



Opportunity is not everything: genetic monogamy and limited brood parasitism in a colonial woodpecker

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Abstract

Avian social and genetic mating systems are influenced by parental care roles as well as by reproductive opportunities. Alternative reproductive tactics, including conspecific brood parasitism and extra-pair mating, are predicted to be most common when females have access to potential host nests and when adults have access to potential mating partners, respectively. We tested these predictions in the facultatively colonial Hispaniolan woodpecker (*Melanerpes striatus*), a socially monogamous species with biparental care. Up to 12 pairs may nest concurrently in the same tree or, less frequently, two adjacent trees, potentially facilitating both conspecific brood parasitism and extra-pair mating. Contrary to our predictions, genotyping with single-nucleotide polymorphisms (SNPs) revealed no evidence of extra-pair paternity in either solitary or colonial nests: all 307 nestlings in 101 broods were matched to their social parents. Two instances of apparent conspecific brood parasitism were detected via changes in clutch size, but these could not be confirmed genetically since none of the apparently parasitic eggs survived to hatching. Therefore, if conspecific brood parasitism did occur, it was not a successful route to reproduction: parents fledged only their genetic offspring. These results suggest that reproductive opportunities alone are insufficient to favor alternative reproductive tactics, and that genetic monogamy can persist despite locally high densities of breeding pairs. Other life-history traits, including high levels of nest attendance and male parental care, may constrain parasitism and extra-pair mating in this long-lived tropical species.

Significance statement

High breeding density, a feature of colonial nesting, should increase opportunities for infidelity and conspecific brood parasitism because of the close proximity of potential extra-pair mates and parasitic females. Yet, we found that Hispaniolan woodpeckers, which nest both solitarily and colonially (two or more pairs in the same tree) in the same population, were genetically monogamous and lacked successful brood parasitism. Colonial nesting is exceptionally rare in the woodpecker family, which is also characterized by high investment in male parental care, including nocturnal incubation. The essential role of paternal care for successful reproduction in the Hispaniolan woodpecker might have selected against extra-pair mating and conspecific brood parasitism despite the apparent ample opportunities provided by nesting so close to others.

Keywords Alternative reproductive tactics · Brood parasitism · Extra-pair paternity · *Melanerpes* · Parentage · Woodpeckers

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Introduction

The majority of bird species are socially monogamous and provide biparental care to their young (Cockburn 2006), but both males and females can use alternative reproductive tactics to opportunistically increase their reproductive success (Arnold and Owens 2002; Berger et al. 2014). Extra-pair mating (EPM), which leads to multiple paternity within the same brood of young, is widespread in birds (occurring in 76% of socially monogamous species; Brouwer and Griffith

2019) and may be viewed as an alternative mating tactic from the perspective of either sex (Griffith et al. 2002; Eliassen and Kokko 2008; Arct et al. 2015). Conspecific brood parasitism (CBP), in which females lay parasitic eggs into conspecific host nests, is a female alternative reproductive tactic that is also widespread but more difficult to detect (documented in ~250 bird species; Lyon and Eadie 2008). Both tactics occur in many lineages across the avian phylogeny, but their frequencies vary widely across and within species (Lyon and Eadie 2017; Brouwer and Griffith 2019). This variation, especially intraspecific variation, provides rich opportunities to test adaptive hypotheses for the origins and maintenance of avian mating behaviors and the selective pressures favoring and constraining parasitic reproduction.

One prominent hypothesis to explain variation in the occurrence of alternative reproductive tactics posits that they are constrained by opportunity, since both EPM and CBP are limited by the availability of local breeding pairs. Both EPM and CBP are therefore predicted to be more frequent in areas with high breeding densities (Rohwer and Freeman 1989; Westneat et al. 1990) and/or locally high synchrony among breeding pairs (Stutchbury and Morton 1995). Empirical support for this prediction is mixed: while some studies have found positive correlations between EPM and breeding density or synchrony (Stewart et al. 2010; Mayer and Pasinelli 2013), many have not (reviewed in Westneat and Sherman 1997; Casey et al. 2011; Ferretti et al. 2019). A recent meta-analysis of EPM rates across species failed to find a strong link with breeding density—or any other ecological predictor—and concluded that studies of different populations within the same species might be more fruitful than comparisons across species (Brouwer and Griffith 2019). Similarly, although breeding density is the most frequently reported correlate of CBP, phylogenetic patterns are typically stronger than environmental factors and much variation remains unexplained (Lyon and Eadie 2017).

Colonial and facultatively colonial species offer promising opportunities to examine the influence of breeding density on alternative reproductive tactics since clear predictions can be made regarding intraspecific variation. In theory, dense breeding aggregations could facilitate both EPM and CBP in at least two, non-mutually exclusive ways. First, both the number of potential extra-pair mates (of either sex) and the number of potential host nests should increase with colony size (Morton et al. 1990; Gowaty and Bridges 1991; Richardson and Burke 1999, 2001). Second, relative to solitary nests, colonies are predicted to be more conspicuous and attractive to floater (non-nesting) males and females who could act as extra-pair mates and parasites, respectively (Gowaty and Bridges 1991). All else being equal, therefore, EPM and CBP should increase with colony size, and, in facultatively colonial species, should be more frequent in colonies than in solitary nesting pairs (Brown and Brown

1988; Brown and Bomberger Brown 1989; Hoi and Hoi-Leitner 1997).

Alternatively, EPM and/or CBP might be constrained by life history, such that colony size is not obviously correlated with the frequency of either tactic. Parents who invest heavily in their young suffer greater costs from being parasitized, as do cuckolded males who raise extra-pair young (Yom-Tov 2001; Griffin et al. 2013; Hauber et al. 2020), and should be under stronger selection to resist rearing unrelated nestlings (Rohwer and Freeman 1989). Species with high levels of parental investment should therefore be characterized by strong pair bonds, vigilance at the nest, and decreased investment in alternative reproductive tactics (both EPM and CBP; Arnold and Owens 2002). By contrast, uncertainty over parentage should select for reduced parental investment. In the context of EPM, this argument has been formalized in 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). This combination of life-history traits—energetically expensive offspring, high levels of male parental care, and strong and long-lasting pair bonds—may help explain the near-absence of alternative reproductive tactics in some colonial lineages, such as seabirds (Quillfeldt et al. 2001, 2012).

In this study, we investigated the frequency of extra-pair paternity (EPP) and conspecific brood parasitism in the Hispaniolan woodpecker (*Melanerpes striatus*), a socially monogamous bird with biparental care. Hispaniolan woodpeckers are endemic to Haiti and the Dominican Republic and are facultatively colonial: pairs may nest singly or in small colonies of 2–26 pairs in separate cavities in the same tree or in two adjacent (~1 m apart) trees (Wallace 1969; Short 1974; LaPergola 2018). This provides an opportunity to test whether alternative reproductive strategies are more frequent in colonies than in solitary nests in the same population. Like the other species in the woodpecker family (Picidae) (Ligon 1993; Winkler et al. 1995), male Hispaniolan woodpeckers provide extensive parental care, including nocturnal incubation (JBL, personal observations). The young are altricial and remain dependent on their parents until fledging at ~32 days of age, and both sexes contribute to incubation, nest sanitation, nestling provisioning, and nest defense (Short 1974). Pairs may remain together for multiple breeding seasons (up to 5; JBL, unpublished data). Several aspects of their life history, therefore, suggest that alternative reproductive tactics may be constrained by

high levels of parental investment. In addition, nesting pairs aggressively defend their cavities against extra-pair conspecifics, which could further limit opportunities for alternative tactics, particularly parasitism. However, the Hispaniolan woodpecker is one of the only colonial woodpeckers ($N=3$ of 254 species), and, in addition to being one of the most abundant birds on Hispaniola (Latta et al. 2006), it exhibits a high breeding density compared to most woodpecker species (Selander 1966; Winkler et al. 1995). Therefore, we predicted that, if alternative reproductive tactics are limited by opportunities, both EPP and conspecific brood parasitism should be more frequent in colony-nesting birds than in solitary pairs in this population.

Methods

Study population and field methods

We studied Hispaniolan woodpeckers in Piedra Blanca, Dominican Republic (19°07'09.5"N, 70° 34' 54.8" W), between April 2012 and July 2017. This region is seasonal with two dry seasons and two wet seasons per year (Climate-data.org 2021); Hispaniolan woodpecker breeding encompasses the long wet season and the short dry season, with clutch initiation beginning in March, peaking in May, and tapering off in July (JBL, unpublished data). Vegetation at the site consists of pine (*Pinus occidentalis* and *Pinus caribaea*) and broadleaf wet forest fragments in a matrix of cattle pastures with isolated or clustered royal palms (*Roystonea hispaniolana*) and small fragments of secondary vegetation and “living tree” (predominantly *Gliricidia sepium*) fences. At our site, Hispaniolan woodpeckers nested overwhelmingly in royal palms (96% of nesting pairs, $N=176$) and occasionally in other substrates (e.g., *Cocos nucifera*, *Sabal* spp., *Syzygium jambos*, and fence posts: 4% of nesting pairs). Pairs typically raise one or two broods per year but might have up to four nesting attempts if first broods are unsuccessful, and the mean (\pm standard error, SE) clutch size in this population was 4.4 ± 0.1 eggs (range = 1–7; LaPergola 2018). Nests were located by searching for cavities and visible woodpecker activity. We inspected cavities using a penlight and small inspection mirror while climbing or with a wireless camera attached to a 15.2 m telescoping pole that broadcast images to a portable digital television (Huebner and Hurteau 2007; Waldstein 2012). We typically checked clutches 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).

We captured adult woodpeckers by “ambushing” adults in nest cavities (Stanback and Koenig 1994) or by mist-netting with an elevated dual-tower system (LaPergola 2018). Ambushing involved using light weight, hollow plastic balls

(Wiffle balls) covered in duct tape and tied to monofilament nylon line to cover cavity entrances after birds entered to feed nestlings, or pre-dawn if birds roosted the previous night. To reduce nest abandonment, we ambushed adults 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 and, using pulleys and ropes, raising two stacked 12 m mist nets in front of nesting trees. This method increased sampling to include woodpeckers nesting in substrates too unstable to climb.

Once captured, each bird received a unique combination of color and numbered aluminum leg bands. We banded a total of 186 adults (89 females, 97 males) and 363 nestlings. For some nests, the cavity entrance was large enough to manually remove nestlings, but for cavities with small entrances, 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 (Stanback and Koenig 1994). Hispaniolan woodpeckers typically returned to normal activity (feeding young, roosting, etc.) after alterations and continued to reuse such cavities within and across breeding seasons. During capture of adults and nestlings, we collected $\sim 50 \mu\text{L}$ 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 because partial brood loss was common in the population (see below). When possible, we also collected broken eggshells, intact eggs if they remained ≥ 2 days after the last chick was known to hatch, and dead nestlings; however, of these samples, only two dead nestlings and one unhatched egg containing a dead embryo yielded DNA of sufficiently high quality to be included in genetic analyses. The remaining 99% of offspring samples ($N=348$) were derived from blood.

We assigned social parents to nests using 2- or 3-h-long nest watches during the incubation and/or nestling phases of the nesting cycle. Nests were observed from burlap hides 10–15 m from the nest tree, and males and females were distinguished visually by plumage dimorphism. Observers recorded the identity of attending parents based on color-band combinations (or lack thereof). Only individuals that incubated eggs or young or provisioned nestlings were considered social parents. Additional birds occasionally visited cavities, but all of these visits were brief and appeared to be antagonistic rather than cooperative (i.e., the individual looked into the cavity but never entered, and, in some cases, they attacked parents and/or nestlings).

We defined nesting attempts as “solitary” or “colonial” based on the spatial clustering of pairs. The distribution of nearest-neighbor distances (NND) among nests in the population was highly bimodal, with nests in colonies being much closer together (mean \pm SD NND = 1.2 ± 1.2 m, range = 0.1–4.9 m, $N = 142$ nests) than solitary nests (mean \pm SD NND = 57.2 ± 34.1 m, range = 18.0–208.4 m, $N = 39$ nests). Thus, solitary nesting attempts were defined as nests with no other pairs on the same tree. Colonial nesting attempts were defined as nests where two or more nesting pairs used the same tree (or, in one case, in two adjacent trees ~ 1 m apart).

Over 6 years, we documented 343 nesting attempts and genotyped 348 offspring from 116 broods (95 offspring from 30 solitary broods and 253 offspring from 86 colonial broods; see Table S1 for summary of sampling by year). Of these, one or both social parents were genotyped for 307 offspring from 101 broods (86 offspring from 26 solitary broods and 219 offspring from 75 colonial broods; Table 1). These 101 broods included 65 unique parent pairs, including 46 pairs where both parents were banded (40 social mothers and 42 social fathers), 7 pairs where only the social mother was banded, and 14 pairs where only the social father was banded. The mean (\pm SD) colony size of sampled colonies was 4.2 ± 3.2 pairs (range = 2–12 pairs, $N = 27$ colony years: 14 colony trees sampled for a mean \pm SD of 1.9 ± 1.1 years, range = 1–4 years).

It was not possible to sample the entire pool of offspring for all nests because hatch failure and partial brood loss occurred in, respectively, 58% and 65% of nests in the study population (LaPergola 2018). Consequently, we sampled 67% ($N = 393$ eggs) of possible eggs across broods of known clutch sizes (mean \pm SD clutch size = 4.5 ± 1.0 eggs, $N = 88$ broods), and a mean (\pm SD) of $69 \pm 23\%$ of possible eggs per brood (range = 17–100%; 20% of these represented full broods). We sampled 86% ($N = 308$ offspring) of hatched offspring across broods with known hatching success ($N = 85$ broods) and a mean (\pm SD) of $87 \pm 18\%$ of hatched offspring per brood (range = 33–100%; 60% of these represented full broods). We were unable to record data blind because our study involved focal animals in the field.

Molecular analyses

We used the ddRAD-seq protocol described in Thrasher et al. (2018), which was modified from Peterson et al. (2012). Briefly, we first extracted genomic DNA from all samples using the Qiagen DNeasy® Blood and Tissue kit (Qiagen, Inc., Valencia, CA) and quantified sample concentrations via Qubit dsDNA BR assay kit (Life Technologies, USA). Sample extractions averaged (\pm SD) 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. Samples were pooled into groups of 20, purified with Sera-Mag Magnetic Speed-beads (Fisher-Sci), and size selected (450–600 bp) using BluePippin (Sage Science). Index groups (P2 adapters) and Illumina sequencing adapters were added using 11 PCR cycles, and cleaned reaction products were pooled in equimolar ratios to create a single library for sequencing on one lane of the Illumina HiSeq 2500 (100 bp single end).

We 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. We then removed reads containing at least a single base with a Phred quality score < 10 (using *fastq_quality_filter*), or if $> 5\%$ of the bases had a Phred quality score < 20 . We used the STACKS version 1.37 pipeline (Catchen et al. 2013) to demultiplex reads and assemble sequences de novo. Following the same STACKS protocol in Thrasher et al. (2018), we used *denovo_map.pl* to assemble and filter RAD loci and the *populations* module to further filter and export SNPs.

Parentage analyses

We used CERVUS version 3.0.7 (Kalinowski et al. 2007) to assign parentage for all nestlings for each year separately. We ran separate allele frequency and parentage simulation analyses (parent-pair, sexes known) for each year, including nestlings and candidate parents in the allele frequency

Table 1 Results of parentage assignments for Hispaniolan woodpeckers using 147 SNPs. For the cases when neither social parent was sampled, none of these offspring were assigned to other adults in the population known to be nesting elsewhere that year

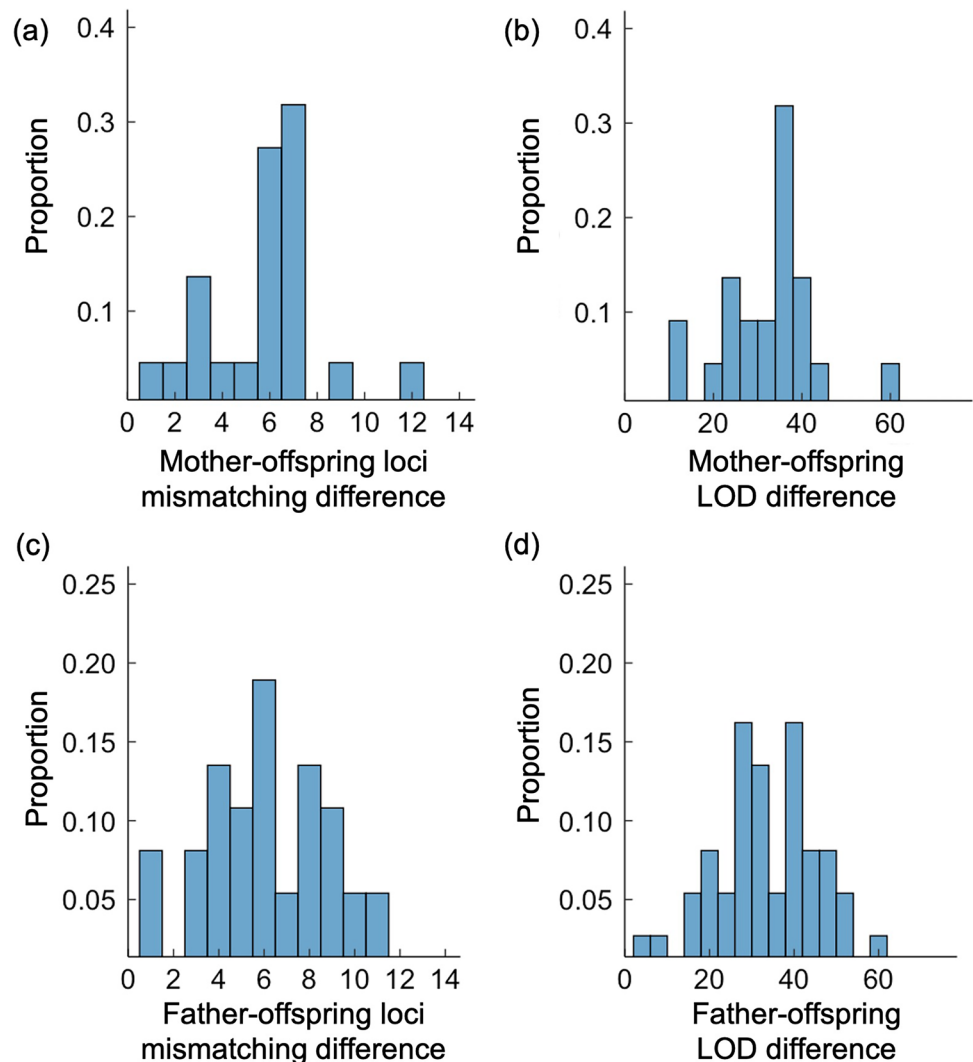
| | Sample sizes | | Assigned to social mother | | Assigned to social father | |
|-------------------------------|--------------------------|---------------------------|---------------------------|------------|---------------------------|------------|
| | Solitary | Colonial | Solitary | Colonial | Solitary | Colonial |
| Both social parents sampled | 71 nestlings (21 broods) | 175 nestlings (56 broods) | 71 (100%) | 175 (100%) | 71 (100%) | 175 (100%) |
| Female sampled, not male | 3 nestlings (1 brood) | 19 nestlings (7 broods) | 3 (100%) | 19 (100%) | — | — |
| Male sampled, not female | 12 nestlings (4 broods) | 27 nestlings (12 broods) | — | — | 12 (100%) | 27 (100%) |
| Neither social parent sampled | 9 nestlings (4 broods) | 32 nestlings (11 broods) | — | — | — | — |
| Total | 95 (30) | 253 (86) | | | | |

calculations. For each year's allele frequency analysis, we included only adults known to be alive that year, all nestlings sampled that year, and any nestlings that had been resighted after fledging in previous years (see Table S2 for allele frequency results broken down by year). For parentage simulation analyses, we used the following parameters: 10,000 offspring, 95% of candidate parents sampled, 85% of loci typed, and minimum number of loci typed was 74. We used the parent pair approach in CERVUS to identify the most likely parent pair, including as candidate parents all adults banded in the year that the nestlings were sampled or in previous years. Because Hispaniolan woodpeckers can be aged using molt limits (Garrod and LaPergola 2018), we also 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. For nestlings with both social parents sampled, we 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. The mean \pm SD trio LOD score was 43.3 ± 11.9 (range = 10.6–69.2), and the mean \pm SD trio loci mismatching was 4.2 ± 2.1 (range = 0–9). For nestlings with only one social parent sampled, we 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 check the quality of assignments for nestlings with only one parent sampled, we 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 (Fig. 1). We included offspring for which neither parent was sampled to increase the chance of documenting EPP or CBP by sampled adults.

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

Fig. 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 ($N=22$ nestlings from 8 broods) or father ($N=37$ nestlings from 16 broods) 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



Results

SNP characteristics

We genotyped 89 adult females, 97 adult males, and 348 nestlings at a total of 147 SNP loci. The mean proportion of loci typed per individual was 0.970. 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). This panel of SNPs had a polymorphic information content (PIC) of 0.349 (mean $H_E = 0.452$; mean $H_O = 0.427$) and high power for assigning parentage (mean non-exclusion probability for first parent, $NEP_1 = 1.2 \times 10^{-7}$; mean non-exclusion probability for second parent, $NEP_2 = 5.8 \times 10^{-13}$; mean non-exclusion probability for parent pair, $NEPP = 2.0 \times 10^{-20}$).

Genetic parentage

There was no genetic evidence for conspecific brood parasitism or extra-pair paternity in any of the broods sampled, in either solitary or colonial nests (Table 1). In all broods for which one or both social parents was genotyped ($N = 307$ nestlings in 101 broods), CERVUS assigned 100% of sampled nestlings to the social parent(s). For broods in which the social father was not sampled, CERVUS did not assign any extra-pair males as the genetic father, and for broods in which the social mother was not sampled, CERVUS did not assign any other females as the genetic mother. In addition, there were 7 nestlings from 3 solitary broods and 17 nestlings from 6 colonial broods for which CERVUS assigned parentage, even though the social parents had not been genotyped at the time of nesting. In all of these cases, the assigned genetic parents were apparently the social parents, but they were trapped and sampled after the nesting attempt (either later in the same breeding season, or in subsequent years; Table S3). Therefore, these assignments were consistent with within-pair parentage. For example, in one colonial nest when the social father had not been sampled during nesting, CERVUS assigned all three nestlings to a male that was banded the next year but mated to the same social mother that had been assigned (suggesting that the same pair had remained together for 2 years and CERVUS correctly identified the social father as the genetic father).

Although we identified no instances of CBP or EPP, we estimated 95% confidence intervals in order to place upper bounds on the frequency of each tactic in our population, given our sample sizes. Pooling offspring for which both parents were banded and sampled with offspring for

which only the social mother was banded and sampled, the overall 95% confidence interval for CBP was $0.0 + 1.7\%$; $N = 268$. These estimates were similarly low for solitary nests ($0.0 + 5.8\%$; $N = 76$) and colonial nests ($0 + 2.3\%$; $N = 194$). At the brood level, the overall 95% confidence interval for CBP was $0.0 + 5.1\%$; $N = 86$ (solitary nests: $0.0 + 16.9\%$; $N = 22$; colonial nests: $0.0 + 6.9\%$; $N = 63$).

Estimates of extra-pair paternity were also low. Pooling offspring for which both parents were banded and sampled with offspring for which only the social father was banded and sampled, the overall 95% confidence interval for EPM was $0.0 + 1.6\%$; $N = 285$ (solitary nests: $0.0 + 5.3\%$, $N = 83$; colonial nests: $0 + 2.2\%$, $N = 202$). At the brood level, the overall 95% confidence interval for EPM was $0.0 + 4.8\%$; $N = 93$ (solitary nests: $0.0 + 15.8\%$, $N = 25$; colonial nests: $0.0 + 6.4\%$, $N = 68$).

Non-genetic evidence for parasitic egg-laying

Only 4% of nesting attempts were followed closely enough to detect brood parasitism via changes in clutch size ($N = 14$ of 343 nests), due to time constraints in the field. Since Hispaniolan woodpeckers lay at most one egg per day, the appearance of more than one egg in a day is suggestive of CBP (an “irregular sequence of appearance of eggs” is commonly inferred to indicate parasitism; Yom-Tov 1980, p. 95). We detected such irregularities at 2 of 14 nests (14.3%). In one solitary nest, five eggs appeared in 3 days, but only two eggs hatched; the other three eggs remained in the cavity intact for 4 days, at which point we collected them. Unfortunately, we were unable to sample either of the nestlings from this nest, and we did not attempt to genotype the failed egg samples. At a second nest in a colony of two pairs, five eggs appeared in 4 days. From this second nest, four of the eggs hatched on 18 May 2015; four chicks and no eggs were present on 26 May 2015; and on 27 May 2015, the nest cavity had filled with water, killing all the chicks and preventing sampling. Observations from a third nest in a colony of three pairs were also suggestive of CBP. For this nest, a clutch of three eggs was completed on 14 April and still comprised three eggs on 15 April, but a fourth egg was present in the nest at the next check on 18 April. Only three of the eggs in this nest hatched, all three of which were sampled as nestlings and assigned to their social parents. We sampled the unhatched egg, which contained a mostly developed chick, but this sample yielded no usable SNPs.

Discussion

We found no difference in the frequency of EPP or CBP in solitary vs. colonial pairs of Hispaniolan woodpeckers. Genetic analyses failed to identify any offspring in either

solitary or colonial nests that were produced by extra-pair birds, although irregularities in the laying sequence at two (possibly three) nests were suggestive of attempted parasitism. These results indicate that, despite facultative coloniality and a locally high breeding density that should enable access to extra-pair mates and potential hosts, Hispaniolan woodpeckers did not successfully achieve extra-pair fertilizations or parasitic laying.

Several potential mechanisms could explain the apparent rarity of alternative reproductive tactics in this population. The relatively high levels of parental investment and nest attendance observed in this species appear to result from both life-history and ecological factors, and may constrain both EPM and CBP. For example, Hispaniolan Woodpeckers exhibit some life-history characteristics that should reduce selection for alternative reproductive behaviors, such as altricial young and high levels of male parental care, including essential male nocturnal incubation (similar to other woodpeckers, discussed below). Nestling Hispaniolan Woodpeckers hatch naked and remain thermally dependent on their parents until ca. 21 days post-hatch (JBL, personal observations). Ecologically, the high population densities of Hispaniolan woodpeckers may lead to intense competition for nest sites, which could also favor investment in cavity defense and high levels of nest attendance (but see Semel and Sherman 2001). Colonial nesting could therefore reduce, rather than increase, opportunities for alternative mating. This hypothesis is plausible in this study population because Hispaniolan woodpeckers preferentially nest in dead royal palms, which are rare relative to live royal palms (LaPergola 2018). Cavities in live palms are prone to flooding, and cavities in dead trees tend to erode and be lost comparatively quickly, creating competition for nest sites in the few available dead palms. In fact, concurrent analyses suggest that nest site limitation is a main driver of coloniality in this species and that pairs aggressively compete for existing cavities (JBL unpublished data). Pairs, and possibly unmated males, attempt to usurp occupied cavities by evicting the residents, which involves attacking nestlings and male (but not female) egg-tossing (JBL personal observations). If competition over cavities necessitates high levels of nest attendance, this could prevent male and female breeders from seeking alternative reproductive opportunities and simultaneously facilitate detection of would-be extra-pair sires and brood parasites by social parents. With regard to CBP, it is also possible that the fitness payoffs of parasitism are simply too low for it to be a profitable strategy for females to pursue, even as a best-of-a-bad-job. The high fecundity of woodpeckers in this population (up to 4 nesting attempts per year) suggests that the energetic costs of providing parental care are not the primary limit on reproductive

output, so the marginal benefits of parasitic laying may fail to outweigh the costs.

Finally, it is possible that limitations in our field sampling methods reduced detection of alternative reproductive tactics, particularly CBP. We were unable to sample approximately 33% of eggs in sampled nests, primarily due to hatching failure and partial brood loss. Hatching success in this population was relatively low (mean \pm SE = $81.9 \pm 1.8\%$; LaPergola 2018) compared to the mean hatching success reported for a sample of 133 bird species (90.6%; Koenig 1982). Hatching failure could, in part, represent failed attempts at brood parasitism, since parasitic eggs that are laid late (after clutch completion and incubation initiation) are substantially less likely to hatch than host eggs (Lyon 1993; Roy Nielsen et al. 2006). Consistent with this hypothesis, irregularities in the laying sequence at one nest suggested CBP, but the apparently parasitic egg failed to hatch despite the rest of the clutch hatching. Although we collected unhatched eggs for genetic analysis, degradation of DNA of all but one prevented genotyping, so genetic identification of parasitic unhatched eggs was not possible. Nevertheless, the absence of parasitic nestlings is strong evidence that successful parasitism was rare. For unhatched eggs to have significantly affected our estimates of CBP, parasitic eggs or offspring would have experienced higher mortality before sampling than genetic offspring. This could happen via recognition and discrimination (Lyon 2003; Shizuka and Lyon 2010), but Hispaniolan woodpecker eggs are immaculate white so discrimination through visual cues is unlikely. The more likely explanation is simply that unhatched eggs are not disproportionately parasitic and that the relatively high hatch failure observed is driven by some other factor(s) (Koenig 1982; Assersohn et al. 2021).

Similarly, it is possible that we failed to detect some instances of EPM since some (14%) nestlings hatched but were depredated or disappeared before sampling; but in this case, there is no reason to suspect that this should have biased our estimates of the overall frequency of EPM. As with CBP, the absence of genotyped extra-pair young suggests that EPM is rarely a successful alternative mating tactic. This point is underscored by the fact that we used a conservative exclusion criterion (i.e., 95% confidence cutoff), which translates to a greater chance of excluding true parents, and thus the absence of genetically detected EPM and CBP is even more compelling.

The 254 species in the woodpecker family (Picidae) are predominantly socially monogamous, although the natural history of many species remain undescribed. A minority of species are known to nest in cooperatively polygamous groups in which multiple males and females reproduce in a single nest and share parental care (Dias et al. 2013; Koenig et al. 2016) or cooperatively breeding families in which a breeding pair is assisted by related and (less

commonly) unrelated non-breeding helpers (Walters 1990; Haig et al. 1994). Despite this variation in breeding group composition, all these woodpeckers exhibit high levels of male parental care and nocturnal incubation by males (Ligon 1993; Winkler et al. 1995). This trait is predicted to reduce the frequency of EPM by nesting males (Li et al. 2009) but potentially facilitate CBP or quasi-parasitism (in which an extra-pair female mates with a nesting male and lays her egg in his nest), since male-biased incubation should theoretically enable nesting females to pursue reproduction elsewhere (Vehrencamp 2000). Although genetic parentage has been examined for only 9 woodpecker species (Table S4), the data available are generally consistent with this hypothesis. Genetic monogamy or low extra-pair paternity is reported in the socially monogamous species (Haig et al. 1994; Michalek and Winkler 2001; Pechacek et al. 2005; Wiebe and Kempnaers 2009) and zero or low extra-group paternity in the cooperatively polygamous species (Dickinson et al. 1995; Haydock et al. 2001; Dias et al. 2013). Rates of CBP are similarly low in most species (e.g., Haig et al. 1994; Michalek and Winkler 2001), but moderately higher in others (e.g., Wiebe and Kempnaers 2009; Dias et al. 2013). The reasons for interspecific variation in CBP rates among woodpeckers remain unknown. Wiebe and Kempnaers (2009) speculated that the combination of high breeding density, large clutch sizes, and relatively small, cheap eggs facilitate CBP in the Northern Flicker (*Colaptes auratus*), which exhibits the highest CBP (17% of broods) known among woodpeckers. Our study, the first to examine parentage in a colonial woodpecker, provides a valuable addition to this literature by revealing that high breeding densities are apparently insufficient to promote EPM in this clade. However, more data are needed on the other members of this family, particularly the two other colonial species, to enable robust comparative studies.

More broadly, our results are consistent with an emerging consensus that patterns of EPM across birds are more strongly influenced by phylogeny than by proximate constraints, and that high rates of EPP are not necessarily characteristic of non-passerines (Macedo 2008; Brouwer and Griffith 2019; Riehl 2020). Despite the seemingly obvious opportunities for alternative reproduction in colonies, colonially nesting birds do not have consistently higher rates of either EPM or CBP than non-colonial species (Griffith et al. 2002; Brouwer and Griffith 2019), nor did our study find support for such a difference intraspecifically. We suggest that the lack of alternative reproductive behaviors observed in this study may be better explained by a suite of life-history traits—including high levels of parental investment, male parental care, and pair bonds that can persist for multiple breeding seasons—than by immediate opportunities.

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Declarations

Ethics statement 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.

Conflict of interest The authors declare no competing interests.

Data availability statement The genotype data and parent and offspring ID data are available at <https://doi.org/10.17605/OSF.IO/FNU5K>.

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