were occupied by heterospecifics, and 9% were unused.

Cavity flooding caused nest failure for 46 (17%) of 269 nesting attempts and accounted for 30% of all 157 nest failures. Across six years, none of the 109 nests in 12 dead palms flooded, but 29% of 160 nests in 34 live palms failed due to flooding. Flooding accounted for 48% of 96 nest failures on 27 live palms. In 34 live palms hosting nests, 66% had one or more nests that failed due to flooding.

Cavity age, but not tree status nor its interaction with cavity age, significantly predicted first egg date for first nesting attempts in a breeding season (Fig. 1.4, Table 1). First nesting attempts of the breeding season began a month earlier on average in old cavities (mean Julian date = 94 ± 2 , $N = 91$ nests) compared to newly constructed cavities (mean Julian date = 125 ± 5 , $N = 29$ nests). Nesting attempts in dead palms had an average first egg date three days earlier (mean Julian date = 100 ± 3 , $N = 62$) than those in live palms (mean Julian date = 103 ± 4 , $N = 58$). Nesting attempts in old cavities on dead palms had a mean first egg date of 87 ± 2 , (range = 62–117, $N = 37$ nests), and those on live palms had a mean first egg date of 99 ± 3 (range = 55–

193, $N = 54$ nests). Nesting attempts in new cavities on dead palms had a mean first egg date of 121 ± 5 , (range = 84–170, $N = 25$ nests), and those in new cavities on live palms had a mean first egg date of 149 ± 13 (range = 117–181, $N = 4$ nests).

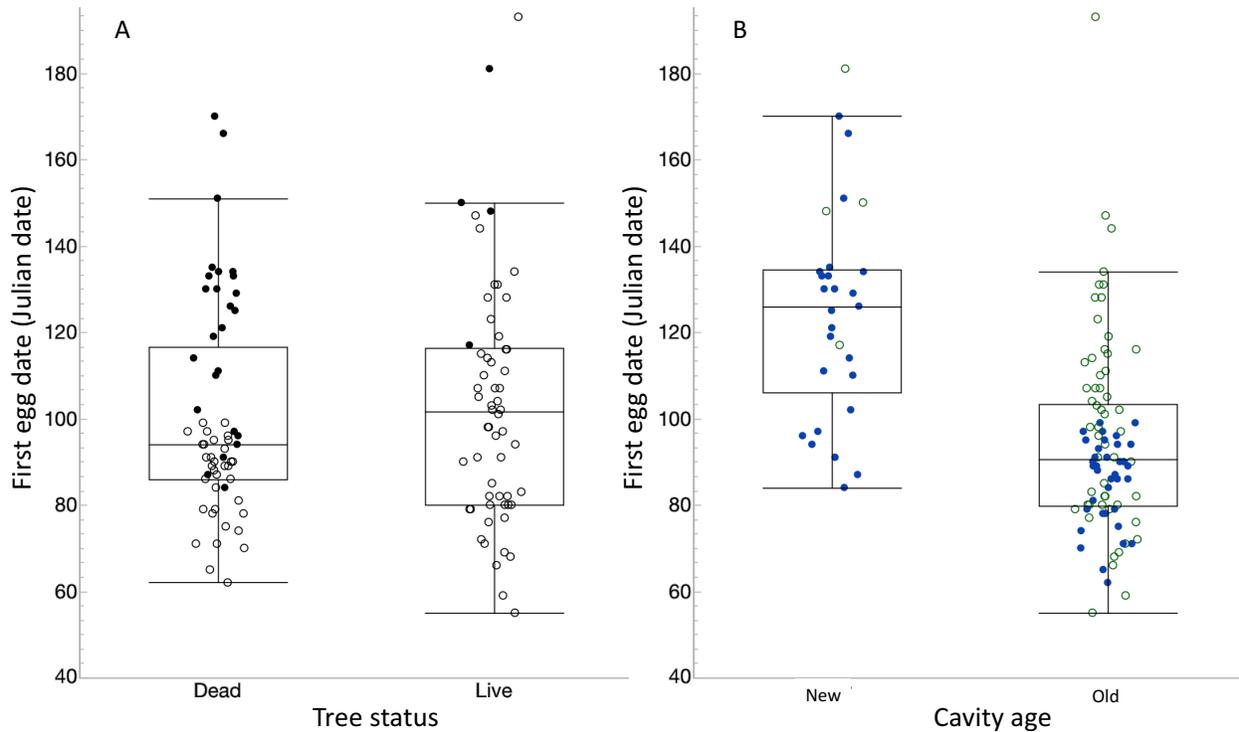


Figure 1.4. (a) First egg date for the first nest in a cavity in a breeding season for Hispaniolan Woodpecker nests in dead and live royal palms (new cavities = full circles, old cavities = open circles). (b) First egg date for the first nest in a cavity for woodpecker nests in old cavities (i.e., constructed in previous years) or new cavities (dead palms = blue, full circles, live palms = green, open circles).

Discussion

The results of this study support the habitat-mediated aggregation hypothesis for colony size variation in the Hispaniolan Woodpecker. Most Hispaniolan Woodpecker nests found during the study were in royal palms, but woodpeckers only used a small proportion of royal palms in the study site. These results indicate that royal palms are an important nest substrate but are not themselves a limiting resource. However, dead palms were much less common than live palms, and colonies were larger on dead than on live palms. Colony size was also positively related to the number of cavities on a palm, but this relationship exhibited a steeper slope on dead palms than on live palms. Dead palms had more cavities than live palms, more cavities were constructed on dead palms, and colony size increased on palms a year after they died. These results suggest that the distribution of dead trees and old cavities influences colony size variation in the Hispaniolan Woodpecker.

Larger colony sizes in dead royal palms were explained in part by at least two advantages that outweigh whatever costs could be incurred by colonial nesting. The first advantage is related to microenvironment: nests in dead palms never failed due to flooding, but nearly one-third of nests in live palms failed due to cavity flooding. Flooding resulted in total loss of a current nesting attempt, and, in some cases, rendered the cavity unusable for the rest of the breeding season.

The second advantage of nesting in dead palms was shorter duration of cavity excavation. Although not specifically assessed here, saving time and energy by excavating in dead palms could translate into greater reproductive output and/or enhanced adult survival, assuming there is a tradeoff between excavation and these other investments (Wiebe et al. 2007). There was also a tendency for birds nesting in dead palms to initiate first clutches of the year earlier than birds in

live palms, but this result was not statistically significant ($P = 0.054$, Table 1g). And the nests in dead palms were only three days earlier on average than those in live palms. Thus, protection from flooding and reduced excavation time were likely the most important factors increasing the quality of dead palms.

In addition to the intrinsic advantages discussed above, cavities in dead palms were more available than cavities in live palms. Although live royal palms accumulated cavities, many of those cavities were unavailable because they were filled with water for all or part of the breeding season and, to a lesser extent, were more likely to be occupied by heterospecifics. Cavity flooding, though, is likely the more important of the two phenomena. Even newly constructed cavities on live palms could quickly become inundated and unusable in the same season they were built. In contrast, cavities on dead palms did not accumulate water and remained available. The internal architecture of a dead palm likely prevents flooding: the ground tissue and vascular bundles remaining in the trunk become dry and loose (pers. obs.), providing many gaps for water to escape. Furthermore, on palms that died, previously water-filled cavities drained and became available for nesting (Fig. 1.3). Thus, when a palm with multiple water-filled cavities died, the newly drained cavities provided a pulse of low-cost, superior (due to flood resistance), and aggregated nest sites, facilitating colonial nesting.

High-quality nest sites—dead palms and old cavities—thus appear to be limiting and clustered in Hispaniolan Woodpeckers. Although palms were not exhaustively sampled, I never encountered a dead palm without at least one visible cavity entrance. Additionally, dead palms were useful to woodpeckers as nest sites for a limited number of years because the dead tissue inside the trunk is increasingly lost as woodpeckers excavate new cavities and maintain old ones. As a result, within a few years, dead palms become empty husks that can support only one or a

small number of cavities. For example, one colony we started monitoring in 2014 had 13 useable cavities and hosted 12 woodpecker pairs, but degradation through continued use, excavation, and maintenance reduced the number of usable cavities to three by 2017, when the colony size was three pairs.

In addition to dead tree abundance and age, cavity flooding greatly impacted cavity availability. In cavity-nesters more generally, flooding or soaking of cavities can reduce reproductive success (Wesołowski et al. 2002, Radford and Du Plessis 2003), and some researchers have argued that nest soaking or flooding is an important cause of nest failure, second only to predation (Wesołowski 2011b). Yet reports of cavity flooding are rare in the literature, suggesting that cavity flooding is only important in a small proportion of habitats or species. Flooding was clearly an important aspect of the Hispaniolan Woodpecker's nesting biology as it accounted for nearly half of nest failures on live trees. Cavity flooding dynamics, combined with dead tree availability, might therefore be a unique ecological mechanism driving colony size variation.

Though the relationships between Hispaniolan Woodpecker colony size, tree status, and cavity availability were consistent with the hypothesis of nest site limitation driving colony size variation, at least two additional approaches would provide complementary tests. First, data on the spatial and temporal variation of palm death and dead palm abundance in combination with woodpecker population size estimates and exhaustive sampling for cavities could be used to determine if colony sizes change with changing availability of high quality nest sites. Even more critically, an experimental manipulation of suitable cavities would provide the strongest test of this hypothesis.

Tree cavity nesting is generally not associated with coloniality in birds (Eberhard 2002),

but nest site limitation driving colony size variation probably applies in other ways to facultatively colonial nesters. Many colonially nesting species do not use cavities, and those species that do typically nest in earthen banks (Hoogland and Sherman 1976, Hegner et al. 1982, Hoi et al. 2015). One of the few other colonial tree cavity nesters, Purple Martins (*Progne subis*), are secondary cavity nesters that likely aggregate because the artificial nesting structures they commonly use are patchily distributed (Davis and Brown 1999). These artificial structures vary in the number of compartments, and colony size variation is likely driven primarily by “how many nesting houses are installed in a given backyard” (Davis and Brown 1999:744). In a more natural system, Red-necked Grebes (*Podiceps grisegena*), variation in optimal nest site availability might be a major driver of colony size variation. Red-necked Grebes nesting on a Minnesota lake were more likely to have one or more pairs within 50m when nesting on floating vegetation mats than when nesting along the lake’s shoreline (Nuechterlein et al. 2003, Sachs et al. 2007). These floating mats provided protection from waves and predators, and as floating mats disintegrated over several years, larger colonies became less frequent (Nuechterlein et al. 2003). Like Red-necked Grebes, Hispaniolan Woodpecker colony size variation appears to be linked to intrinsic differences in nest site quality and nest site abundance. The observations that colony size variation is related to habitat quality in these species but not, apparently, others, begs an explanation (Brown 2016).

Habitat-mediated aggregation as an explanation for colony size variation might be most applicable to facultatively colonial (or semi-colonial) species if settlement decisions in these species are driven more by intrinsic habitat quality than by socially-influenced factors (Safran 2007, Safran et al. 2007). In other words, individuals in facultatively colonial species might choose habitats based primarily on the presence, absence, or quantity of non-social resources,

such as nesting substrate or physical protection from predators. This habitat choice strategy might be especially favored if grouping yields no socially-derived benefits (social resources), such as extra-pair mates (Hoi and Hoi-Leitner 1997), social foraging (Greene 1987), or group defense against predators (Robinson 1985). In contrast, colony size variation in species that experience benefits of grouping might be driven more by settlement decisions based on the presence or absence of conspecifics (Wagner 1993, Serrano et al. 2004). Thus, to convincingly demonstrate that Hispaniolan Woodpecker colony size variation is driven by nest site limitation and that colonies are habitat-mediated aggregations will require an investigation of the relationship between colony size and fitness.

Acknowledgments

I gratefully acknowledge the following individuals for providing invaluable assistance in the field: M. Angelucci, H. Boyle, C. Cerrilla, W. Coleman, A. Diaz, L. Emerson, N. Gilbert, A. Janik, K. Kauffman, T. Lacerda, A. Lascher-Posner, M. Larrieu, K. Larsen, C. Mathers-Winn, K. Nelsen, A. Occhialini, S. Schubert, H. Stapleton, M. Walters, A. Waterman-Snow, P. Werner, A. Wichtendahl. I thank W. D. Koenig, J. L. Dickinson, P. W. Sherman, M. S. Webster, H. K. Reeve, and I. J. Lovette for feedback on the manuscript and constructive criticism at various points in the development of this project. F. Vermeulen and D. Akdemir at the Cornell Statistical Consulting Unit provided statistical advice. I thank C. LaPergola, A. Savagian, M. G. Smith, and M. J. Strong for providing independent counts for the satellite imagery analysis. The following sources provided funding support: Cornell Lab of Ornithology Athena Fund, Department of Neurobiology Animal Behavior Research Grant, Society for the Study of Evolution Rosemary Grant Award, and Sigma Xi Grant in Aid of Research. I was also supported by the following

fellowships during fieldwork: Charles Walcott Graduate Fellowship, Linda and Samuel Graduate Student Fellowship, Eleanore Stuart Graduate Fellowship, Andrew '78 and Margaret Paul Graduate Fellowship, Kramer Graduate Fellowship, Halberstadt Graduate Fellowship, Anne Marie Brown Summer Graduate Fellowship, and Lab of Ornithology Summer Graduate Fellowship. All research activities described here were approved by the Dominican Republic's Ministerio de Medio Ambiente y Recursos Naturales and conducted in accordance with IACUC protocol 2008-0185 at Cornell University.

References

- Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics* 5:325–383.
- Brown, C. R. (2016). The ecology and evolution of colony-size variation. *Behavioral Ecology and Sociobiology* 70:1613–1632. doi: 10.1007/s00265-016-2196-x
- Brown, C. R., and M. Bomberger Brown (1996). *Coloniality in the Cliff Swallow*. The University of Chicago Press, Chicago.
- Brown, C. R., and M. B. Brown (2001). Chapter 1: Avian coloniality. In *Current Ornithology* (Nolan, V., and C. F. Thompson, Editors). Kluwer Academic/Plenum Publishers, pp. 1–82. doi: 10.1007/978-1-4615-1211-0_1
- Brown, C. R., M. B. Brown, and E. A. Roche (2013). Spatial and temporal unpredictability of colony size in Cliff Swallows across 30 years. *Ecological Monographs* 83:511–530. doi: 10.1890/12-2001.1
- Brown, C. R., B. J. Stutchbury, and P. D. Walsh (1990). Choice of colony size in birds. *Trends in Ecology & Evolution* 5:398–403. doi: 10.1016/0169-5347(90)90023-7
- Casey, J. (2010). Jarabacoa, Dominican Republic: climate, global warming, and daylight charts and data. *Climate-Charts.com*. [Online.] Available at <https://www.climate-charts.com/Locations/d/DR78000000000203.php>.

- Danchin, E., L.-A. Giraldeau, and R. H. Wagner (2008). Animal aggregations: hypotheses and controversies. In *Behavioural Ecology* (E. Danchin, L.-A. Giraldeau and F. Cézilly, Editors). Oxford University Press, Oxford, pp. 503–545.
- Danchin, E., and R. H. Wagner (1997). The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology and Evolution* 12:342–347. doi: 10.1016/S0169-5347(97)01124-5
- Davis, J. A., and C. R. Brown (1999). Costs of coloniality and the effect of colony size on reproductive success in Purple Martins. *The Condor* 101:737–745.
- Eberhard, J. R. (2002). Cavity adoption and the evolution of coloniality in cavity-nesting birds. *The Condor* 104:240–247.
- Edworthy, A. B., K. L. Wiebe, and K. Martin (2012). Survival analysis of a critical resource for cavity-nesting communities: patterns of tree cavity. *Ecological Applications* 22:1733–1742. doi: 10.1890/11-1594.1
- Fretwell, S. D., and H. L. J. Lucas (1969). On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19:16–36. doi: 10.1007/BF01601953
- Gibbs, J. P., S. Woodward, M. L. Hunter, and E. Hutchinson (1987). Determinants of Great Blue Heron colony distribution in coastal Maine. *The Auk* 104:38–47. doi: 10.2307/4087230
- Greene, E. (1987). Individuals in an Osprey colony discriminate between high and low quality information. *Nature* 329:239–241. doi: 10.1038/329239a0
- Hegner, R. E., S. T. Emlen, and N. J. Demong (1982). Spatial organization of the White-fronted Bee-eater. *Nature* 298:264–266. doi: 10.1038/298264a0
- Hoi, H., and M. Hoi-Leitner (1997). An alternative route to coloniality in the Bearded Tit: females pursue extra-pair fertilizations. *Behavioral Ecology* 8:113–119. doi: 10.1093/beheco/8.2.113
- Hoi, H., J. Krištofik, and A. Darolová (2015). All you can eat: Is food supply unlimited in a colonially breeding bird? *Ecology and Evolution* 5:450–458. doi: 10.1002/ece3.1355

- Hoogland, J. L., and P. W. Sherman (1976). Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. *Ecological Monographs* 46:33–58.
- Huebner, D. P., and S. R. Hurteau (2007). An economical wireless cavity-nest viewer. *Journal of Field Ornithology* 78:87–92. doi: 10.1111/j.1557-9263.2006.00089.x
- Kaiser, G. W., and L. S. Forbes (1992). Climatic and oceanographic influences on island use in four burrow-nesting alcids. *Ornis Scandinavica* 23:1–6. doi: 10.2307/3676419
- Lack, D. (1968). *Ecological adaptations for breeding in birds*. In. Methuen, London.
- Nuechterlein, G. L., D. Buitron, J. L. Sachs, and C. R. Hughes (2003). Red-necked Grebes become semicolonial when prime nesting substrate is available. *The Condor* 105:80–94. doi: 10.1650/0010-5422(2003)105[80:RNGBSW]2.0.CO;2
- R Core Team (2017). *R: A language and environment for statistical computing*.
- Radford, A. N., and M. A. Du Plessis (2003). The importance of rainfall to a cavity-nesting species. *Ibis* 145:692–694. doi: 10.1046/j.1474-919X.2003.00198.x
- Robinson, S. K. (1985). Coloniality in the Yellow-rumped Cacique as a defense against nest predators. *The Auk* 102:506–519.
- Rolland, C., E. Danchin, and M. de Fraipont (1998). The evolution of coloniality in birds in relation to food, habitat, predation, and life- history traits: a comparative analysis. *The American Naturalist* 151:514–529. doi: 10.1086/286137
- Sachs, J. L., C. R. Hughes, G. L. Nuechterlein, and D. Buitron (2007). Evolution of coloniality in birds: a test of hypotheses with the Red-necked Grebe (*Podiceps grisegena*). *The Auk* 124:628. doi: 10.1642/0004-8038(2007)124[628:EOCIBA]2.0.CO;2
- Safran, R. J. (2007). Settlement patterns of female Barn Swallows *Hirundo rustica* across different group sizes: Access to colorful males or favored nests? *Behavioral Ecology and Sociobiology* 61:1359–1368. doi: 10.1007/s00265-007-0366-6
- Safran, R. J., V. A. J. Doerr, P. W. Sherman, E. D. Doerr, S. M. Flaxman, and D. W. Winkler (2007). Group breeding in vertebrates: linking individual- and population-level approaches. *Evolutionary Ecology Research* 9:1163–1185.

- Selander, R. K. (1966). Sexual dimorphism and differential niche utilization in birds. *The Condor* 68:113–151. doi: 10.2307/1365712
- Serrano, D., M. G. Forero, J. A. Donázar, and J. L. Tella (2004). Dispersal and social attraction affect colony selection and dynamics of Lesser Kestrels. *Ecology* 85:3438–3447. doi: 10.1890/04-0463
- Short, L. L. (1974). Habits of three endemic West Indian woodpeckers (Aves, Picidae). *American Museum Novitates* 2549:1–44.
- Wagner, R. H. (1993). The pursuit of extra-pair copulations by female birds: a new hypothesis of colony formation. *Journal of Theoretical Biology* 163:333–346. doi: 10.1006/jtbi.1993.1123
- Waldstein, A. L. (2012). An inexpensive camera system for monitoring cavity nests. *Journal of Field Ornithology* 83:302–305. doi: 10.1111/j.1557-9263.2012.00379.x
- Wallace, R. A. (1974). Ecological and social implications of sexual dimorphism in five melanerpine woodpeckers. *The Condor* 76:238–248.
- Wesołowski, T. (2011a). “Lifespan” of woodpecker-made holes in a primeval temperate forest: A thirty year study. *Forest Ecology and Management* 262:1846–1852. doi: 10.1016/j.foreco.2011.08.001
- Wesołowski, T. (2011b). Reports from nestbox studies: a review of inadequacies. *Acta Ornithologica* 46:13–17. doi: 10.3161/000164511X589866
- Wesołowski, T., D. Czeszczewik, P. Rowiński, and W. Walankiewicz (2002). Nest soaking in natural holes - A serious cause of breeding failure? *Ornis Fennica* 79:132–138.
- Wetmore, A., and B. H. Swales (1931). The birds of Haiti and the Dominican Republic. *Bulletin of the United States National Museum*. doi: 10.5479/si.03629236.155.i
- Wiebe, K. L. (2001). Microclimate of tree cavity nests: Is it important for reproductive success in Northern Flickers? *The Auk* 118:412–421. doi: 10.1642/0004-8038(2001)118[0412:MOTCNI]2.0.CO;2
- Wiebe, K. L., W. D. Koenig, and K. Martin (2007). Costs and benefits of nest reuse versus excavation in cavity-nesting birds. *Annales Zoologici Fennici* 44:209–217.

Winkler, H., and D. A. Christie (2018). Woodpeckers (Picidae). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie and E. de Juana, Editors). Lynx Edicions, Barcelona, retrieved from <https://www.hbw.com/node/52286> on 2 August 2018.

Wittenberger, J. F., and G. L. Hunt (1985). The adaptive significance of coloniality in birds. In Avian Biology (D. S. Farner and J. R. King, Editors). Academic Press, San Diego, pp. 1–78. doi: 10.1016/B978-0-12-249408-6.50010-8

CHAPTER 2: REPRODUCTIVE SUCCESS AND COLONIAL NESTING IN THE HISPANIOLAN WOODPECKER

Abstract

Both socially-derived benefits and spatial clustering of resources constitute non-mutually exclusive hypotheses for why animals breed in colonies, despite the costs of doing so. I studied the Hispaniolan Woodpecker (*Melanerpes striatus*), a facultative colonial breeder, to test for the effects of colony size on various components of reproductive success, with the goal of distinguishing between these two hypotheses. Clutch size, hatching success, partial brood loss, and the number of fledglings produced were unrelated to colony size. Overall nesting success (fledging one or more chicks) was positively associated with colony size, but this relationship was likely driven by tree status (live vs. dead) rather than colony size per se. Nest failures due to flooding occurred almost exclusively in live trees (mainly *Roystonea* palms), which were more likely to host singular nests and small colonies (2–4 nesting pairs), whereas dead *Roystonea* palms, which were immune to cavity flooding, were more likely to host larger colonies (≥ 5 pairs). The relationship between colony size and nesting success, though, remained statistically significant when failures due to flooding were omitted. However, neither annual fledging success nor annual nesting success (number of successful nesting attempts) were associated with colony size. Colonial nesting in the Hispaniolan Woodpecker does not appear to yield social benefits for reproductive success. Instead, coloniality is more likely driven by limited availability of dead trees and cavities.

Introduction

Why do some organisms live in groups whereas others lead mostly solitary existences? This question remains a challenge for behavioral ecologists because the underlying factors that promote grouping are not as obvious or automatic as the costs, which include increased competition for resources and mates, exposure to parasites and pathogens, and conspicuousness to predators of densely aggregating (Alexander 1974).

Coloniality, a social breeding system in which individuals or pairs are clustered during breeding (Wittenberger and Hunt 1985), provides an opportunity to test hypotheses and theories for the maintenance and origin of group living, in part because colonial species exhibit extensive intra- and inter-specific natural variation in group size (Brown and Brown 2001, Brown 2016). A productive paradigm for studying coloniality has been to document the relationship between fitness and natural variation in colony size (Hoogland and Sherman 1976, Snapp 1976).

One major hypothesis for the evolution and maintenance of group-living and thus coloniality is that grouping yields social benefits, including protection from predators (Hoogland and Sherman 1976, Serrano et al. 2004, Jungwirth et al. 2015), social enhancement of foraging (Brown 1988, Herbert-Read et al. 2016, Jones et al. 2018), or thermoregulatory benefits (Leighton and Echeverri 2014, Paquet et al. 2016). For example, predation could influence the evolution of coloniality by promoting aggregation via various anti-predator defenses, such as group defense and mobbing (Hoogland and Sherman 1976, Picman et al. 1988, Kazama and Watanuki 2010), predator dilution (Stier et al. 2013), predator confusion (Ioannou et al. 2008), or enhanced vigilance and detection of predators (Brown and Brown 1987, Uetz et al. 2002). Conspecifics could also benefit through use of colonies as “information centers” in which naïve individuals follow knowledgeable individuals to food (Emlen and Demong 1975, Greene 1987,

Brown 1988). Such social benefits would manifest as a positive relationship between colony size and one or more components of reproductive success.

An alternative to social benefits, the resource limitation (or habitat-mediated aggregation) hypothesis posits that individuals aggregate due to the spatiotemporal clustering of resources (Alexander 1974, Danchin et al. 2008). In the absence of socially-mediated benefits, the automatic detriments of grouping should yield a decrease in fitness with group size (Alexander 1974). For example, aggregations increase attraction of predators, potentially resulting in increased adult mortality or nest predation (Varela et al. 2007), and high local density of conspecifics is likely to increase competition for food (Ashmole 1963) and mates (Wagner 1993). The risk of inadvertent harm, such as burrow collapse (Boland 2004), could also increase with group size. If such costs of grouping are substantial, the relationship between group size and reproductive success should be negative. Alternatively, if these costs are minimal, reproductive success could be unrelated to group size, akin to an ideal-free distribution (Fretwell and Lucas 1969, Davis and Brown 1999).

An ideal species for testing these hypotheses would exhibit facultative coloniality, having both singular and colonial nests (Nuechterlein et al. 2003, Sachs et al. 2007, Brown 2016). The Hispaniolan Woodpecker, *Melanerpes striatus* (Class: Aves, Family: Picidae) is one such candidate. Although coloniality is rare among picids, the Hispaniolan Woodpecker nests both singularly and colonially, with as many as 26 pairs occupying a single tree (Short 1974, Wallace 1974, Chapter 1). Hispaniolan Woodpecker colonies are larger on dead trees than live trees, and dead trees are relatively rare. The species is the major cavity excavator on its namesake island, yet while the number of old cavities on a tree is positively associated with colony size, cavities appear to be limiting because they frequently flood in live trees and eventually collapse in dead

trees (Chapter 1). Additionally, new cavities in dead trees take less time to construct, and nests in live trees are susceptible to flooding while dead tree cavities are nearly impervious to flooding. The positive association between tree status (dead vs. alive), the number of existing cavities, and colony size suggests a possible role for resource limitation. However, the relationship between colony size and fitness for this species has not previously been investigated.

The primary objective of this study is to test the social benefits hypothesis for group living in the Hispaniolan Woodpecker by analyzing the relationship between colony size and reproductive success. The social benefits hypothesis predicts that success should increase with colony size. In contrast, the resource limitation hypothesis predicts either a negative relationship or no relationship between colony size and reproductive success.

Materials and Methods

Study area

In the following paragraphs, I use “we” where appropriate to reflect the involvement of assistants in all aspects of field work. We studied a population of Hispaniolan Woodpeckers in Piedra Blanca, 3 km east of Jarabacoa (19°07'09.5"N, 70°34'54.8"W; 550–700 m a.s.l.), La Vega, Dominican Republic, between April 2012 and July 2017. The site consists of several private properties in a landscape of pine (*Pinus occidentalis* and *Pinus caribaea*) and broadleaf wet forest fragments immersed in a matrix of cattle pastures with isolated or clustered *Roystonea* palms and small fragments of secondary vegetation and “living tree” (predominantly *Gliricidia sepium*) fences. This region experiences a mild, dry winter season (January - March), followed by a short, wet spring wet season (April - May), a long, dry summer season (June - September), and a short, wet fall season (October - December) coinciding with the latter half of the Atlantic

hurricane season (Casey 2010).

Individual capture and identification

We captured adult woodpeckers via two approaches: (1) ambushing adults in nest cavities (Stanback and Koenig 1994) and (2) an elevated, dual-tower mist-net system (LaPergola & Kenyon in prep.). Ambushing involved monitoring active cavities by checking contents to determine the stage of nesting (see below). We set up traps using a plastic ball (Wiffle ball) covered in duct tape and tied to monofilament nylon line to cover cavity entrances after birds entered to feed chicks or pre-dawn when birds were in roost. To reduce nest abandonment, we used the ambush capture method one or more weeks before egg-laying or ≥ 22 days post-hatch. The mist net tower system involved erecting two 15.2 m tower poles supported with a series of guy lines (ropes) and, using pulleys and ropes, raising two stacked 12 m mist nets in front of targeted nesting trees. This method reduced disturbance at nests and enabled us to include woodpeckers nesting in substrates too unstable to climb. Once captured, each bird received a unique four-band combination consisting of two color bands on one leg and a color band and numbered aluminum band on the other.

In total, we banded 186 adult birds (89 females, 97 males) and 260 nestlings. Of the 260 nestlings, six were recaptured as adults. We determined adult sex based on crown color, which is black in females and red in males, but we were unable to determine nestling sex because all nestlings had black crowns.

Nest monitoring

The vast majority of nesting attempts (~98%) occurred in native royal palms, *Roystonea*

hispaniolana (Chapter 1). We selected trees for monitoring based on the presence of cavities and activity of woodpeckers. Dead palms were easily distinguished from live palms by the absence of the green crownshaft on the former. We inspected cavities using a penlight and small inspection mirror (1-2" diameter) while climbing or with a wireless camera attached to a 15.2 m telescoping pole that broadcasted images to a portable digital television (Huebner and Hurteau 2007, Waldstein 2012).

In total, we monitored 263 full cavities in 59 palms, which included 48 palms that remained alive during the study, 7 palms that died during the study, and 4 palms that were dead at the start of the study. We checked cavities that were inundated with water or guano less frequently (typically two or three times per month) than dry cavities, unless we observed woodpeckers occupying them or if the cavities occurred on trees with active nests. Once we detected a nesting attempt, we checked the clutch every 3-5 days and, when possible, daily if I did not know the clutch completion date. Because incubation typically last 11 days (range = 9–14 days, unpubl. data) and birds lay only 1 egg per day, I back-calculated first egg dates when nests were found after clutch completion.

Overall, we documented 343 nesting attempts. Of these attempts, 164 involved 65 unique pairs of marked birds (45 females, 47 males), and 97 nesting attempts involved one marked individual paired with an unmarked individual (17 banded males paired to unmarked females and 7 females paired to unmarked males). To account for repeated measures of unmarked pairs, I attributed an additional 82 nesting attempts to 71 unique pairs comprising pairs of unmarked individuals. I used this approach because individuals rarely changed nesting cavities within a season: of marked pairs with two or more nesting attempts in a season, 8% ($N = 79$) changed cavities once, and one marked pair lost their cavity to another pair. I included pair identity (pair

ID) as a random effect in all models.

We recorded the following components of reproductive success: clutch size, hatching success, fledging success, partial brood loss, and nesting success. I calculated hatching success as the number of chicks present divided by clutch size for nests where all eggs hatched or ≥ 1 intact egg remained 2-3 days after the first egg hatched. We recorded fledging success as the number of chicks that were either known or likely to have fledged. Partial brood loss occurred when ≥ 1 nestling disappeared from the nest or died in the nest prior to fledging but ≥ 1 nestling successfully fledged (Mock 1994). I recorded nesting success as a binary response: complete failure or fledging ≥ 1 chick.

In addition to nesting success, we recorded the stage of failure (i.e., the egg, hatching, or nestling stages) and inferred causes of failure when possible. During checks of complete cavities, we recorded the presence/absence of eggs and their condition (intact or broken eggshells), the presence/absence of nestlings and their condition (alive or dead), the presence of moisture or standing water, and the condition of the cavity itself (intact or collapsed into lower cavity). If the cavity was empty, we searched a ~ 1 m radius area around the base of the nest tree for evidence of eggs or dead chicks.

We assigned the following causes of nest failure: flooding, collapse, abandonment, heterospecific competition, parasitism by botflies, infanticide of nestlings, and egg tossing. Nests were considered to fail due to flooding if the cavity contained standing water and was either missing eggs or nestlings or contained partially submerged eggs, floating eggs, or dead nestlings. We considered collapse the cause of failure when the contents of one or both nests were lost after the floor or wall separating adjacent cavities collapsed. We considered nests to be abandoned if eggs never hatched but were present longer than 14 days, the longest known incubation period

leading to successful hatching. Nests were considered to fail due to heterospecific competition when bats and/or bat guano appeared in a cavity. Nest failure was assigned to botfly (*Philornis* sp.) parasitism if nestlings were known to be infested and disappeared before fledging.

Infanticide of nestlings and egg tossing by adult Hispaniolan Woodpeckers were identified as causes of nest failure directly during nest watches.

We monitored a subset of banded birds (88 unique pairs) sufficiently to calculate annual reproductive success. This sample included both pairs that fledged one or more young and pairs that fledged none. Pairs were monitored for an average of 1.2 ± 0.1 breeding seasons (range = 1–3). Of these pairs, 21 were only observed nesting singularly, 62 were only observed nesting colonially, and 5 nested singularly and colonially. Annual fledging success was the total number of fledglings produced by a pair within a breeding season, and annual nesting success was the total number of successful nesting attempts for a pair within a breeding season. Pairs were only included in these analyses if their nest cavities were checked early and frequently enough to detect all successful nesting attempts in a breeding season. For these analyses, I included pairs with one ($N = 21$) or both ($N = 50$) parents banded and unbanded pairs ($N = 17$).

Statistical analysis

All summary statistics are presented as mean \pm standard error unless otherwise noted. In all models utilizing individual nesting attempts, I included first egg date as a fixed effect because of its demonstrated relationship to clutch size in temperate latitudes (Rowe et al. 1994). I also included tree status (live vs. dead) and its interaction with colony size as fixed effects in all models because of the importance of tree status on reproductive success (Short 1974, Chapter 1).

I included year as a random effect in all analyses because I was not confident that

interannual variation was sampled adequately enough to interpret the fixed effects of year (Bennington and Thayne 1994). The breakdown of monitoring by years was as follows: 21 nesting attempts in 13 trees in 2012, 35 nesting attempts in 11 trees in 2013, 77 nesting attempts in 19 trees in 2014, 86 nesting attempts in 21 trees in 2015, 36 nesting attempts in 10 trees in 2016, and 88 nesting attempts in 25 trees in 2017.

I analyzed clutch size and fledging success with linear mixed-effects models (LMMs), and I analyzed hatching success (including clutch size as a weight in the model), partial brood loss (yes or no), and nesting success with generalized linear mixed-effects models (GLMMs). I fitted all GLMMs with a binomial distribution and logit link. I analyzed both annual fledging success and annual nesting success with GLMMs fitted with a poisson distribution, and I included Tree ID and Pair ID nested within Year as random effects. I conducted all statistical analyses in R v. 3.4.3 (R Core Team 2017) using the *lmer* (LMMs) and *glmer* (GLMMs) functions in the *lme4* package (Bates et al. 2015).

I fitted a second GLMM of nesting success in which nest failures due to cavity flooding were omitted from the analysis. Compared with dead trees, live trees hosted smaller colonies (2–4 pairs) and were more likely to host singular nests, but cavity flooding was almost exclusively restricted to live trees (Chapter 1). Flooding thus disproportionately impacted singular and small colony nests compared to larger colonies (≥ 5 pairs), so a statistically significant positive association between nesting success and colony size might be due to tree status rather than colony size. If so, removing failures due to flooding from the nesting success analysis would result in a non-significant association with colony size.

Table 2.1. Results of linear mixed models for clutch size and fledging success and generalized linear mixed models for hatching success, partial brood loss, and nesting success.

	<i>N</i>	Estimate ± S.E.	<i>d.f.</i>	<i>z</i>	<i>P</i>
(a) Clutch size					
Colony size	208	0.065 ± 0.118	176.1	0.55	0.58
First egg date		-0.369 ± 0.068	183.5	-5.46	< 0.001
Tree status (live) x Colony size		-0.550 ± 0.297	161.3	-1.85	0.07
(b) Hatching success					
Colony size	118	-0.260 ± 0.247		-1.05	0.29
Tree status (live)		-0.767 ± 0.612		-1.26	0.21
First egg date		0.265 ± 0.129		2.05	0.04
Colony size x Tree status		-0.072 ± 0.657		-0.11	0.91
(c) Partial brood loss					
Colony size	96	-0.084 ± 0.455		-0.19	0.85
Tree status (live)		-0.147 ± 1.179		-0.13	0.90
Brood size		0.952 ± 0.329		2.89	0.004
First egg date		0.388 ± 0.276		1.40	0.16
Colony size x Tree status		-0.551 ± 1.313		-0.42	0.68
(d) Fledging success					
Colony size	109	0.009 ± 0.188	63.4	0.05	0.96
Tree status (live)		-0.122 ± 0.338	94.9	-0.36	0.72
First egg date		0.032 ± 0.106	91.1	0.30	0.76
Tree status (live) x Colony size		-0.195 ± 0.358	98.9	-0.55	0.59
(e) Nesting success					
Colony size	259	0.666 ± 0.277		2.41	0.016
Tree status (live)		0.840 ± 0.537		1.56	0.12
First egg date		-0.966 ± 0.172		-5.62	<0.001
Tree status (live) x Colony size		-0.527 ± 0.559		-0.94	0.35

For all analyses, colony size and first egg date were standardized by centering with the mean and dividing by the standard deviation.

Results

Colony size and measures of reproductive success

Clutch size averaged 4.4 ± 0.1 eggs (range = 1–7 eggs, $N = 208$ nests). Neither colony size, tree status, nor their interaction significantly influenced clutch size (Table 2.1a). Clutch size was significantly associated with first egg date, decreasing as the season progressed (Table 2.1a, $P < 0.001$).

Most nests (58%) had ≥ 1 egg that failed to hatch, with mean hatching success of $81.9 \pm$

1.8% (range = 20 – 100%; $N = 118$ nesting attempts). However, none of the predictors considered was significantly associated with hatching success (Table 2.1b).

Partial brood loss occurred in 65% of nesting attempts ($N = 96$), and nests lost 1.8 ± 0.1 nestlings (range = 1 – 4, $N = 61$ nesting attempts). Colony size, tree status, the interaction between colony size and tree status, and first egg date were not significantly associated with the occurrence of partial brood loss. Brood size was the only significant predictor: the probability of experiencing partial brood loss increased with brood size (Table 2.1c).

Successful nests produced an average of 2.8 ± 0.1 fledglings ($N = 109$ nests). However, neither colony size, tree status, the interaction between colony size and tree status, nor first egg date significantly predicted the number of fledglings produced (Table 2.1d).

Overall Nesting Success and Causes of Nest Failure

Although tree status and its interaction with colony size were not significant in the model, first egg date and colony size were significantly associated with nesting success, i.e., complete failure vs. fledging ≥ 1 young (Table 2.1e, Fig. 2.1). Nesting success decreased seasonally but was positively associated with colony size (Fig. 2.1). Overall, 4 (50%) singular nests were successful in dead trees ($N = 8$), 30 (47%) singular nests were successful in live trees ($N = 64$), 41 (42%) colonial nests were successful in dead trees ($N = 97$), and 34 (38%) colonial nests were successful in live trees ($N = 90$).

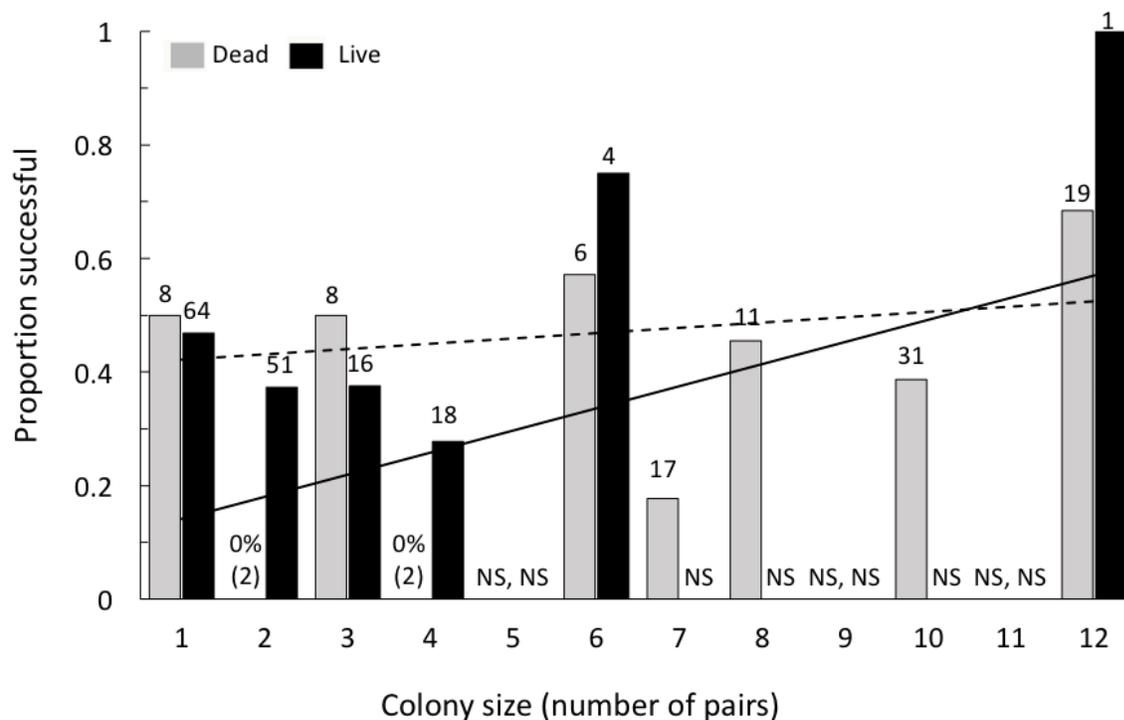


Figure 2.1. Proportion of Hispaniolan Woodpecker nesting attempts that were successful as related to colony size and tree status. “NS” indicates that no nesting attempts were sampled for the corresponding colony size. Numbers of above or immediately adjacent to each bar indicate the number of nesting attempts, and for clarity, the number of nesting attempts are presented parenthetically for colony sizes with no successful nests. The dashed and solid lines are the predicted relationship for live and dead palms, respectively, based on a generalized mixed effects model.

Table 2.2. Hispaniolan Woodpecker nest fates, including known stages and causes of failure.

Fate	Singular nests		Colonial nests	
	Dead tree	Live tree	Dead tree	Live tree
Success	4	30	41	34
Failure - total	4	34	56	56
Failed while hatching (Predation)	0	0	5	2
Failed with eggs	1	27	34	39
Predation	0	7	27	15
Eggs tossed	0	0	0	1
Flooded	1	17	0	19
Collapsed	0	0	2	0
Abandoned	0	2	2	1
Heterospecific competition	0	1	0	1
Insufficient checks	0	0	3	2
Failed with nestlings	3	7	17	15
Dead in nest (Starvation)	0	2	6	2
Predation	1	1	4	3
Flooded	0	2	0	6
Heterospecific competition	0	0	0	1
Infanticide	0	0	1	0
Collapsed	0	0	1	0
Botflies	2	1	2	3
Insufficient checks	0	1	3	0

Nest records with unknown colony size, number of fledglings, and/or clutch initiation date were omitted.

The cause of failure was determined for 66 (44%) failed nests ($N = 150$) (Table 2.2, Fig. 2.2), and predation was inferred as the cause for a further 65 (43%) nests. Overall, 9 (24%) singular nest failures ($N = 38$) were attributed to predation whereas 56 (50%) colonial nest failures ($N = 112$) were attributed to predation. Flooding, however, was the most common known cause of failure in live trees, accounting for 44 (49%) failed nests ($N = 90$). Among dead trees, only 1 failure (2%, $N = 60$ failed nests) was attributable to flooding: a nest in a non-palm species was soaked but not fully inundated.

Omitting nest failures due to flooding from the analysis did not qualitatively change the model results. First egg date and colony size were both significantly associated with nesting success.

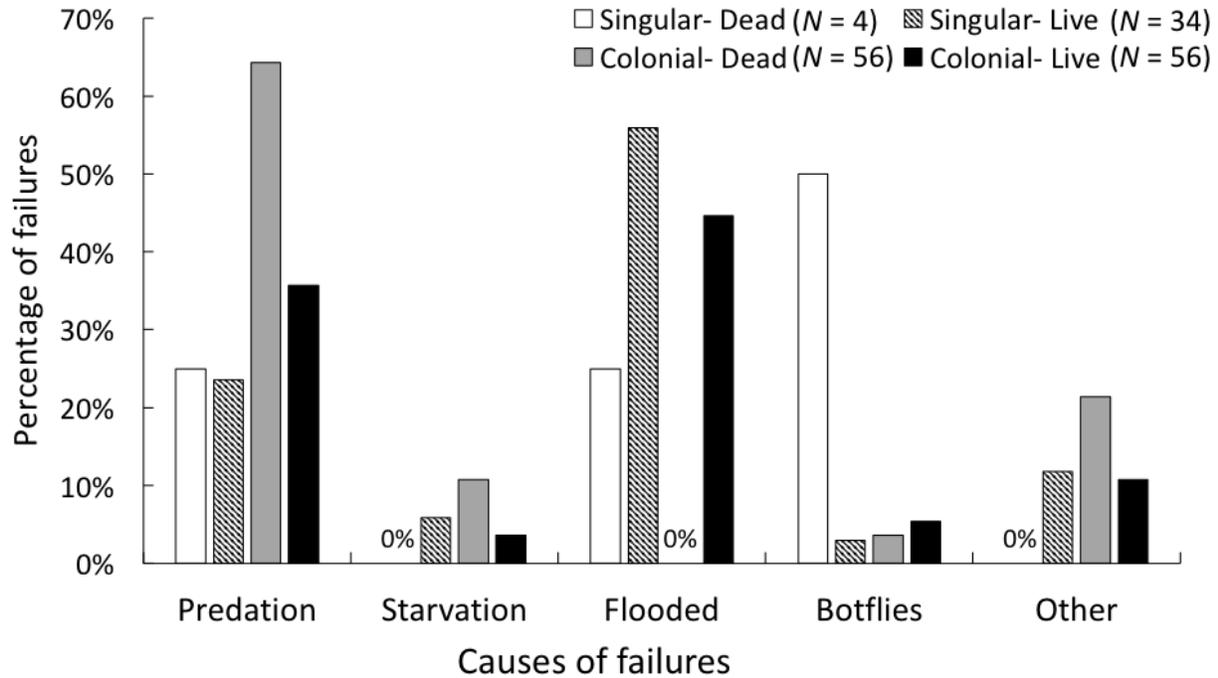


Figure 2. Proportion of Hispaniolan Woodpecker nest failures attributed to predation, starvation, flooding, botfly parasitism, and other causes for singular nests in dead or live trees and colonial nests in dead or live trees. Other causes occurred a relatively low frequency and included abandonment, cavity collapse, egg-tossing, infanticide, heterospecific competition, and nests checked with insufficient frequency to attribute cause or stage of failure.

Annual Reproductive Success

The mean annual fledging success for singular pairs was 2.4 ± 0.4 ($N = 30$ pair-years), and the mean annual fledging success for colonial pairs was 2.0 ± 0.2 ($N = 79$ pair-years). Combining singular and colonially nesting pairs, the mean annual fledging success was 2.1 ± 0.2 fledglings (range = 0–6, $N = 109$ pair-years). Neither colony size, tree status, nor their interaction were significantly associated with annual fledging success (Table 2.3a).

Mean annual nesting success (number of successful nesting attempts) was 0.8 ± 0.1 ($N = 30$ pair-years) for singular pairs 0.7 ± 0.1 ($N = 79$ pair-years) for colonial pairs. Across all pairs, mean annual nesting success was 0.7 ± 0.1 (range = 0–2, $N = 109$ pair-years), and pairs made an average of 1.9 ± 0.1 nesting attempts per season (range = 1–4). Neither colony size, tree status, nor their interaction were significantly associated with annual nesting success (Table 2.3b).

Table 2.3. Results of generalized linear mixed effects models for (a) annual fledging success and (b) annual nesting success.

	<i>N</i>	Estimate \pm S.E.	<i>z</i>	<i>P</i>
(a) Annual fledging success	109			
Colony size		0.151 ± 0.184	0.82	0.41
Tree Status (live)		-0.186 ± 0.478	-0.39	0.70
Tree status (live) * Colony size		-0.732 ± 0.573	-1.28	0.20
(b) Annual nesting success	109			
Colony size		0.239 ± 0.235	1.02	0.31
Tree Status (live)		0.109 ± 0.556	0.20	0.84
Tree status (live) * Colony size		-0.563 ± 0.653	-0.86	0.39

Colony size was standardized by centering with the mean and dividing by standard deviation. Random effects included tree ID and pair ID nested within year.

Discussion

Colony size was not significantly associated with any of the components of reproductive success examined, including clutch size, hatching success, partial brood loss, and fledging success.

Nesting success (complete failures vs. fledging ≥ 1 young), though, was marginally positively associated with colony size (Fig. 2.2, Table 2.1e), even when flooded nests were omitted. At first, these results would seem to support the social benefits hypothesis. However, colony size was not significantly associated with either annual fledging success or annual nesting success. The social benefits hypothesis was unlikely to explain the positive association between colony size and nesting success. The lack of association between colony size and the components of reproductive success and annual reproductive success are more consistent with the resource limitation hypothesis. Instead, the positive association between colony size and nesting success was probably due to large colonies (≥ 5 pairs) being in dead trees, which were immune to flooding and easier to excavate than live trees (Chapter 1). Flooding occurred almost exclusively on live trees (Table 2.2, Fig. 2.2), which were more likely to host singular nests and smaller (2–4 pairs) colonies (Chapter 1).

The findings of this study indicate that Hispaniolan Woodpeckers experience few if any social benefits that affect reproductive success per nesting attempt or annual reproductive success. It is, however, still possible that social benefits could be manifested through increased adult survival. That is, coloniality and group living might have no impact on reproductive success in a given breeding season but could be adaptive if breeding birds in colonies experienced greater survival due, for example, to reduced predation (Serrano et al. 2005).

The effects of colony size on adult Hispaniolan Woodpecker survival are not known. Few predators are known for adult Hispaniolan Woodpeckers, and it has been suggested that

predation might be of minimal importance for the species (Short 1974). However, colonial nesting could have the opposite effect on adult survival if, for example, predators of adults were more attracted to colonies than to singular nests (Wiklund and Andersson 1994). Either a negative or flat relationship between adult survival and increasing colony size would falsify the hypothesis of socially derived survival benefits, making it more likely that Hispaniolan Woodpecker colonies are habitat-mediated aggregations (Danchin et al. 2008, Chapter 1).

One alternative interpretation for the lack of a relationship between colony size and annual reproductive success is that colony sizes in the study were not large enough to detect an effect of social benefits (Davis and Brown 1999, Weaver and Brown 2005). Weaver and Brown (2005) suggested that for Cave Swallows (*Petrochelidon fulva*), whose annual reproductive success was not related to colony size, social benefits might require a certain threshold size before they are realized. The largest colonies observed in the present study comprised 12 pairs, but colonies as large as 19 and 26 pairs have been reported (Wallace 1969, Short 1974). However, if there is a net benefit to group living, analyses including singular nests should be able to detect a positive association between reproductive success and colony size because singular nests would not enjoy any social benefits from coloniality. In other words, the threshold at which pairs experience social benefits might be the smallest colony size of two. This “threshold” argument is therefore unlikely to apply to Hispaniolan Woodpeckers because it included singular nests, which fared as well as nests in different colony sizes.

Another interpretation for no relationship between colony size and annual reproductive success is that the costs and benefits of group living balance across colony sizes (Brown and Bomberger Brown 1996). For example, parents might increase foraging efficiency by foraging in groups but increased ectoparasitism of nestlings might heighten nutritional demands, keeping

pace with heightened foraging success. Such a balance might explain why in Cliff Swallows (*P. pyrrhonota*) fledging success was only associated with colony size in some years (Brown and Bomberger Brown 1996). Determining whether the relationship between reproductive success and colony size of Hispaniolan Woodpeckers results because costs and benefits balance across colony sizes will require additional work, including analysis of behaviors that might constitute social benefits. Such work will be an important next step because this interpretation is inconsistent with the resource limitation hypothesis.

What is currently known about the Hispaniolan Woodpecker makes a strong case for the resource limitation hypothesis and a lack of social benefits. Colony size variation in this species appears to be driven by variation in dead tree and cavity availability (Chapter 1). In the study population, colonies were larger on dead royal palms than on live royal palms, and dead palms were rarer on the landscape, immune to cavity flooding, and more quickly excavated than live palms. Thus, dead royal palms, especially recently dead palms, appear to be high quality nest sites. Cavity flooding on live trees is a major cause of nest failure for Hispaniolan Woodpeckers, yet despite the protection from cavity flooding on dead palms, nesting success was not consistently higher on dead palms. This was likely due to differences in the prevalence of different causes of nest failure between nests in live and dead palms and singular and colonial nests. Specifically, although predation was rarely directly observed, predation was inferred to be a more prevalent cause of nest failure for colonial nests than for singular nests (Table 2.2, Fig. 2.2). This pattern is consistent with increased attraction of predators in colonies. Since colonies were larger on dead palms, the lack of an association between reproductive success and colony size is consistent with Hispaniolan Woodpeckers settling in an ideal free distribution (Fretwell and Lucas 1969), enjoying no significant socially derived benefits, and experiencing socially

derived costs that balance the benefits of breeding in a higher quality nest tree.

The significant positive association between colony size and nesting success (Table 2.1e) was also intriguing because 47% of singular nests were successful while only 40% of colonial nests were successful (Table 2.2). Instead of social benefits explaining the positive association in the analysis, I suggest that how long a palm has been dead also impacted nesting success, but I was unable to attempt such an analysis owing a small sample size. However, it could be that trees that have been dead for several years, which can only host singular nests or small colonies of two or three pairs, offer less protection from weather or predators. Trees that recently died, however, are still relatively intact but offer protection from flooding, leading to higher nesting success. How long the tree has been dead might also interact significantly with how many cavities it had at the time of death. For example, a tree that dies with many cavities would deteriorate more quickly and offer less protection from weather and predators sooner than a tree that dies with no or few cavities.

That Hispaniolan Woodpeckers fared equally well in terms of annual reproductive success when nesting singularly and colonially is intriguing because it suggests an absence of socially derived benefits for a species in a family (Picidae) where coloniality is exceptionally rare. Work is needed on the effects of colony size on reproductive success in the other two colonial woodpeckers (*Melanerpes lewis* and *Colaptes rupicola*) to determine if the resource limitation hypothesis can more broadly explain the rare occurrence of coloniality in the family.

Acknowledgements

I gratefully acknowledge the following individuals for providing invaluable assistance in the field: M. Angelucci, H. Boyle, C. Cerrilla, W. Coleman, A. Diaz, L. Emerson, N. Gilbert, A.

Janik, K. Kauffman, T. Lacerda, A. Lascher-Posner, M. Larrieu, K. Larsen, C. Mathers-Winn, K. Nelsen, A. Occhialini, S. Schubert, H. Stapleton, M. Walters, A. Waterman-Snow, P. Werner, A. Wichtendahl. I thank W. D. Koenig, J. L. Dickinson, P. W. Sherman, M. S. Webster, H. K. Reeve, and I. J. Lovette for feedback on the manuscript and constructive criticism at various points in the development of this project. F. Vermeulen and D. Akdemir at the Cornell Statistical Consulting Unit provided statistical advice. The following sources provided funding support: Cornell Lab of Ornithology Athena Fund, Department of Neurobiology Animal Behavior Research Grant, Society for the Study of Evolution Rosemary Grant Award, and Sigma Xi Grant in Aid of Research. I was also supported by the following fellowships during fieldwork: Charles Walcott Graduate Fellowship, Linda and Samuel Graduate Student Fellowship, Eleanore Stuart Graduate Fellowship, Andrew '78 and Margaret Paul Graduate Fellowship, Kramer Graduate Fellowship, Halberstadt Graduate Fellowship, Anne Marie Brown Summer Graduate Fellowship, and Lab of Ornithology Summer Graduate Fellowship. Lastly, I wish to thank PB05-16, the royal palm that tried, but narrowly failed, to kill me. All research activities described here were approved by the Dominican Republic's Ministerio de Medio Ambiente y Recursos Naturales and conducted in accordance with IACUC protocol 2008-0185 at Cornell University.

References

- Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics* 5:325–383.
- Ashmole, N. P. (1963). The regulation of numbers of tropical oceanic birds. *Ibis* 103 b:458–473. doi: 10.1111/j.1474-919X.1963.tb06766.x
- Bates, D., M. Mächler, B. Bolker, and S. Walker (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48. doi: 10.18637/jss.v067.i01

- Bennington, C. C., and W. V. Thayne (1994). Use and misuse of mixed model analysis of variance in ecological studies. *Ecology* 75:717–722.
- Boland, C. R. J. (2004). Breeding biology of Rainbow Bee-eaters (*Merops ornatus*): a migratory, colonial, cooperative bird. *The Auk* 121:811–823. doi: 10.1642/0004-8038(2004)121[0811:BBORBM]2.0.CO;2
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S. White (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24:127–135. doi: 10.1016/j.tree.2008.10.008
- Brown, C. R. (1988). Enhanced foraging efficiency through information centers: a benefit of coloniality in Cliff Swallow. *Ecology* 69:602–613.
- Brown, C. R. (2016). The ecology and evolution of colony-size variation. *Behavioral Ecology and Sociobiology* 70:1613–1632. doi: 10.1007/s00265-016-2196-x
- Brown, C. R., and M. Bomberger Brown (1996). *Coloniality in the Cliff Swallow*. The University of Chicago Press, Chicago.
- Brown, C. R., and M. B. Brown (1987). Group-living in Cliff Swallows as an advantage in avoiding predators. *Behavioral Ecology and Sociobiology* 21:97–107. doi: 10.1007/BF02395437
- Brown, C. R., and M. B. Brown (2001). Chapter 1: Avian coloniality. In *Current Ornithology* (Nolan, V., and C. F. Thompson, Editors). Kluwer Academic/Plenum Publishers, pp. 1–82. doi: 10.1007/978-1-4615-1211-0_1
- Casey, J. (2010). Jarabacoa, Dominican Republic: climate, global warming, and daylight charts and data. *Climate-Charts.com*. [Online.] Available at <https://www.climate-charts.com/Locations/d/DR78000000000203.php>.
- Danchin, E., L.-A. Giraldeau, and R. H. Wagner (2008). Animal aggregations: hypotheses and controversies. In *Behavioural Ecology* (E. Danchin, L.-A. Giraldeau and F. Cézilly, Editors). Oxford University Press, Oxford, pp. 503–545.
- Danchin, E., and R. H. Wagner (1997). The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology and Evolution* 12:342–347. doi: 10.1016/S0169-5347(97)01124-5

- Davis, J. A., and C. R. Brown (1999). Costs of coloniality and the effect of colony size on reproductive success in Purple Martins. *The Condor* 101:737–745.
- Emlen, S. T., and N. J. Demong (1975). Adaptive significance of synchronized breeding in a colonial bird: a new hypothesis. *Science* 188:1029–1031. doi: 10.1126/science.1145188
- Evans, J. C., S. C. Votier, and S. R. X. Dall (2016). Information use in colonial living. *Biological reviews of the Cambridge Philosophical Society* 91:658–672. doi: 10.1111/brv.12188
- Fretwell, S. D., and H. L. J. Lucas (1969). On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19:16–36. doi: 10.1007/BF01601953
- Greene, E. (1987). Individuals in an Osprey colony discriminate between high and low quality information. *Nature* 329:239–241. doi: 10.1038/329239a0
- Herbert-Read, J. E., P. Romanczuk, S. Krause, D. Strömbom, P. Couillaud, P. Domenici, R. H. J. M. Kurvers, S. Marras, J. F. Steffensen, A. D. M. Wilson, and J. Krause (2016). Proto-cooperation: Group hunting sailfish improve hunting success by alternating attacks on grouping prey. *Proceedings of the Royal Society B: Biological Sciences* 283. doi: 10.1098/rspb.2016.1671
- Hoogland, J. L., and P. W. Sherman (1976). Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. *Ecological Monographs* 46:33–58.
- Huebner, D. P., and S. R. Hurteau (2007). An economical wireless cavity-nest viewer. *Journal of Field Ornithology* 78:87–92. doi: 10.1111/j.1557-9263.2006.00089.x
- Ioannou, C. C., C. R. Tosh, L. Neville, and J. Krause (2008). The confusion effect—from neural networks to reduced predation risk. *Behavioral Ecology* 19:126–130. doi: 10.1093/beheco/arm109
- Jones, T. B., S. C. Patrick, J. P. Y. Arnould, M. R. Wells, and J. A. Green (2018). Evidence of sociality in the timing and location of foraging in a colonial seabird. *Biology Letters* 14:20180214. doi: 10.1098/rsbl.2018.0214
- Jungwirth, A., D. Josi, J. Walker, and M. Taborsky (2015). Benefits of coloniality: Communal defence saves anti-predator effort in cooperative breeders. *Functional Ecology* 29:1218–1224. doi: 10.1111/1365-2435.12430

- Kazama, K., and Y. Watanuki (2010). Individual differences in nest defense in the colonial breeding Black-tailed Gulls. *Behavioral Ecology and Sociobiology* 64:1239–1246. doi: 10.1007/s00265-010-0938-8
- Leighton, G. M., and S. Echeverri (2014). Non-linear influence of nest size on thermal buffering of Sociable Weaver nests and the maintenance of cooperative nest construction. *Avian Biology Research*. doi: 10.3184/175815514X14151918723245
- Mock, D. W. (1994). Brood reduction: narrow sense, broad sense. *Journal of Avian Biology* 25:3–7. doi: 10.2307/3677288
- Nuechterlein, G. L., D. Buitron, J. L. Sachs, and C. R. Hughes (2003). Red-necked Grebes become semicolonial when prime nesting substrate is available. *The Condor* 105:80–94. doi: 10.1650/0010-5422(2003)105[80:RNGBSW]2.0.CO;2
- Paquet, M., C. Doutrelant, M. Loubon, F. Theron, M. Rat, and R. Covas (2016). Communal roosting, thermoregulatory benefits and breeding group size predictability in cooperatively breeding Sociable Weavers. *Journal of Avian Biology* 47:749–755. doi: 10.1111/jav.00916
- Picman, J., M. Leonard, and A. Horn (1988). Antipredation role of clumped nesting by marsh-nesting Red-winged Blackbirds. *Behavioral Ecology and Sociobiology* 22:9–15. doi: 10.1007/BF00395693
- R Core Team (2017). R: A language and environment for statistical computing.
- Rowe, L., D. Ludwig, and D. Schluter (1994). Time, condition, and the seasonal decline of avian clutch size. *The American Naturalist* 143:698–722. doi: 10.1086/285627
- Sachs, J. L., C. R. Hughes, G. L. Nuechterlein, and D. Buitron (2007). Evolution of coloniality in birds: a test of hypotheses with the Red-necked Grebe (*Podiceps grisegena*). *The Auk* 124:628. doi: 10.1642/0004-8038(2007)124[628:EOCIBA]2.0.CO;2
- Safran, R. J. (2004). Adaptive site selection rules and variation in group size of Barn Swallows: individual decisions predict population patterns. *The American Naturalist* 164:121–131. doi: 10.1086/422198
- Safran, R. J., V. A. J. Doerr, P. W. Sherman, E. D. Doerr, S. M. Flaxman, and D. W. Winkler (2007). Group breeding in vertebrates: linking individual- and population-level approaches. *Evolutionary Ecology Research* 9:1163–1185.

- Serrano, D., M. G. Forero, J. A. Donázar, and J. L. Tella (2004). Dispersal and social attraction affect colony selection and dynamics of Lesser Kestrels. *Ecology* 85:3438–3447. doi: 10.1890/04-0463
- Serrano, D., D. Oro, E. Ursúa, and J. L. Tella (2005). Colony size selection determines adult survival and dispersal preferences: Allee effects in a colonial bird. *The American Naturalist* 166:E22–E31. doi: 10.1086/431255
- Short, L. L. (1974). Habits of three endemic West Indian woodpeckers (Aves, Picidae). *American Museum Novitates* 2549:1–44.
- Snapp, B. D. (1976). Colonial breeding in the Barn Swallow (*Hirundo rustica*) and its adaptive significance. *Condor* 78:471–480. doi: 10.2307/1367096
- Stanback, M. T., and W. D. Koenig (1994). Techniques for capturing birds inside natural cavities. *Journal of Field Ornithology* 65:70–75.
- Stier, A. C., S. W. Geange, and B. M. Bolker (2013). Predator density and competition modify the benefits of group formation in a shoaling reef fish. *Oikos* 122:171–178. doi: 10.1111/j.1600-0706.2012.20726.x
- Uetz, G. W., J. Boyle, C. S. Hieber, and R. S. Wilcox (2002). Antipredator benefits of group living in colonial web-building spiders: The “early warning” effect. *Animal Behaviour* 63:445–452. doi: 10.1006/anbe.2001.1918
- Varela, S. A. M., É. Danchin, and R. H. Wagner (2007). Does predation select for or against avian coloniality? A comparative analysis. *Journal of Evolutionary Biology* 20:1490–1503. doi: 10.1111/j.1420-9101.2007.01334.x
- Wagner, R. H. (1993). The pursuit of extra-pair copulations by female birds: a new hypothesis of colony formation. *Journal of Theoretical Biology* 163:333–346. doi: 10.1006/jtbi.1993.1123
- Waldstein, A. L. (2012). An inexpensive camera system for monitoring cavity nests. *Journal of Field Ornithology* 83:302–305. doi: 10.1111/j.1557-9263.2012.00379.x
- Wallace, R. A. (1969). Sexual dimorphism, niche utilization, and social behavior in insular species of woodpeckers. Ph.D. dissertation, University of Texas, Austin, TX, USA.

- Wallace, R. A. (1974). Ecological and social implications of sexual dimorphism in five melanerpine woodpeckers. *The Condor* 76:238–248.
- Weaver, H. B., and C. R. Brown (2005). Colony size, reproductive success, and colony choice in Cave Swallows *Petrochelidon fulva*. *Ibis* 147:381–390. doi: 10.1111/j.1474-919x.2005.00417.x
- Wiklund, C. G., and M. Andersson (1994). Natural selection of colony size in a passerine bird. *Journal of Animal Ecology* 63:765–774. doi: 10.2307/5254
- Wittenberger, J. F., and G. L. Hunt (1985). The adaptive significance of coloniality in birds. In *Avian Biology* (D. S. Farner and J. R. King, Editors). Academic Press, San Diego, pp. 1–78. doi: 10.1016/B978-0-12-249408-6.50010-8

CHAPTER 3: GENETIC MONOGAMY AND ABSENCE OF BROOD PARASITISM IN THE COLONIAL HISPANIOLAN WOODPECKER

Abstract

Living in groups entails automatic costs related to density and frequency of interactions, as well as potential socially derived benefits, but these costs and benefits vary across species depending on differences in ecology and life-history. In colonially nesting species with biparental care, one possibility is that individuals are more likely to gain or lose reproductive success via conspecific brood parasitism (CBP) or extra-pair paternity (EPP) compared to species with dispersed nests. In contrast to this “opportunity hypothesis”, the “parental care hypothesis” predicts that regardless of density, colonially nesting species will have no CBP and will be genetically monogamous when high levels of maternal and paternal care are essential for successful reproduction. To test these hypotheses, I studied the social and genetic mating system of a color-banded population of the facultatively colonial Hispaniolan Woodpecker over six years. I quantified the incidence of CBP and EPP using single nucleotide polymorphisms identified via double-digest restriction-site associated DNA sequencing. All young analyzed matched genetically with their social parents. Rare instances of possible CBP were identified via changes in clutch size, but genetic analyses confirmed that parents only fledged their genetic offspring. These results reject the opportunity hypothesis for CBP and EPP but are consistent with the parental care hypothesis. The exact behavioral mechanism remains unknown for the Hispaniolan Woodpecker, but it might involve retaliation to infidelity or CBP or high levels of nest attendance reducing opportunities for CBP and EPP.

Introduction

Living in groups entails automatic costs related to density and frequency of interactions, but also confers potential socially derived benefits (Alexander 1974), but the considerable behavioral variation that exists among social species demonstrates that these species experience different selective pressures or evolve different solutions to the challenges of social life. Understanding why this variation exists remains a challenge for behavioral ecology. Colonially breeding organisms offer an excellent opportunity to test different hypotheses to explain this variation (Danchin and Wagner 1997; Brown and Brown 2001; Brown 2016).

While colonial species are unified by their habit of densely aggregating in time and space for the sole purpose of breeding (Wittenberger and Hunt 1985; Danchin et al. 2008), they vary in the ways they have adapted to this sociality (Brown and Brown 2001). One of the potential consequences of coloniality is the increased opportunity for mixed mating strategies and parentage loss/gain (Alexander 1974; Hoogland and Sherman 1976). For colonial species with social monogamy and biparental care, these consequences manifest as conspecific brood parasitism (CBP), where a female lays one or more eggs in another female's nest and provides no parental care (Lyon and Eadie 2008), and extra-pair paternity (EPP), where a pair-bonded female produces one or more offspring from matings outside the pair-bond (Westneat and Stewart 2003). The extent of CBP and EPP varies across colonial nesting bird species (Westneat and Sherman 1997; Miño et al. 2011), and whether a colonial species evolves mixed mating strategies or alternative reproductive tactics depends on various ecological and life-history factors, including those affecting opportunities for mixed mating strategies and those affecting the cost-benefit trade-offs of these strategies (Westneat et al. 1990; Klug 2018).

For both CBP and EPP, living at high density should increase the risk for parentage

loss/gain via increased opportunities for both reproductive parasitism (Eadie et al. 1998) and extra-pair matings (Westneat et al. 1990; Stewart et al. 2010). In colonial species, this “opportunity hypothesis” could apply in at least two different, non-mutually exclusive ways. First, both the number or proportion of resident parasitic females and the number of potential extra-pair mates resident in a colony increase with increasing colony size (Gowaty and Bridges 1991). Similarly, from a female’s perspective, the likelihood of having one or more colony males of higher quality than her social mate increases with colony size (Morton et al. 1990; Richardson and Burke 1999, 2001). Second, relative to solitary nests, colonies are more conspicuous and attractive to floater females and males that could act as parasites and extra-pair mates, respectively (Gowaty and Bridges 1991). This opportunity hypothesis predicts that CBP and EPP will increase with colony size and be higher in colonies relative to solitary nests within a species (Brown and Brown 1988; Brown and Bomberger Brown 1989; Hoi and Hoi-Leitner 1997), and both CBP and EPP should be higher in colonial than non-colonial species (Møller and Birkhead 1992, 1993; Beauchamp 1997).

An alternative explanation for parentage patterns hypothesizes that the need for high levels of parental care and high parental investment selects against CBP and EPP. In other words, species for which extensive parental care is necessary for successful reproduction incur greater costs due to CBP and should therefore be under stronger selection to prevent or resist parasitism (Rohwer and Freeman 1989). This “parental care hypothesis” predicts that species with high parental investment will have lower levels of or no CPB compared to species with lower parental investment or lower post-hatch parental care (Arnold and Owens 2002).

A similar argument has been made from game theory models hypothesizing that paternity is the result of transactional negotiations between partners (Shellman-Reeve and Reeve 2000).

According to these models, the social mate's paternity (within-pair paternity) is expected to increase as the value of male parental care increases. If males reduce parental care in response to female infidelity but male care is essential for successful reproduction (Dixon et al. 1994; Suter et al. 2009), infidelity should be selected against because females cannot afford to lose the social father's care (Møller 2000). As for CBP, the parental care hypothesis predicts that species with a high need for paternal care or high male parental investment will have reduced levels of EPP compared to species with low need for paternal care (Arnold and Owens 2002). Thus, the opportunity and parental care hypotheses make opposite predictions about the level of CBP and EPP in colonial species.

The Hispaniolan Woodpecker (*Melanerpes striatus*) is a facultative colonial breeder and provides an excellent system for testing the opportunity and parental care hypotheses. For this woodpecker, both singular and colonial nesting (two or more pairs concurrently on a single tree) can occur within the same population (Wallace 1969; Short 1974; Chapter 1), providing the basis for a natural experiment testing whether CBP and EPP are elevated or reduced compared to non-colonial species.

As one of only three (1.2%, $N = 254$ species) colonial woodpecker species (Winkler et al. 1995; Winkler and Christie 2018), the Hispaniolan Woodpecker exhibits a high breeding density compared to other woodpeckers. At both the intra- and inter-specific levels, then, the opportunity hypothesis predicts that Hispaniolan Woodpeckers should exhibit CBP and EPP, and that levels of each should be higher than for other woodpecker species. At the intraspecific level, the opportunity hypothesis predicts that CBP and EPP should occur at higher rates in colonial than in singular nests. The absence of CBP and EPP would thus falsify the opportunity hypothesis.

Regarding the parental care hypothesis, woodpeckers generally exhibit extensive parental

care (Wiebe 2008; Wiebe and Kempnaers 2009) that is shared nearly equally between the sexes (Ligon 1993). The Hispaniolan Woodpecker is no exception, having altricial young that remain thermally dependent until ~21 days after hatching and fledge at ~32 days after hatching (mean \pm standard error = 32.4 ± 0.4 days, $N = 39$ nests, present study). Both females and males contribute to incubation, nest sanitation, nestling provisioning, and nest defense (Short 1974; JBL unpublished data), suggesting that both maternal and paternal investment are high.

My primary objective here is to describe the genetic mating system of the Hispaniolan Woodpecker. By quantifying rates of CBP and EPP, I test the opportunity hypothesis and parental care hypothesis to explain intraspecific variation in the Hispaniolan Woodpecker's genetic mating system and interspecific variation in the genetic mating system of woodpeckers.

Materials and Methods

Study population and field methods

I studied a Hispaniolan Woodpecker population in the small community of Piedra Blanca (19°07'09.5"N, 70°34'54.8"W; 550–700 m a.s.l.), 3 km east of Jarabacoa, La Vega, Dominican Republic, between April 2012 and July 2017. This region experiences a mild, dry winter season (January - March), followed by a short, wet spring wet season (April - May), long, dry summer season (June - September), and a short, wet fall season (October - December) coinciding with the latter half of the Atlantic hurricane season (Casey 2010).

My field assistants and I selected trees for monitoring based on the presence of cavities and detectable activity of woodpeckers. We inspected cavities using a penlight and small inspection mirror (1-2" diameter) while climbing or with a wireless camera attached to a 15.2 m telescoping pole that broadcasted images to a portable digital television (Huebner and Hurteau

2007; Waldstein 2012). Once we detected a nesting attempt, we typically checked the clutch every 3-5 days and, when possible, daily if we did not know the clutch completion date. Incubation typically lasted 11 days (range = 9–14 days). For some nests, I checked the nest every day during egg-laying to determine whether parasitic egg-laying could have occurred.

Additional details for methods of searching for and monitoring nests and capturing adult and nestling woodpeckers are reported in Chapters 1 and 2. In short, we capture adults via “ambushing” them in nest cavities (Stanback and Koenig 1994) and using an elevated, dual-tower mist-net system (LaPergola & Keynon in prep.). Once captured, each bird received a unique four-band combination consisting of two color bands on one leg and a color band and numbered aluminum band on the other. In total, we banded 186 adult birds (89 females, 97 males) and 363 nestlings. For some nests, the cavity entrance was large enough for one of us to reach in and manually remove chicks, but for other cavities, the entrance was too small. To extract nestlings from these cavities, we used a manual or handheld portable power saw to cut a triangular or rectangular door that could be held in place with nails or screws and occasionally reinforced with wood glue. During capture of adults and nestlings, we collected ~50 μ L of blood via ulnar venipuncture, and stored samples in 2% SDS lysis buffer solution (100 mM Tris pH 8, 100 mM Na₂ EDTA, 10 mM NaCl). For nestlings sampled from 2012–2015, we took blood samples and banded nestlings with the aluminum band at ~14 days post-hatch, and at ~21 days post-hatch, we color-banded nestlings and took additional blood samples for individuals that yielded little blood the first time. Starting in 2016, we started metal banding and blood sampling nestlings at ~7 days post-hatch to try to increase the proportion of the brood sampled because partial brood loss was common in the population (65% of nests, N = 96; Chapter 2). When possible, we also collected broken eggshells, intact eggs if they remained \geq 2 days after the last

chick was known to hatch, and dead nestlings.

We assigned social parents to nests using two- or three-hour long nest watches during the incubation and/or nestling phases of the nesting cycle. Nest watches involved sitting 10–15 m from the nest tree with a spotting scope trained on the cavity entrance (in most cases, observers sat inside hides constructed of burlap). Observers used digital voice records to record the identity of attending parents based on color-band combinations (or lack thereof), and, during the nestling phase, the number and kinds of food items delivered. Only those individuals that incubated eggs or young or provisioned nestlings were considered social parents. Restricting social parentage assignment to these cases was necessary because additional birds occasionally visited cavities; however, most of these visits by additional birds involved one-time visits (i.e., the individual was never observed again at the nest), looking into the cavity but never entering, and/or attacking parents and chicks.

In total, we documented 343 nesting attempts. Of these, I included 348 offspring from 116 nesting attempts for parentage analyses, covering all 6 years of the study. Combining years, we sampled a total of 95 offspring from 30 singular nesting attempts and 253 offspring from 86 colonial nesting attempts. Singular nesting attempts were defined as nests with no other pairs on the same tree, and colonies were defined as nest trees with two or more nesting pairs. I also considered one instance of two adjacent trees as one colony because each tree hosted one or more nesting pairs, and the trees were ~1 m apart. The mean colony size of sampled colonies was 4.7 ± 0.7 pairs (range = 2–12 pairs, $N = 22$ colony years: 14 colony trees sampled for a mean of 1.9 ± 0.3 years, range = 1–4 years).

One or both social parents were banded and sampled at the time of nesting for 307 (88%) of 348 sampled offspring and 101 (87%) of 116 nesting attempts. The breakdown for these

samples was as follows: 246 offspring from 77 nests where both social parents were banded and sampled, 24 offspring from 9 nests where only the social mother was banded and sampled while the father was unbanded, and 37 offspring from 15 nests where only the social father was banded and sampled while the mother was unbanded. The remaining 41 offspring from 15 nests fell into two different sampling-assignment categories. The first category included those offspring for which neither parent was banded and sampled at the time of nesting, and subsequent parentage analyses (see below) assigned none of the candidate parents (15 offspring from 5 nests). The second category included those offspring for which neither parent was banded and sampled at the time of the nesting attempt, but subsequent parentage analyses assigned offspring to a candidate male, candidate female, or candidate parent pair (26 offspring from 10 nests) that were included in the candidate parent pool because they were determined to be old enough based on plumage characteristics (Garrod and LaPergola 2018). Additionally, some offspring (see Results) for which only one parent was banded and sampled at the time of nesting were nevertheless assigned with 95% confidence to parent pairs that included the social parent and a parent sampled after nesting.

It was not possible to sample the entire pool of offspring for all nests because hatch failure and partial brood loss occurred in more than half of nests in the study population (Chapter 2). Consequently, for sampled nests with known clutch sizes (mean clutch size = 4.5 ± 0.1 eggs, $N = 88$), the mean percentage of potential offspring sampled was $69 \pm 2\%$ (range = 17–100%, $N = 88$ nests), and 20% of these nests represented full broods.

ddRAD sequencing

I followed the double-digest restriction site-associated DNA sequencing (ddRAD-seq) protocol

described in Thrasher et al. (2018), which was modified from Peterson et al. (2012). I first extracted genomic DNA from all samples using the Qiagen DNeasy® Blood and Tissue kit (Qiagen, Inc., Valencia, CA), including overnight digestion at 64°C and final elutions using nuclease free water warmed to 64°C. I quantified sample concentrations via Qubit dsDNA BR assay kit (Life Technologies, USA). Sample extractions averaged 28.7 ± 12.5 ng DNA/ μ L (range = 2.54 – 67.6 ng/ μ L). For each individual, 100–500 ng of DNA was digested with SbfI and MspI and ligated with one of 20 P1 adapters, each adapter having a unique inline barcode. After this digestion and ligation, I pooled samples into groups of 20 and purified them with 1.5x volumes of homemade MagNA made with Sera-Mag Magnetic Speed-beads (FisherSci) as described by Rohland and Reich (2012). Fragments were then size selected (450-600 bp) using BluePippin (Sage Science) by the Cornell University Biotechnology Resource Center (BRC). After size selection, I added index groups (P2 adapters) and Illumina sequencing adapters using 11 PCR cycles with Phusion DNA Polymerase (NEB). I cleaned these reactions with 0.79 volumes of MagNA. I then pooled the reactions in equimolar ratios to create a single library for sequencing on one lane of the Illumina HiSeq 2500 (100 bp single end, performed by BRC). Sequencing was done with ~10% PhiX spike-in to introduce diversity to the library. Samples were sequenced in four different bouts: 2 full lanes were used for 240 samples each, 20 samples were included as 1 index group in a lane with 2 sets of fairy-wren (*Malurus lamberti* and *Ma. melanocephalus*) samples, and 80 samples were included as 4 index groups in a lane with three other species (*Tockus erythrorhynchus*, *T. deckeni*, and *Sapayoa aenigma*).

SNP data analysis

I assessed read quality using FASTQC version 0.11.5

(www.bioinformatics.babraham.ac.uk/projects/fastqc) and then trimmed all sequences to 97 bp using *fastX_trimmer* (FASTX-Toolkit), excluding low-quality calls near the 3' of the reads. I then removed reads containing at least a single base with a Phred quality score < 10 (using *fastq_quality_filter*). In addition, I removed sequences if more than 5% of the bases had a Phred quality score < 20. I used *process_radtags* from the STACKS version 1.37 pipeline (Catchen et al. 2013) to demultiplex the reads to generate files with sequences specific to each individual.

Because a sequenced genome does not exist for the Hispaniolan Woodpecker, I assembled the sequences *de novo* using the STACKS pipeline (Catchen et al. 2013). I used *denovo_map.pl* to assemble reads into a catalog allowing minimum stack depth of 5 (*m* parameter), up to five mismatches per locus within an individual (*M* parameter), and five mismatches between loci of different individuals when building the catalog (*n* parameter). I then ran the *rxstacks* module to filter loci with a log-likelihood < -50 (*lnl_lim* -50) or that were confounded in at least 25% of the population (*conf_lim* 0.25). I then built a new catalog by rerunning *cstacks* and obtained individual genotype calls with *sstacks*.

I exported SNPs using the *populations* module of the STACKS pipeline. All samples were grouped in one population, and a locus was exported if it was present in 95% of individuals in the population (*r* parameter) at a stack depth of ≥ 10 (*m* parameter). To avoid SNPs in high linkage disequilibrium, I restricted data to the first SNP when a RAD locus had more than one (*-write_single_snp*). I required a minor allele frequency of ≥ 0.25 to process a nucleotide site (*-min_maf*). I initially included 15 samples from unhatched eggs, but 14 (93%) of these samples were too degraded, resulting in too few SNPs, and I omitted these 14 samples from the final *populations* module run and parentage analyses. Three of these samples (2 mixed egg contents and 1 partial embryo) were missing >75% of SNPs in preliminary discovery stages, and the

remaining 11 samples (1 eggshell, 7 mixed egg contents, 2 partial embryos, and 1 nearly hatched embryo) yielded no SNPs. Ultimately, I obtained 147 SNPs for the final data set.

Parentage analyses

I used CERVUS version 3.0.7 (Kalinowski et al. 2007) to assign parentage for all nestlings for each year separately. Because Hispaniolan Woodpeckers can be aged using molt limits (Garrod and LaPergola 2018), I included as candidate parents those birds that were old enough to be breeders in the year of nestling sampling but were caught and sampled in later seasons. I ran separate allele frequency and parentage simulation analyses (parent-pair, sexes known) for each year, including nestlings and candidate parents in the allele frequency calculations (Table 1). For parentage simulation analyses, I used the following parameters: 10,000 offspring, 95% of candidate parents sampled, 85% of loci typed, and minimum number of loci typed was 74. The number of candidate parents for simulations varied across years (Table 1). I used the parent pair approach in CERVUS to identify the most likely parent pair because I was interested in identifying cases of EPP and CBP.

I considered the following possible assignment results for offspring: within-pair offspring (WPO), quasi-parasitism (QP), extra-pair paternity (EPP), brood parasitism (BP), and unassigned. For nestlings with both social parents sampled, I accepted CERVUS's parentage assignment at the 95% confidence level for the parent pair with the highest trio LOD score and the lowest number of trio loci mismatches. For nestlings with only one social parent sampled, I accepted CERVUS's maternity or paternity assignment at 95% confidence for the female or male, respectively, with the highest LOD score and lowest number of parent-offspring loci mismatches. To double-check the quality of assignments for nestlings with only one parent

sampled, I calculated the difference between the two top-ranked females and between the two top-ranked males for the number of parent-offspring loci mismatches and the parent-offspring LOD score. I used assignments based on these criteria to categorize assignment results as WPO, QP, EPP, or BP. For nestlings with both parents sampled or only one parent sampled, I considered offspring to be WPO if CERVUS assigned them to both known social parents or the known social parent, respectively. For nestlings with both parents sampled, I considered offspring the results of QP if they were assigned to the social father but not the social mother. I considered nestlings to be the result of EPP if they were assigned to the social mother and to a male other than the social father, and I considered nestlings to be the result of BP if they were assigned to neither the social mother and father. Unassigned offspring were offspring with no confident assignments to any of the sampled parents. I included offspring for which neither parent was sampled to increase the chance of documenting EPP or BP by sampled adults.

All summary statistics are presented as mean \pm standard error (SE) unless otherwise noted. I used the modified Wald method (Agresti and Coull 1998) to calculate 95% confidence intervals for proportions of offspring and nests.

Results

Table 3.1. SNP characteristics*

Year	N			Mean percent loci typed	Mean PIC	Mean H_E	Mean H_o	NEP1	NEP2	NEPP
	Candidate Parents		Young							
	F	M								
2012	45	51	9	0.978	0.348	0.453	0.419	1.2 x 10^{-7}	6.1 x 10^{-13}	2.2 x 10^{-20}
2013	51	57	28	0.971	0.347	0.450	0.422	1.5 x 10^{-7}	7.0 x 10^{-13}	2.6 x 10^{-20}
2014	62	76	71	0.976	0.348	0.451	0.426	1.3 x 10^{-7}	6.2 x 10^{-13}	2.2 x 10^{-20}
2015	70	89	129	0.973	0.349	0.452	0.426	1.2 x 10^{-7}	5.9 x 10^{-13}	2.1 x 10^{-20}
2016	80	92	7	0.978	0.349	0.453	0.423	1.2 x 10^{-7}	5.8 x 10^{-13}	2.1 x 10^{-20}
2017	84	100	104	0.975	0.349	0.452	0.423	1.2 x 10^{-7}	5.8 x 10^{-13}	2.0 x 10^{-20}
Total	89	97	348	0.970	0.349	0.452	0.427	1.2 x 10^{-7}	5.8 x 10^{-13}	2.0 x 10^{-20}

*N = number of individuals genotyped; PIC = polymorphic information content; NEP1 = combined non-exclusion probability for first parent; NEP2 = combined non-exclusion probability for second parent; NEPP = combined non-exclusion probability for parent pair.

SNP characteristics

For blood samples ($N = 345$), the mean number of loci compared for top ranked parents was 140.1 ± 0.3 for mother-offspring pairs (range = 89-147), 138.9 ± 0.7 for father-offspring pairs (range = 73-147), and 143.3 ± 0.3 for trios (range = 96-147). For two dead nestling samples, the number of loci compared was 131 for both mother-offspring pairs, 128 for both father-offspring pairs, and 131 for both trios. The number of loci compared for one embryo from unhatched egg sample was 33 (22% of 147 identified SNPs) for the mother-offspring pair, father-offspring pair, and the trio. Non-exclusion probabilities were very low for all years (Table 3.1).

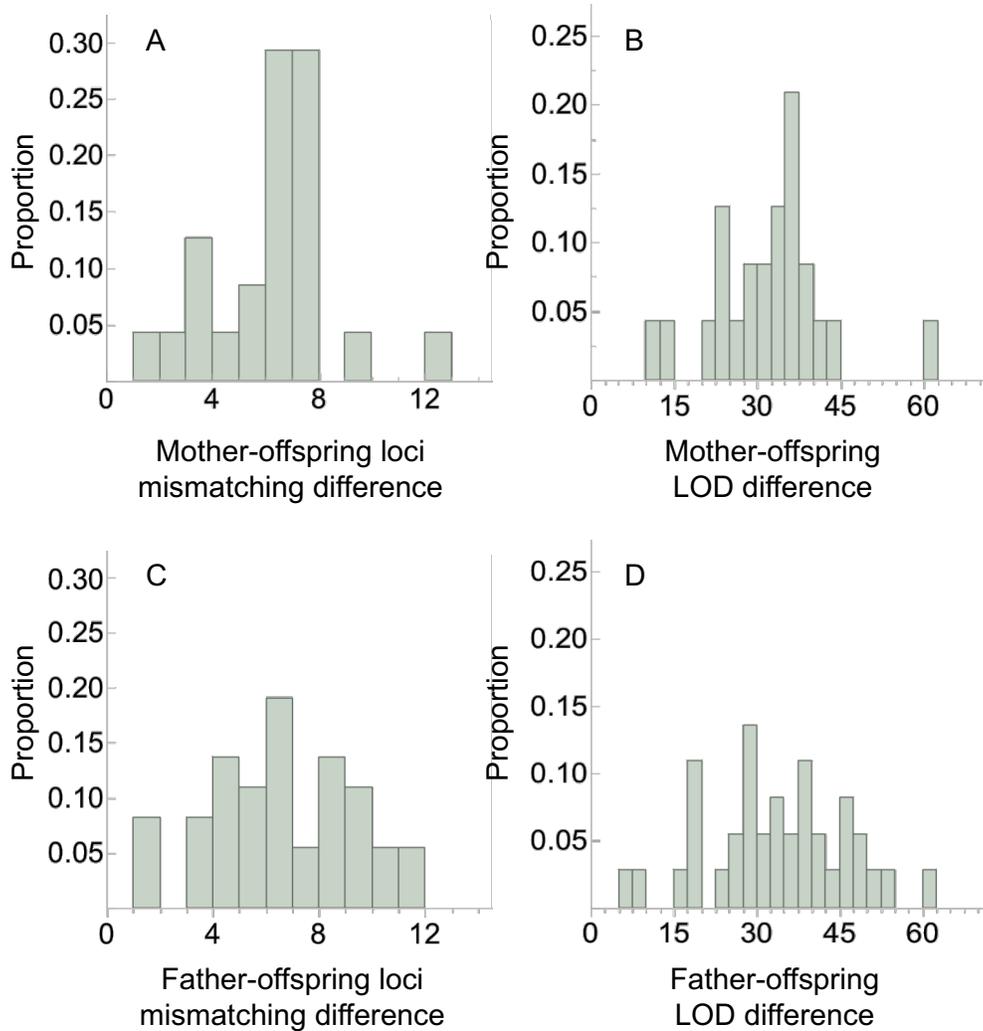


Figure 3.1. Differences between the top two scoring candidate mothers (A, B) and fathers (C, D) for parentage assignments of Hispaniolan Woodpecker nestlings with only the social mother ($N = 24$ nestlings from 9 nests) or father ($N = 37$ nestlings from 15 nests) sampled. The parent-offspring loci mismatching difference (A, C) was calculated by subtracting the number of loci mismatching with the highest ranked parent (social mother or social father) from the number of loci mismatching with the second highest ranked parent. The parent-offspring LOD difference (B, D) was calculated by subtracting the second highest ranked parent's LOD score from the highest ranked parent's LOD score.

Maternity

There was no genetic evidence for either QP or BP for nests where both parents were banded and sampled at the time of nesting. For 71 nestlings from 21 singular nests and 175 nestlings from 56 colonial nests, CERVUS assigned 100% of sampled nestlings to the social mother with 95% confidence based on the trio LOD score. These assignments included 7 females that nested only singularly, 26 females that nested only colonially, and 8 females that nested singularly and colonially in different seasons. The mean trio LOD score was 43.6 ± 0.8 (range = 10.6–69.2), and the mean trio loci mismatching was 4.2 ± 0.1 (range = 0–9).

There was also no genetic evidence for QP or BP for nests where the social mother was banded and sampled at the time of nesting but the father was not. For 5 nestlings from 2 singular nests and 19 nestlings from 7 colonial nests, CERVUS assigned 100% of offspring to the social mother ($N = 8$ females) with 95% confidence. The mean number of loci mismatching was 2.8 ± 0.4 (range = 0–6), and the mean pair LOD score = 14.5 ± 1.8 (range = 2.5–31.6). In all cases, the second highest ranking candidate female mismatched with the nestling at more loci (Fig. 3.1A) and had a lower LOD score (Fig. 3.1B) than the social mother. For 21 of these offspring (2 singular nests and 6 colony nests), the social father was not sampled and none of the sampled males matched. For 3 offspring in 1 colony nest, however, CERVUS assigned a male that was banded 1 year later but mated to the same social mother. No evidence for BP was found for 14 offspring from 4 singular nests and 38 offspring from 13 colonial nests where the social mother was not banded and sampled during the season. CERVUS assigned no females with a positive pair LOD score (mean top pair LOD = -27.5 ± 1.5 , range = -53.0– -5.5; mean loci mismatching = 10 ± 0.4 , range = 2–16).

Pooling offspring for which both parents were banded and sampled with offspring for

which only the social mother was banded and sampled, the 95% confidence interval for CBP was 0.0 + 1.7% ($N = 270$). The 95% confidence interval for CBP was 0.0 + 5.8% ($N = 76$) for offspring from singular nests and 0 + 2.3% ($N = 194$) for offspring from colonial nests. Pooling nests for which both parents were banded and sampled with nests for which only the social mother was banded and sampled, the 95% confidence interval for CBP was 0.0 + 5.1% ($N = 86$). The 95% confidence interval CBP was 0.0 + 16.9% ($N = 23$) for singular nests and 0.0 + 6.9% ($N = 63$) for colonial nests.

Paternity

There was no genetic evidence for EPP. As with females, with both parents banded and sampled at the time of nesting, CERVUS assigned 100% of sampled offspring to the social father with 95% confidence based on the trio LOD (71 offspring from 21 singular nests (16 pairs) and 175 offspring from 56 colonial nests (39 pairs)). The mean trio LOD score and mean trio loci mismatching were the same as those reported for females (see above).

There was also no evidence for EPP when the social father was banded and sampled at the time of nesting but the mother was not. For these samples, CERVUS assigned 12 nestlings from 4 singular nests (4 males) and 25 nestlings from 11 nests (10 males) at the 95% confidence level (mean number of loci mismatching = 1.4 ± 0.2 , range = 0–5; mean pair LOD score = 17.0 ± 1.0 , range = 2.8–32.3). The social father was assigned as the genetic parent in all cases ($N = 14$ males). In all cases, the second highest ranking candidate male mismatched with the nestling at more loci (Fig. 3.1C) and had a lower LOD score (Fig. 3.1D) than the social father. For 27 of these offspring, no candidate mothers were assigned by CERVUS. For 8 offspring from 5 colony nests and 2 offspring from 1 singular nest, CERVUS assigned 6 females with trio assignments at

the 95% confidence level. One of these females bred with the same male in that and three subsequent nesting seasons. Another of the females was not documented breeding again. The third female was documented breeding in later seasons with a different male because her former mate had died. No evidence was found for EPP for 6 offspring from 3 singular nests and 36 offspring from 12 colonial nests where the social father was not banded and sampled at the time of nesting. For these offspring, CERVUS assigned no males with a positive pair LOD score (mean = -20.2 ± 1.6 , range = -47.0 – -1.1 ; mean loci mismatching = 8.0 ± 0.4 , range = 4–15).

Pooling offspring for which both parents were banded and sampled with offspring for which only the social father was banded and sampled, the 95% confidence interval for EPO was $0.0 + 1.6\%$ ($N = 283$). The 95% confidence interval for EPO was $0.0 + 5.3\%$ ($N = 83$) for offspring from singular nests and $0 + 2.3\%$ ($N = 200$) for offspring from colonial nests. Pooling nests for which both parents were banded and sampled with nests for which only the social father was banded and sampled, the 95% confidence interval for EPP was $0.0 + 4.8\%$ ($N = 92$). The 95% confidence interval for EPP was $0.0 + 15.8\%$ ($N = 25$) for singular nests and $0.0 + 6.5\%$ ($N = 67$) for colonial nests.

Mating system

Overall, when both parents were sampled, CERVUS assigned all nestlings to the social parents with 95% confidence as the top-ranking trio. Assignments included 47 unique pairs representing 43 fathers and 41 mothers. Of assignments, 71 nestlings from 21 singular nests by 16 pairs were assigned to the social parents, and 175 nestlings from 56 colonial nests attempts by 39 pairs were assigned to the social parents. For the full sample of colonial nests, mean group size was 6.2 ± 3.7 pairs (range = 2–12 pairs, $N = 56$ nests). Eight pairs bred both singularly and colonially in

different years.

Non-genetic evidence for parasitic egg-laying

Of all nesting attempts, 4% were followed closely enough to detect brood parasitism via changes in clutch size ($N = 343$ nests). Given that Hispaniolan Woodpeckers, like all birds, lay at most one egg per day, clutch size changes in three nests that were closely followed ($N = 14$ nests) suggest possible egg-dumping. In one singular nest, five eggs appeared in three days. At another nest in a colony of two pairs, five eggs appeared in four days. At another nest in a colony of three pairs, a clutch of three eggs was completed on 14 April and a fourth egg appeared between 15 and 18 April. Eleven colony nests that were checked frequently increased in clutch size as expected, suggesting no parasitism.

Discussion

I found no relationship between patterns of genetic parentage and colony size in the Hispaniolan Woodpecker. Parentage analyses indicated that singular and colonial nests from the same population had no offspring resulting from CBP nor EPP, rejecting the opportunity hypothesis. These results demonstrate that despite high local breeding density that should correspond to high access to potential hosts and extra-pair mates, Hispaniolan Woodpeckers did not successfully parasitize nests nor achieve successful extra-pair fertilizations: that is, parentage was neither lost nor gained as a consequence of coloniality. Because male and female Hispaniolan Woodpeckers invest heavily in parental care, the results are consistent with the parental care hypothesis, which posits that both sexes are under strong selection to prevent parentage loss.

Alternative explanations and limitations

While the Hispaniolan Woodpecker's genetic mating system is consistent with the parental care hypothesis, the behavioral mechanism driving the observed patterns is unknown. The parental care hypothesis traditionally posits that reduction of parental care (i.e., retaliation) is a response to infidelity or CBP and selects for high within-pair parentage and low/no CBP. However, high levels of nest attendance might be selected for by pressures other than CBP and EPP, including defense against nest predators or nest site competitors. Consequently, social parents can easily detect and successfully defend against would-be brood parasites or potential extra-pair sires. At the same time, high nest attendance levels prevent both male and female breeders from seeking alternative reproductive strategies. Since females are constrained to producing no more than one egg per day, nesting females might not be able to successfully time parasitic egg-laying to match the breeding stage of a nearby host nest. And males forced to spend a lot of time in or near the nest might be constrained from leaving to mate with nearby extra-pair females. Colonial nesting itself might amplify selection for high nest attendance if colonies increase the attraction of predators or competitors. Defense against and failure to pursue CBP and EPP would therefore be consequences of high levels of nest attendance.

The above behavioral mechanism (high nest attendance) would apply if, for example, high predation risk selected for greater investment in nest defense resulting in more time spent at or near the nest. Similarly, intense competition for nest sites might also select for greater investment in cavity defense and higher levels of nest attendance. This mechanism is plausible for Hispaniolan Woodpeckers because cavity flooding reduces cavity availability in live *Roystonea* palms, flood immune, dead *Roystonea* palms are relatively rare (Chapter 1), and there appears to be intense competition over existing nest cavities (pers. obs.).

Differentiating between the behavioral mechanisms of retaliation and high nest attendance would be practical only to the extent that there is variability in the selective pressure proposed to favor high nest attendance levels. A comparative analysis of CBP and EPP across species that included nest attendance levels as a predictor variable and incorporated other relevant factors, such as nest predation levels and nest site competition intensity, might provide a fruitful means of discriminating between the two mechanisms. Traditionally, nest predation has been considered a selective pressure favoring CBP as a bet-hedging strategy (McRae 1997; Pöysä and Pesonen 2007), and recently, a similar argument has been made for predation selecting for EPP (Yuta and Koizumi 2016; Abbey-Lee et al. 2018). More work is clearly needed on the relationship between parental care and parentage and what factors, if any, mediate this relationship.

The methods used for parentage sampling did not rule out the possibility of failed parasitism. Parasitic eggs that are laid late (after clutch completion and incubation initiation) are substantially less likely to hatch than host eggs, which means that such late parasitic eggs comprise a larger proportion of eggs that fail to hatch than host eggs (Lyon 1993; Roy Nielsen et al. 2006). This disproportionate contribution of parasitic eggs to hatch failure is potentially relevant for Hispaniolan Woodpeckers because hatching success in this species was lower (mean = $81.9 \pm 1.8\%$; Chapter 2) than the mean hatchability (90.6%) found for a sample of 113 avian species (Koenig 1982).

Hispaniolan Woodpecker eggs that failed to hatch could, at least in part, represent poorly timed attempts at CBP. In the present study, ~31% of eggs in sampled nests went unsampled, primarily due to hatching failure and partial brood loss, and while all sampled hatched young (and one advanced embryo from an unhatched egg) were within-pair offspring, omitting

unhatched eggs and young lost before fledging might lead to an underestimate of CBP. Three cases of possible CBP were suspected based on clutch size observations; however, only a small proportion (4%) of all nesting attempts were followed closely enough to detect CBP in this way. In all but one of the few nests for which I collected unhatched eggs, degradation of DNA prevented genotyping so I was unable to determine whether unhatched eggs were sometimes (or often) parasitic. If any of these unhatched eggs were from brood parasites, the apparent complete failure of CBP as an alternative reproductive tactic would require further attention as it would suggest Hispaniolan Woodpeckers have evolved highly effective countermeasures (Lyon 2003, 2007; Shizuka and Lyon 2010). Nevertheless, the absence of genetically detected CBP and EPP is strong evidence that Hispaniolan Woodpeckers rarely if ever fledged extra-pair young, and such strategies do not represent successful means of pursuing reproduction in the species.

Parentage in woodpeckers and colonial species

Although the breeding biology of many woodpecker species, especially those breeding in the tropics, are poorly known (Mikusiński 2006), most species that have been sufficiently studied exhibit social monogamy (Winkler et al. 1995). However, only 9 (3.5%) of the 254 woodpecker species have been the focus of genetic parentage analyses (Table 3.2). Those species showed low to moderate levels of CBP (Wiebe and Kempnaers 2009; Dias et al. 2013), very low levels of EPP (Haig et al. 1994; Pechacek et al. 2005; Wink et al. 2011), or genetic monogamy (Michalek and Winkler 2001), and, in cooperatively breeding species, within-group paternity and maternity (Dickinson et al. 1995; Haydock et al. 2001). High breeding density might facilitate CBP in some woodpecker species (Wiebe and Kempnaers 2009), but that relationship was clearly not the case for Hispaniolan Woodpeckers. Furthermore, even the high breeding density associated

with coloniality was insufficient to promote extra-pair mating in this woodpecker. The parental care hypothesis is thus consistent with the high levels of paternal care and within-pair paternity exhibited in woodpeckers (Li et al. 2009). But the genetic mating systems of more picids, especially the two other colonial species, need to be studied before a robust comparative test of these hypotheses can be fruitfully attempted in the family.

Table 3.2. Genetic parentage of woodpecker species.

Species	CBP (<i>N</i> *)		EPP (<i>N</i> *)		Reference
	Offspring	Nests	Offspring	Nests	
<i>Melanerpes formicivorus</i>	2% (51)	5% (19)	0% (51)	0% (19)	(Dickinson et al. 1995)**
<i>M. striatus</i>	0% (270)	0% (86)	0% (283)	0% (92)	present study
<i>Colaptes auratus</i>	4% (367)	17% (53)	<1% (367)	2% (53)	(Wiebe and Kempenaers 2009)
<i>C. campestris</i>	12% (51)	10% (20)	0% (51)	0% (51)	(Dias et al. 2013)†
<i>Leuconotopicus borealis</i>	0%? (80)	0%? (44)	1% (80)	2% (44)	(Haig et al. 1994)
<i>Picooides tridactylus</i>	3% (40)	5% (19)	7% (46)	9% (22)	(Pechacek et al. 2005)
<i>P. tridactylus</i>	4% (80)	8% (26)	3% (80)	8% (26)	(Li et al. 2009)
<i>P. major</i>	0% (114)	0% (24)	0% (161)	0% (36)	(Michalek and Winkler 2001)
<i>P. medius</i>	0% (33)	0% (8)	0% (61)	0% (13)	(Michalek and Winkler 2001)
<i>Jynx torquilla</i>	0%? (292)	0%? (50)	1% (292)	2% (50)	(Wink et al. 2011)

**N* = number of offspring or nests sampled

** Single-male groups; † socially monogamous nests only

Among colonial species more broadly, the Hispaniolan Woodpecker adds to the growing list of species with high parental investment with no or little CBP or EPP (Quillfeldt et al. 2012), yet it remains to be seen whether the parental care hypothesis adequately explains variation in parentage across colonial nesters. Even among colonial seabirds with small clutches, large eggs, long durations of brood care, and high levels of parental care, CBP and EPP can be entirely absent in some species (Quillfeldt et al. 2001) but common in others (Ležalová-Piálková 2011). Hispaniolan Woodpeckers have larger clutches of proportionately smaller eggs compared to many colonial seabirds, and so clutch size and egg size might therefore be unimportant features in the evolution of CBP and EPP among colonial species. This hypothesis would require a proper comparative analysis.

Other key differences in natural history among species might drive variation in opportunity for CBP and EPP. For example, differences in the duration of time away from the nest or colony required for successful foraging might prevent successful timing of egg-dumping or extra-pair copulations. Differences in nest loss rates, whether due to predation, conspecific nest destruction, or weather, might also account for variation among colonial nesters if CBP and EPP function as bet-hedging strategies.

Some researchers have hypothesized that sexual selection drives the evolution of nesting aggregations and can account for variation in EPP among species (Morton et al. 1990; Wagner 1993, 1998; Wagner et al. 1996). This “hidden lek” hypothesis postulates that males in species with biparental care cluster territories because females prefer to copulate with high-quality males but cannot pair with them due to strict social monogamy. The complete absence of EPP, however, rejects the hidden lek hypothesis as a plausible mechanism for colony formation in Hispaniolan Woodpeckers and many other colonial birds (Masello et al. 2002; Quillfeldt et al.

2012; Indykiewicz et al. 2017). Indeed, few empirical studies have found support for the hidden lek hypothesis for coloniality (Morton et al. 1990; Hoi and Hoi-Leitner 1997). A satisfactory explanation for the evolutionary causes of interspecific variation in parentage systems among colonial nesters thus remains unclear.

Conclusions

Strict genetic monogamy and lack of CBP in the Hispaniolan Woodpecker demonstrate that the ways in which social organisms adapt to sociality depends upon more than the automatic detriments of group living. Interspecific differences in sharing of parental investment between the sexes might be an important determinant of whether CBP or EPP occur in a colonial species. Understanding the consequences of coloniality and, more broadly, of group living will ultimately depend on studying the genetic parentage systems of more colonial species, especially in lineages such as the woodpecker family where coloniality is itself rare.

Acknowledgements

I am very grateful to B. Butcher for her patient guidance and assistance with lab work and genomic data analyses. Many thanks to D. Thrasher for suggestions on bioinformatics and parentage logistics. I gratefully acknowledge the following individuals for providing invaluable assistance in the field: M. Angelucci, H. Boyle, C. Cerrilla, W. Coleman, A. Diaz, L. Emerson, N. Gilbert, A. Janik, K. Kauffman, T. Lacerda, A. Lascher-Posner, M. Larrieu, K. Larsen, C. Mathers-Winn, K. Nelsen, A. Occhialini, S. Schubert, H. Stapleton, M. Walters, A. Waterman-Snow, P. Werner, A. Wichtendahl. I thank W. D. Koenig, J. L. Dickinson, P. W. Sherman, M. S. Webster, H. K. Reeve, and I. J. Lovette for feedback on the manuscript and constructive

criticism at various points in the development of this project. J. L. Dickinson and H. K. Reeve in particular provided critical discussion on the manuscript's framing. F. Vermeulen and D. Akdemir at the Cornell Statistical Consulting Unit provided statistical advice. The following sources provided funding support: Cornell Lab of Ornithology Athena Fund, Department of Neurobiology Animal Behavior Research Grant, Society for the Study of Evolution Rosemary Grant Award, and Sigma Xi Grant in Aid of Research. I was also supported by the following fellowships during fieldwork: Charles Walcott Graduate Fellowship, Linda and Samuel Graduate Student Fellowship, Eleanore Stuart Graduate Fellowship, Andrew '78 and Margaret Paul Graduate Fellowship, Kramer Graduate Fellowship, Halberstadt Graduate Fellowship, Anne Marie Brown Summer Graduate Fellowship, and Lab of Ornithology Summer Graduate Fellowship. All research activities described here were approved by the Dominican Republic's Ministerio de Medio Ambiente y Recursos Naturales and conducted in accordance with IACUC protocol 2008-0185 at Cornell University.

References

- Abbey-Lee, R. N., Y. G. Araya-Ajoy, A. Mouchet, M. Moiron, E. F. Stuber, B. Kempenaers, and N. J. Dingemanse (2018). Does perceived predation risk affect patterns of extra-pair paternity? A field experiment in a passerine bird. *Functional Ecology* 32:1001–1010. doi: 10.1111/1365-2435.13052
- Agresti, A., and B. A. Coull (1998). Approximate is better than “exact” for interval estimation of binomial proportions. *American Statistician* 52:119–126. doi: 10.1080/00031305.1998.10480550
- Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics* 5:325–383.
- Arnold, K. E., and I. P. F. Owens (2002). Extra-pair paternity and egg dumping in birds: life history, parental care and the risk of retaliation. *Proceedings of the Royal Society B*:

Biological Sciences 269:1263–1269. doi: 10.1098/rspb.2002.2013

Beauchamp, G. (1997). Determinants of intraspecific brood amalgamation in waterfowl. *Auk* 114:11–21. doi: 10.2307/4089061

Brown, C. R. (2016). The ecology and evolution of colony-size variation. *Behavioral Ecology and Sociobiology* 70:1613–1632. doi: 10.1007/s00265-016-2196-x

Brown, C. R., and M. Bomberger Brown (1989). Behavioural dynamics of intraspecific brood parasitism in colonial Cliff Swallows. *Animal Behaviour* 37:777–796. doi: 10.1016/0003-3472(89)90063-8

Brown, C. R., and M. B. Brown (1988). A new form of reproductive parasitism in Cliff Swallows. *Nature* 331:66–68. doi: 10.1038/331066a0

Brown, C. R., and M. B. Brown (2001). Chapter 1: Avian coloniality. In *Current Ornithology* (Nolan, V., and C. F. Thompson, Editors). Kluwer Academic/Plenum Publishers, pp. 1–82. doi: 10.1007/978-1-4615-1211-0_1

Casey, J. (2010). Jarabacoa, Dominican Republic: climate, global warming, and daylight charts and data. *Climate-Charts.com*. [Online.] Available at <https://www.climate-charts.com/Locations/d/DR78000000000203.php>.

Catchen, J., P. A. Hohenlohe, S. Bassham, A. Amores, and W. A. Cresko (2013). Stacks: an analysis tool set for population genomics. *Molecular Ecology* 22:3124–3140. doi: 10.1111/mec.12354

Danchin, E., L.-A. Giraldeau, and R. H. Wagner (2008). Animal aggregations: hypotheses and controversies. In *Behavioural Ecology* (E. Danchin, L.-A. Giraldeau and F. Cézilly, Editors). Oxford University Press, Oxford, pp. 503–545.

Danchin, E., and R. H. Wagner (1997). The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology and Evolution* 12:342–347. doi: 10.1016/S0169-5347(97)01124-5

Dias, R. I., R. H. Macedo, D. Goedert, and M. S. Webster (2013). Cooperative breeding in the Campo Flicker II: patterns of reproduction and kinship. *The Condor* 115:855–862. doi: 10.1525/cond.2013.120143

- Dickinson, J., J. Haydock, W. Koenig, M. Stanback, and F. Pitelka (1995). Genetic monogamy in single-male groups of Acorn Woodpeckers, *Melanerpes formicivorus*. *Molecular Ecology* 4:765–770. doi: 10.1111/j.1365-294X.1995.tb00277.x
- Dixon, A., D. Ross, S. L. C. O'Malley, and T. Burke (1994). Paternal investment inversely related to degree of extra-pair paternity in the Reed Bunting. *Nature* 371:698–700. doi: 10.1038/371698a0
- Eadie, J., P. Sherman, and B. Semel (1998). Conspecific brood parasitism, population dynamics, and the conservation of cavity-nesting birds. In *Behavioral Ecology and Conservation Biology* (T. Caro, Editor). Oxford University Press, pp. 306–340.
- Garrod, H. M., and J. B. LaPergola (2018). Overlap in molt and breeding phenology in the Hispaniolan Woodpecker (*Melanerpes striatus*). *Ornitología Neotropical Special Is*:29–36.
- Gowaty, P. A., and W. C. Bridges (1991). Nestbox availability affects extra-pair fertilizations and conspecific nest parasitism in Eastern Bluebirds, *Sialia sialis*. *Animal Behaviour* 41:661–675. doi: 10.1016/S0003-3472(05)80904-2
- Haig, S. M., J. R. Waiters, and J. H. Plissner (1994). Genetic evidence for monogamy in the cooperatively breeding Red-cockaded Woodpecker. 295–303.
- Haydock, J., W. D. Koenig, and M. T. Stanback (2001). Shared parentage and incest avoidance in the cooperatively breeding Acorn Woodpecker. *Molecular Ecology* 10:1515–1525. doi: 10.1046/j.1365-294X.2001.01286.x
- Hoi, H., and M. Hoi-Leitner (1997). An alternative route to coloniality in the Bearded Tit: females pursue extra-pair fertilizations. *Behavioral Ecology* 8:113–119. doi: 10.1093/beheco/8.2.113
- Hoogland, J. L., and P. W. Sherman (1976). Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. *Ecological Monographs* 46:33–58.
- Huebner, D. P., and S. R. Hurteau (2007). An economical wireless cavity-nest viewer. *Journal of Field Ornithology* 78:87–92. doi: 10.1111/j.1557-9263.2006.00089.x
- Indykiewicz, P., P. Podlasczuk, and P. Minias (2017). Extra-pair paternity in the Black-headed Gull: Is it exceptional among colonial waterbirds? *Behaviour* 154:1081–1099. doi: 10.1163/1568539X-00003459

- Kalinowski, S. T., M. L. Taper, and T. C. Marshall (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* 16:1099–1106. doi: 10.1111/j.1365-294X.2007.03089.x
- Klug, H. (2018). Why monogamy? A review of potential ultimate drivers. *Frontiers in Ecology and Evolution* 6:1–6. doi: 10.3389/fevo.2018.00030
- Koenig, W. D. (1982). Ecological and social factors affecting hatchability of eggs. *The Auk* 99:526–536.
- Ležalová-Piálková, R. (2011). Molecular evidence for extra-pair paternity and intraspecific brood parasitism in the Black-headed Gull. *Journal of Ornithology* 152:291–295. doi: 10.1007/s10336-010-0581-1
- Li, M. H., K. Välimäki, M. Piha, T. Pakkala, and J. Merilä (2009). Extrapair paternity and maternity in the Three-toed Woodpecker, *Picoides tridactylus*: Insights from microsatellite-based parentage analysis. *PLoS ONE* 4:2–7. doi: 10.1371/journal.pone.0007895
- Ligon, J. D. (1993). The role of phylogenetic history in the evolution of contemporary avian mating and parental care systems. In *Current Ornithology* (D. M. Power, Editor). Springer, Boston, Massachusetts, pp. 1–46. doi: 10.1007/978-1-4615-9582-3_1
- Lyon, B. E. (1993). Tactics of parasitic American Coots: host choice and the pattern of egg dispersion among host nests. *Behavioral Ecology and Sociobiology* 33:87–100. doi: 10.1007/BF00171660
- Lyon, B. E. (2003). Egg recognition and counting reduce costs of avian conspecific brood parasitism. *Nature* 422:495–499. doi: 10.1038/nature01505
- Lyon, B. E. (2007). Mechanism of egg recognition in defenses against conspecific brood parasitism: American Coots (*Fulica americana*) know their own eggs. *Behavioral Ecology and Sociobiology* 61:455–463. doi: 10.1007/s00265-006-0273-2
- Lyon, B. E., and J. M. Eadie (2008). Conspecific brood parasitism in birds: a life-history perspective. *Annual Review of Ecology, Evolution, and Systematics* 39:343–363. doi: 10.1146/annurev.ecolsys.39.110707.173354
- Masello, J. F., A. Sramkova, P. Quillfeldt, J. T. Epplen, and T. Lubjuhn (2002). Genetic monogamy in Burrowing Parrots *Cyanoliseus patagonus*? *Journal of Avian Biology* 33:99–

103. doi: 10.1034/j.1600-048X.2002.330116.x

- McRae, S. B. (1997). A rise in nest predation enhances the frequency of intraspecific brood parasitism in a moorhen population. *Journal of Animal Ecology* 66:143–153. doi: 10.2307/6017
- Michalek, K. G., and H. Winkler (2001). Parental care and parentage in monogamous Great Spotted Woodpeckers (*Picoides major*) and Middle Spotted Woodpeckers (*Picoides medius*). *Behaviour* 138:1259–1285.
- Mikusiński, G. (2006). Woodpeckers: distribution, conservation, and research in a global perspective. *Annales Zoologici Fennici* 43:86–95.
- Miño, C. I., M. A. Russello, P. F. Mussi Gonçalves, and S. N. Del Lama (2011). Reconstructing genetic mating systems in the absence of parental information in colonially breeding waterbirds. *BMC Evolutionary Biology* 11. doi: 10.1186/1471-2148-11-196
- Møller, A. P. (2000). Male parental care, female reproductive success, and extrapair paternity. *Behav. Ecol.* 11:161–168. doi: 10.1093/beheco/11.2.161
- Møller, A. P., and T. R. Birkhead (1992). A pairwise comparative method as illustrated by copulation frequency in birds. *The American Naturalist* 139:644–656. doi: 10.1086/285348
- Møller, A. P., and T. R. Birkhead (1993). Cuckoldry and sociality: a comparative study of birds. *The American Naturalist* 142:118–140.
- Morton, E. S., L. Forman, and M. Braun (1990). Extrapair fertilizations and the evolution of colonial breeding in Purple Martins. *The Auk* 107:275–283. doi: 10.2307/4087610
- Pechacek, P., K. G. Michalek, H. Winkler, and D. Blomqvist (2005). Monogamy with exceptions: Social and genetic mating system in a bird species with high paternal investment. *Behaviour* 142:1093–1114. doi: 10.1163/156853905774405281
- Peterson, B. K., J. N. Weber, E. H. Kay, H. S. Fisher, and H. E. Hoekstra (2012). Double digest RADseq: An inexpensive method for de novo SNP discovery and genotyping in model and non-model species. *PLoS ONE* 7. doi: 10.1371/journal.pone.0037135
- Pöysä, H., and M. Pesonen (2007). Nest predation and the evolution of conspecific brood

- parasitism: from risk spreading to risk assessment. *The American naturalist* 169:94–104. doi: 10.1086/509943
- Quillfeldt, P., J. F. Masello, and G. Segelbacher (2012). Extra-pair paternity in seabirds: a review and case study of Thin-billed Prions *Pachyptila belcheri*. *Journal of Ornithology* 153:367–373. doi: 10.1007/s10336-011-0751-9
- Quillfeldt, P., T. Schmoll, H.-U. Peter, J. T. Epplen, and T. Lubjuhn (2001). Genetic monogamy in Wilson's Storm-Petrel. *The Auk* 118:242–248. doi: 10.2307/4089775
- Richardson, D. S., and T. Burke (1999). Extra-pair paternity in relation to male age in Bullock's Orioles. *Molecular Ecology* 8:2115–2126. doi: 10.1046/j.1365-294X.1999.00832.x
- Richardson, D. S., and T. Burke (2001). Extrapair paternity and variance in reproductive success related to breeding density in Bullock's Orioles. *Animal Behaviour* 62:519–525. doi: 10.1006/anbe.2001.1778
- Rohland, N., and D. Reich (2012). Cost-effective, high-throughput DNA sequencing libraries for multiplexed target capture. *Genome Research* 22:939–946. doi: 10.1101/gr.128124.111.22
- Rohwer, F. C., and S. Freeman (1989). The distribution of conspecific nest parasitism in birds. *Canadian Journal of Zoology* 67:239–253. doi: 10.1139/z89-035
- Roy Nielsen, C., P. G. Parker, and R. J. Gates (2006). Intraspecific nest parasitism of cavity-nesting Wood Ducks: costs and benefits to hosts and parasites. *Animal Behaviour* 72:917–926. doi: 10.1016/j.anbehav.2006.03.004
- Shellman-Reeve, J. S., and H. K. Reeve (2000). Extra-pair paternity as the result of reproductive transactions between paired mates. *Proceedings of the Royal Society B: Biological Sciences* 267:2543–2546. doi: 10.1098/rspb.2000.1318
- Shizuka, D., and B. E. Lyon (2010). Coots use hatch order to learn to recognize and reject conspecific brood parasitic chicks. *Nature* 463:223–226. doi: 10.1038/nature08655
- Short, L. L. (1974). Habits of three endemic West Indian woodpeckers (Aves, Picidae). *American Museum Novitates* 2549:1–44.
- Stanback, M. T., and W. D. Koenig (1994). Techniques for capturing birds inside natural

- cavities. *Journal of Field Ornithology* 65:70–75.
- Stewart, S. L. M., D. F. Westneat, and G. Ritchison (2010). Extra-pair paternity in Eastern Bluebirds: Effects of manipulated density and natural patterns of breeding synchrony. *Behavioral Ecology and Sociobiology* 64:463–473. doi: 10.1007/s00265-009-0862-y
- Suter, S. M., J. Bielańska, S. Röthlin-Spillmann, L. Strambini, and D. R. Meyer (2009). The cost of infidelity to female Reed Buntings. *Behavioral Ecology* 20:601–608. doi: 10.1093/beheco/arp037
- Thrasher, D. J., B. G. Butcher, L. Campagna, M. S. Webster, I. J. Lovette, and I. J. L. D. J. T. B. G. B. L. C. Michael S. Webster (2018). Double-digest RAD sequencing outperforms microsatellite loci at assigning paternity and estimating relatedness: A proof of concept in a highly promiscuous bird. *Molecular Ecology Resources* in press:1–13. doi: 10.1111/1755-0998.12771
- Wagner, R. H. (1993). The pursuit of extra-pair copulations by female birds: a new hypothesis of colony formation. *Journal of Theoretical Biology* 163:333–346. doi: 10.1006/jtbi.1993.1123
- Wagner, R. H. (1998). Hidden leks: sexual selection and the clustering of avian territories. *Ornithological Monographs* 49:123–145.
- Wagner, R. H., M. D. Schug, and E. S. Morton (1996). Condition-dependent control of paternity by female Purple Martins: Implications for coloniality. *Behavioral Ecology and Sociobiology* 38:379–389. doi: 10.1007/s002650050255
- Waldstein, A. L. (2012). An inexpensive camera system for monitoring cavity nests. *Journal of Field Ornithology* 83:302–305. doi: 10.1111/j.1557-9263.2012.00379.x
- Wallace, R. A. (1969). Sexual dimorphism, niche utilization, and social behavior in insular species of woodpeckers. Ph.D. dissertation, University of Texas, Austin, TX, USA.
- Westneat, D. F., and P. W. Sherman (1997). Density and extra-pair fertilizations in birds: A comparative analysis. *Behavioral Ecology and Sociobiology* 41:205–215. doi: 10.1007/s002650050381
- Westneat, D. F., P. W. Sherman, and M. L. Morton (1990). The ecology and evolution of extra-pair copulations in birds. *Current Ornithology* 7:331–369.

- Westneat, D. F., and I. R. K. Stewart (2003). Extra-pair paternity in birds: causes, correlates, and conflict. *Annual Review of Ecology, Evolution, and Systematics* 34:365–396. doi: 10.1146/annurev.ecolsys.34.011802.132439
- Wiebe, K. L. (2008). Division of labour during incubation in a woodpecker *Colaptes auratus* with reversed sex roles and facultative polyandry. *Ibis* 150:115–124. doi: 10.1111/j.1474-919X.2007.00754.x
- Wiebe, K. L., and B. Kempenaers (2009). The social and genetic mating system in flickers linked to partially reversed sex roles. *Behavioral Ecology* 20:453–458. doi: 10.1093/beheco/arn138
- Wink, M., D. Becker, D. Tolkmitt, V. Knigge, H. Sauer-Gürth, and H. Staudter (2011). Mating system, paternity and sex allocation in Eurasian Wrynecks (*Jynx torquilla*). *Journal of Ornithology* 152:983–989. doi: 10.1007/s10336-011-0684-3
- Winkler, H., and D. A. Christie (2018). Woodpeckers (Picidae). In *Handbook of the Birds of the World Alive* (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie and E. de Juana, Editors). Lynx Edicions, Barcelona, retrieved from <https://www.hbw.com/node/52286> on 2 August 2018.
- Winkler, H., D. A. Christie, and D. Nurney (1995). Woodpeckers: an identification guide to the woodpeckers of the world. In: Houghton Mifflin, Boston, Massachusetts.
- Wittenberger, J. F., and G. L. Hunt (1985). The adaptive significance of coloniality in birds. In *Avian Biology* (D. S. Farner and J. R. King, Editors). Academic Press, San Diego, pp. 1–78. doi: 10.1016/B978-0-12-249408-6.50010-8
- Yuta, T., and I. Koizumi (2016). Does nest predation risk affect the frequency of extra-pair paternity in a socially monogamous passerine? *Journal of Avian Biology* 47:153–158. doi: 10.1111/jav.00713