IBIS
international journal of avian science
Ibis (2026)
doi: 10.1111/ibi.70051

Fine-scale genetic structure in co-operatively breeding Palmchats (*Dulus dominicus*) suggests mixed kinship in compound nests

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Fine-scale genetic structure in animal populations can create opportunities for both kin-directed co-operation and kin competition. Knowledge of kinship is therefore key to understanding the selective pressures shaping sociality as well as the effects of social behaviour on local genetic structure. Here we investigate patterns of relatedness in compound nests of Palmchats *Dulus dominicus*, a co-operatively breeding bird endemic to Hispaniola. Compound nests are large stick structures that contain separate nesting chambers attended by different breeding pairs and putative family groups (breeding pairs and non-breeding helpers); nests are occupied and maintained year-round. We captured and genetically sampled 102 Palmchats from 10 compound nests (range = 6–17 birds captured per nest) and genotyped them with 779 single-nucleotide polymorphisms (SNPs). Both relatives and non-relatives were associated with compound nests: the majority of dyads were unrelated, but some dyads were consistent with first- or second-order kin relationships. Average genetic relatedness, although low, was higher within nests than between nests for all types of dyads (female–female, female–male and male–male). Patterns of spatial autocorrelation revealed no association between relatedness and distance between compound nests for either males or females. The population exhibited weak (though significant) overall genetic structuring as measured by F_{ST}, indicating that low levels of genetic variance within the population existed between compound nesting groups. However, we detected no significant patterns of isolation-by-distance nor significant differences between the sexes. Groups of Palmchats using compound nests appear to be composed of kin and non-kin, suggesting that social nesting involves both direct and indirect fitness benefits.

Keywords: colonial nesting, Dominican Republic, Dulidae, population genetics, social evolution.

Genetic structure in animal populations occurs when gene flow is limited, resulting in the spatial clustering of relatives and decreased genetic relatedness with geographical distance (isolation-by-distance; Wright 1943). Limited gene flow can be a consequence of demographic processes (Méndez *et al.* 2011), physical barriers to dispersal (Adams & Burg 2015), constraints on the availability of mates (Lackey *et al.* 2024) or breeding habitat (Row *et al.* 2018), or behavioural traits that restrict dispersal, such as natal philopatry (Piertney *et al.* 1999, Avise 2004, Temple *et al.* 2006, Garroway *et al.* 2013, Dawson Pell *et al.* 2021). Conversely, genetic structure can also play a crucial role in the evolution of social and mating behaviours, because local clustering of kin can create opportunities for kin-directed co-operation (Hamilton 1964, Hatchwell 2010, Leedale *et al.* 2018, Morinay *et al.* 2025) as well as kin competition

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(Taylor 1992, Ronce *et al.* 2000, Taylor & Buckling 2010) and inbreeding (Koenig & Haydock 2004, Riehl & Stern 2015). Knowledge of kin relationships between individuals is therefore key to understanding their social relationships as well as local genetic structure.

As birds are capable of long-distance dispersal, wild populations were previously assumed to have little fine-scale genetic structure (Avise 1996), but recent work has revealed significant genetic structuring in bird populations across a diverse array of social systems (reviewed in Hatchwell 2010). These range from co-operative breeders with kin-biased helping, in which the importance of family living has long been recognized (Painter *et al.* 2000, Double *et al.* 2005, Temple *et al.* 2006, Aguillon *et al.* 2017), to other types of social associations that are not traditionally considered to be co-operative breeding, including nesting colonies (McKinnon *et al.* 2006), male leks (Höglund & Shorey 2003, Bouzat & Johnson 2004) and non-breeding flocks (Lee *et al.* 2010). In some cases, local genetic structure is presumed to be adaptive and yield indirect fitness benefits (Cornwallis *et al.* 2009), whereas in others it may result from constraints on breeding opportunities or other, non-adaptive limitations on dispersal (Sonsthagen *et al.* 2010). However, local genetic structure is not universal in birds: other studies of similar aggregations have found little or no evidence of genetic structure, even in species with strong natal philopatry (Austin *et al.* 1994), stable lekking associations (Lebigre *et al.* 2008) or interannual site fidelity (Arnberg *et al.* 2015). This variation suggests that, at least in some cases, the costs of interacting with kin (including kin competition and inbreeding) may favour dispersal that effaces local genetic structure. Alternatively, the direct fitness benefits of dispersal (e.g. to larger aggregations or to more favourable habitats) may outweigh any potential indirect fitness benefits that might result from remaining with relatives (Lebigre *et al.* 2008).

Very few studies have investigated fine-scale genetic structure in birds that breed in compound nests, a phenomenon that provides an opportunity to examine the selective pressures favouring social reproduction. Compound nesting occurs when multiple individuals collectively build and defend a single, large nest (i.e. nest building and nest defence are co-operative public goods), but smaller breeding units or pairs tend young within separate chambers inside the nest. Compound nesting has evolved independently in at least four lineages of birds (including Monk Parakeets *Myiopsitta monachus* (Dawson Pell 2021, Dawson Pell *et al.* 2021), Sociable Weavers *Philetarius socius* (Covas *et al.* 2006, Leighton & Echeverri 2016), buffalo weavers *Bubalornis niger* and *B. albirostris* (Winterbottom *et al.* 2001), and Palmchats *Dulus dominicus* (Wetmore & Swales 1931, Schubert *et al.* 2022)). All species share a similar nest architecture—compound nests are large, arboreal stick structures with separate enclosed chambers used for nesting or roosting—and all are facultative co-operative breeders, with breeding units containing multiple same-sex breeding adults, non-reproductive helpers or both. Furthermore, compound nests are often spatially clustered, with different compound nests located in adjacent or nearby trees. Social interactions may therefore occur at several levels of social organization, including the breeding unit, the compound nest or among adjacent nests (Dhondt *et al.* 2019).

Patterns of kinship, group composition and population genetic structure are well described for only two compound nesting species. In Monk Parakeets, breeding units contain a mix of relatives and non-relatives, but at least in an introduced population, short dispersal distances (median natal dispersal distances of 15 and 144 m for males and females, respectively) and high breeding site fidelity led to significant genetic structuring over small spatial scales (< 400 m), particularly among males (Dawson Pell *et al.* 2021). In Sociable Weavers, in contrast, while breeding units tend to be composed of relatives (a breeding pair and related non-breeding helper(s); Covas *et al.* 2006), genetic structuring was weak within compound nests and across larger spatial scales (~6 km) (Leighton & Echeverri 2016). The population genetic structure is consistent with the comparatively longer dispersal distances observed in this species (median natal dispersal distances of 641.5 and 751.2 m for males and females, respectively, in a different population; Van Dijk *et al.* 2015). Genetic evidence from Red-billed Buffalo Weavers *Bubalornis niger* is limited: co-operative males in polygynandrous groups are typically unrelated, but genetic structure is not described at the level of the compound nest or population (Winterbottom *et al.* 2001). Overall, therefore, compound nesting typically involves multi-tiered co-operative interactions between both kin and non-kin, but analyses of

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kinship and genetic structure in these societies are scarce.

In this study, we investigate patterns of genetic relatedness and population genetic structure in the Palmchat, an abundant but understudied bird endemic to Hispaniola (Haiti and the Dominican Republic). Palmchats build large stick nests, typically in palm trees, that contain between one and five separate chambers that are used by different breeding units (we define 'compound nests' as those containing more than one chamber; Keys 1991). Each compound nest is collectively built and defended by multiple individuals, but breeding pairs are thought to be socially monogamous and tend their own young within separate chambers. Data on Palmchat breeding biology and natural history are extremely sparse. Previous research indicates that they are facultative co-operative breeders: most social breeding units comprise three to five individuals, but it is not known whether helpers are retained offspring of the breeding pair or non-relatives (Keys 1991). Furthermore, irregularities in clutch size suggest that more than one female may occasionally lay eggs in the same clutch (Temple 2013). No detailed data are available on dispersal, group composition or genetic structure within compound nests or at larger spatial scales.

Our goals in this paper were: (i) to quantify kin relationships and patterns of genetic relatedness within and between compound nests to test the hypothesis that social nesting is associated with fine-scale genetic structure; and (ii) to infer patterns of natal philopatry or dispersal that could give rise to the observed patterns. If compound nesting groups are primarily composed of relatives, we predicted that: (a) genetic relatedness within nesting groups should be significantly higher than average genetic relatedness in the study area, and (b) compound nesting groups should contain closely related dyads (first- and second-order kin relationships). If offspring are more likely to disperse to nearby nests than to nests that are comparatively far away, and/or if Palmchats exhibit strong natal philopatry, we predicted that: (a) genetic relatedness between individuals should decline with geographical distance, (b) compound nests should exhibit significant genetic structure as measured by F_{ST} and (c) genetic differentiation should be positively correlated with geographical distance, as measured by isolation-by-distance (Temple *et al.* 2006, Van Dijk *et al.* 2015).

To address these questions, we captured and genetically sampled adult Palmchats at 10 compound nests at a field site in the Dominican Republic and genotyped them using next-generation sequencing techniques. First, to test the hypothesis that individuals within compound nests are more closely related to each other than expected by chance, we calculated pairwise genetic relatedness between dyads of individuals within and between compound nests. Second, to test the hypothesis that limited dispersal creates local genetic structure (at the scale of the compound nest or the study area), we used spatial autocorrelation analyses to quantify genetic relatedness as a function of geographical distance between compound nests, and computed differentiation resulting from genetic structure (F_{ST}) and tested for isolation-by-distance within our c. 500-ha study area. For each question, we also conducted separate analyses for males and females to test for possible sex biases in dispersal or philopatry.

METHODS

Study site and sample collection

We trapped groups of adult Palmchats in Piedra Blanca, La Vega, Dominican Republic (19.119306°N, 70.581889°W), in 2016 and 2017. Vegetation at this site consists of pine (*Pinus occidentalis* and *P. caribaea*) and broadleaf wet forest fragments in a matrix of cattle pastures with isolated or clustered royal palms and small fragments of secondary vegetation and 'living tree' (predominantly *Gliricidia sepium*) fences. Palmchat compound nests were located in Royal Palms *Roystonea hispaniolana* and Cana Palms *Sabal domingensis*. We sampled 10 groups associated with distinct compound nests (one in mid-April 2016 and nine between mid-April and early July 2017; Fig. S1) across our c. 500-ha study area, with a maximum distance of 2740 m between nests. Although compound nests are often spatially clustered into loose aggregations (Kent *et al.* 2020), these clusters are often difficult to define, so we conducted our analyses at the level of the compound nest. We captured birds using two mist-net systems that allowed netting at maximum heights of 9.1 m (https://batmanagement.com/products/triple-high-mist-net-pole-system) or 15.2 m (Garrod & LaPergola 2018). We adjusted sampling

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effort at each nest to try to catch a similar number of individuals from each compound nest, although our sampling did not perfectly balance the number of individuals from each nest. Palmchat nests are abundant in the study area, and we did not sample all of the individuals associated with each compound nest, nor all of the nests within the study area. We collected ~80 μL of blood from the brachial vein and stored samples at room temperature in 2% SDS lysis buffer. Each individual also received a unique four-band combination (one numbered aluminium band and three coloured plastic bands). In total, we sampled 102 individuals (46 females and 56 males) with a mean (± sd) of 10.2 ± 3.9 individuals (range = 6–17 individuals) per compound nest (see Table S1 for details). All of the individuals sampled in this study were adults (i.e. none were offspring from the current year). Thus, any relatives detected are either adults breeding in the same compound nest or non-dispersed offspring delaying breeding, not simply fledglings trapped with their parents.

Although the Palmchat's breeding phenology remains poorly characterized, the breeding season is thought to last from March through June (Wetmore & Swales 1931, Keys 1991). We can confirm that our capture periods overlapped with the breeding season based on the following observations. Some of our captured birds possessed a vascularized brood patch (30%, $n = 46$ females) or an egg visible in the abdomen (4%). Young nestlings have also been observed as early as 7 May (J.B.L. pers. obs.) at the field site. Considering all capture records (including individuals not used for the present study), we have observed vascularized brood patches as early as 11 April and as late as 30 June (J.B.L. unpubl. data).

Sequencing

We extracted DNA using QIAGEN DNeasy® or Gentra PureGene kits, following the manufacturer's protocols. After isolating the genomic DNA, we assessed DNA quality with a NanoDrop (Thermo-Fisher) and quantified DNA with a Qubit® Fluorometer (Life Technologies) dsDNA BR Assay Kit following the manufacturer's protocol. We aimed to have concentrations of 20 ng/μL (mean ± se = 18.8 ± 0.2 ng/μL, range = 13.8–26.5 ng/μL, $n = 102$ samples). As Palmchats appear sexually monochromatic and are not known to display sexual size dimorphism (Schubert *et al.* 2022), we used the P2/P8 primer set to the determine the genetic sex of each individual (Griffiths *et al.* 1998).

We used double-digest restriction site-associated DNA sequencing (ddRADseq) to characterize single-nucleotide polymorphisms (SNPs) following a modified version of the protocols described by Peterson *et al.* (2012) and Thrasher *et al.* (2018) and reported in LaPergola *et al.* (2022). Briefly, we digested genomic DNA with the restriction enzymes *Eco*RI and *Msp*I, ligated adapters, ran low-cycle PCR to add index primers (eight index adapters and 16 barcode adapters), size selected fragments between 340 and 600 bp via BluePippin (Sage Science) and pooled index libraries in equimolar ratios into a final library. We submitted the final library for sequencing on an Illumina NovaSeq SP v.1.5 machine, using both lanes of the flowcell, at the Princeton University Lewis-Sigler Institute for Integrative Genomics, which produced 138-bp single-end reads.

Sequencing produced 990 520 375 reads, which we processed using the STACKS 2 pipeline (Rochette *et al.* 2019). First, we demultiplexed reads using *process_radtags*. Because we lack a reference genome for the Palmchat, we then used the STACKS 2 *denovo_map* program to assemble RAD loci with the following parameter settings: *-M* 5; *-n* 5; and *-m* 10. Demultiplexing yielded 132 048 loci. We then used the *populations* module within STACKS 2 to further filter SNPs, tuning the following parameters with the respective values: *-R* 0.95, *-p* 1, *--write-single-snp*, *--min-maf* 0.05 and *--max-obs-het* 0.95. This filtering step, which retained 883 SNPs, was fairly restrictive because we wanted to reduce the chances of spurious results resulting from high proportions of missing loci in some individuals while having a high proportion of overlapping loci. Thus, we used a high *-R*, which sets the minimum threshold proportion of individuals across populations needed to retain a locus. We then excluded any loci deviating from Hardy–Weinberg equilibrium, which was calculated using the *--hwe* flag in *populations*. After filtering, we retained 779 high-quality variable loci. For relatedness analyses, we used a second SNP panel (3068 loci) generated with a more permissive filtering setting (STACKS: *-m* 5, and no filtering for Hardy–Weinberg equilibrium) to determine if filtering influenced our results. Results from this panel were qualitatively similar to those with the more restrictive filtering (see Figs S2 & S3) so we

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only report the results from the former (779 loci) panel in the article.

Statistical analyses

Unless otherwise noted, we performed all analyses in Rstudio v.2021.9.2.382 (RStudio Team 2022) using R v.4.2.2 (R Core Team 2022), and we report all means as ± se. We used the *lmer* function in the R package 'lmerTest' (Kuznetsova *et al.* 2017) for linear mixed effects models (LMMs), and we used the *glmer* function in the 'lme4' package (Bates *et al.* 2015) for generalized linear mixed effects models (GLMMs). We used the *emmeans* function from its eponymous package (Lenth 2023) to conduct *post hoc* comparisons using Tukey's honestly significant difference (HSD) method.

Relatedness and compound nest group composition

To test for within- and between-group kin structuring, we used two complementary approaches. First, we used the full SNP panel to calculate dyadic relatedness using the R package 'related' (Pew *et al.* 2015) and the Wang estimator (hereafter, *r*; Wang 2002). We then tested the prediction that compound nests comprise kin-based groups with an LMM in which *r* was the response variable. The LMM included a fixed effect of compound nest comparison (i.e. within or between compound nests), and we included the sex pairing of dyads (among males, among females or between sexes). We also included an interaction between sex pairings of dyads with compound nest comparison to determine whether sex influenced patterns of relatedness within and between compound nests, as would be predicted by sex-biased philopatry. We included the ID of the first and second individuals in dyads as separate random effects to account for repeated measures.

Second, we used the same SNP panel in the program ML-RELATE (Kalinowski *et al.* 2006) to estimate genealogical relationships among Palmchats. ML-RELATE uses a maximum-likelihood approach to assign different kinship categories to dyads of individuals (e.g. unrelated, half sibling, full sibling or parent–offspring). Because we lacked demography data for our sampled individuals, we could not reliably infer parent–offspring status, so we classified dyads as unrelated, second-order kin (half sibling) or first-order kin (consistent with parent–offspring or full sibling relationships). As a secondary test of the hypothesis that compound nests are kin-based, we used ML-RELATE's genealogical assignments to categorize Palmchat dyads as being either kin or non-kin, treated as a binary response variable (kin = 1, non-kin = 0). ML-RELATE offers a method for constructing confidence sets that include a list of all the plausible relationships for a dyad given the genetic data. In a few cases ($n = 2$ out of 5151 dyads), ML-RELATE assigned both 'unrelated' and 'second-order kin' as plausible relationships, and in these cases, we accepted the more conservative (unrelated) of the two assignments. We then conducted a GLMM of this kinship binary in which dyads assigned as either full or half siblings were considered kin (i.e. first- or second-order kin) and the remainder were considered non-kin. The GLMM thus had a binomial response, with 0 = non-kin and 1 = kin, and a logit link function. We tested for an association of this kinship classification with the fixed effect of compound nest comparison (i.e. within or between compound nests). As with the analysis of *r*, we also included the sex pairing of dyads and its interaction with compound nest comparison. The model included random effects of ID of the first and second individuals in a dyad to account for repeated measures.

We tested the fine-scale genetic relatedness patterns of our population via spatial autocorrelation analyses with the same pairwise genetic relatedness estimator, *r*, as a function of the geographical distance between compound nests. We calculated the inter-nest distances using the *distm* function in the 'geosphere' package (Hijmans *et al.* 2022). We used the program SPAGeDi v.1.3a (Hardy & Vekemans 2002) to test for correlations over seven distance classes (0 m or from the same nest, > 0 to 300 m, > 300 to 600 m, > 600 to 900 m, > 900 to 1200 m, > 1200 to 2000 m, > 2000 to 2800 m) that we chose for ease of visual interpretation while attempting to ensure sufficiently large sample sizes for each distance band. We ran separate analyses for relatedness among all individuals and for each sex, and used 999 permutations each of individual nest locations and individuals, and specified jackknifing over loci. We used two-tailed tests and considered the observed relatedness to be statistically significant if it fell outside of the 95% confidence interval (CI) generated by SPAGeDi's permutations.

Because population structure could affect relatedness results, we also conducted exploratory

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analyses of population structure using a principal component analysis (PCA) of the 779 loci SNP panel following approaches used by Aguillon *et al.* (2017). These results would probably be more helpful in understanding higher-order patterns of population genetic structure than what might be detectable at the spatial scale and resolution of the present study. Nonetheless, we report the results of these analyses in Table S4 and Figures S4 and S5.

Genetic structure and isolation-by-distance

To test for genetic structure, we computed the overall F_{ST} using the *wc* function in the 'hierfstat' R package (Goudet 2005) to calculate the Weir and Cockerham (1984) estimate of F_{ST} (F_{ST}^{WC}), which is considered to have lower bias than other estimators (Weir & Cockerham 1984). We then tested the significance of this value using the *test.within* function in 'hierfstat' with 1000 permutations. To test whether females and males differed in genetic structuring among compound nests, we used the *sexbias.test* in the 'hierfstat' package with 100 permutations. To test for potential genetic structuring via isolation by distance, we performed Mantel tests using the 'ecodist' package (Goslee & Urban 2007). We used the *pairwise.WCfst* function in the 'hierfstat' package to calculate the Weir and Cockerham (1984) estimate of F_{ST} (F_{ST}^{WC}). We performed three Mantel tests for these three groupings, each with 10 000 permutations, and we report the results based on the Spearman correlation (including the 95% CI) and two-tailed tests. We repeated these analyses using the analysis of molecular variance (AMOVA) F_{ST} calculation based on Weir (Weir 1996) as implemented with the 'fstats' flag in the *populations* module of STACKS (Rochette *et al.* 2019). These results were comparable, so we report them only in the Figure S6.

RESULTS

Relatedness and compound nest group composition

For the 10 compound nests, the mean inter-nest distance was 989 ± 97 m (range = 100–2740 m, $n = 45$ nest dyads). The unweighted mean r within compound nests was 0.042 ± 0.005 ($n = 536$ dyads) and 0.012 ± 0.002 ($n = 4615$ dyads) between compound nests. Within compound nests, r was 0.037 ± 0.009 for males ($n = 157$ dyads), 0.048 ± 0.012 for females ($n = 115$ dyads), and 0.042 ± 0.008 between males and females ($n = 264$ dyads). Model results revealed that r was significantly associated with the interaction between compound nest comparison and sex pairings of dyads (Wald $\chi^2 = 6.175$, $P = 0.046$; Table 1a): overall, relatedness was significantly higher within compound nests than between them (Fig. 1). The significant interaction meant there were 15 possible comparisons (between nest of origin (same vs different) and sex pairings (among females, among males or between sexes; Table S2)), but of these, only five were significant. Notably, all three contrasts within sex pairings (i.e. female–female, male–male and between sexes) were significantly higher within compound nests than between compound nests. Additionally, females from the same nest had higher relatedness than between sex pairings from different nests, and females from different compound nests had lower relatedness than between sex pairings from the same nest (Fig. 1).

Results of the genealogical relationship assignments were partially consistent with the genetic relatedness estimators. Of all possible within-nest dyads ($n = 536$), ML-RELATE assigned 12 (2.2%) as first-order kin, 39 (7.3%) as second-order kin and the rest as unrelated. Of all possible between-nest dyads ($n = 4615$), 16 (0.3%) were first-order kin, 32 (0.7%) were second-order kin and the rest were unrelated (including two dyads assigned as either unrelated or half siblings). Considering only within-nest dyads, six of the 10 compound nests had at least one full-sibling dyad (mean = 1.2 ± 0.4 dyads, range = 0–3), and nine of the 10 compound nests had at least one full- or half-sibling dyad (mean = 5.1 ± 1.4 dyads, range = 0–15). Results of a GLMM of the binary kinship category revealed a significant association with compound nest comparisons: within-nest dyads were more likely to be kin (Wald $\chi^2 = 116.382$, $P < 0.001$; Table 1b). The interaction between sex pairings of dyads with compound nest comparison was non-significant so we omitted this term from the final model (Table S3). However, sex pairings of dyads was significant in the model (Wald $\chi^2 = 6.415$, $P = 0.040$). Overall, 2.7% ($n = 1035$ dyads) of female dyads were kin, 1.2% ($n = 1540$ dyads) of male–male dyads were kin and 2.1% ($n = 2576$ dyads) of female–male dyads were kin. Tukeys HSD *post hoc* comparisons

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Table 1. Models predicting (a) genetic relatedness between all dyads of individuals in the study population and (b) the presence of kin (half or full sibling) dyads, all with compound nest of origin (same vs. different) and sex pairings (F-F = among females, M-M = among males, between = between sexes) as fixed effects.

	Estimate ± se	df	*t*- or *Z*-value	*P*
(a) Genetic relatedness				
Intercept	0.058 ± 0.015	270.1	3.839	0.0002
Compound nest (same)	**−0.049 ± 0.007**	**5048.0**	**−6.836**	**9.08e-12**
Sex: F-F vs M-M	−0.018 ± 0.020	264.2	−0.904	0.367
Sex: F-F vs Between	−0.006 ± 0.015	159.8	−0.386	0.700
Nest (different): Sex (F-F vs M-M)	0.007 ± 0.008	5053.0	0.829	0.407
Nest (different): Sex (F-F vs Between)	**0.021 ± 0.009**	**5113.0**	**2.29**	**0.022**
(b) Presence of kin dyads				
Intercept	−2.146 ± 0.293		−7.339	**< 0.001**
Compound nest (same)	**−2.399 ± 0.222**		**−10.788**	< 0.001
Sex: F-F vs M-M	**−0.947 ± 0.379**		**−2.497**	**0.013**
Sex: F-F vs Between	**−0.318 ± 0.292**		−1.089	0.276

The reference level for the model (same) is given in parentheses. Model (a) was a linear mixed-effects model with dyadic relatedness as the response variable and an interaction between compound nest and sex comparisons; model (b) was a generalized linear mixed-effects model with a binomial distribution and a binary response variable (whether dyads were either non-kin or kin, including both half and full siblings). All models included the ID of the first and second individuals in a dyad as random effects. Values in bold type emphasize significant predictors.

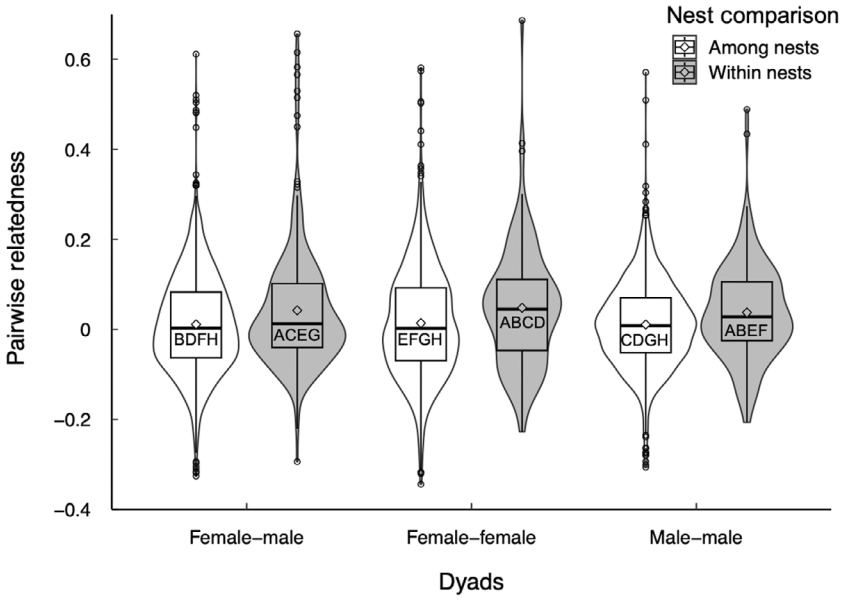

Figure 1. Violin plots of among and within compound nests pairwise relatedness (Wang estimator) values for between sexes (within compound nests: $n = 264$ dyads; among compound nests: $n = 2312$ dyads) and within each sex (females, within compound nests: $n = 115$ dyads; females, among compound nests: $n = 920$ dyads; males, within compound nests: $n = 157$ dyads; males, among compound nests: $n = 1383$ dyads). The violin outlines show kernel probability density traces. The lower and upper edges of the boxplots represent the lower 25th and 75th percentiles, respectively. The solid midline represents the median, diamonds represent the means, and the whiskers represent the smallest or largest observations less than or equal to 1.5 times the interquartile range for each grouping. Points represent outliers. Letters within boxes indicate comparisons that are not significantly different based on Tukey's HSD method.

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revealed that male–male dyads were less likely to be kin than female–female dyads ($P = 0.03$), but neither of the other pairwise comparisons were significant (male–male vs female–male: $P = 0.12$; female–female vs female–male: $P = 0.52$).

Spatial autocorrelation analyses showed overall similar patterns of fine-scale genetic relatedness (Fig. 2a–c). In particular, r within compound nests was higher than expected by chance among all individuals ($P = 0.003$, Fig. 2a), among females ($P = 0.047$, Fig. 2b) and among males ($P = 0.013$, Fig. 2c). There was no significant relationship between relatedness and distance for any of the comparisons.

Genetic structure

We found weak but significant genetic structuring between compound nests ($F_{ST}^{WC} = 0.014$, $G = 20\,911$, $P = 0.03$). Genetic structure based on all individuals, and comparing between compound nests was low (mean $F_{ST}^{WC} = 0.015 \pm 0.001$, $n = 45$ dyads, Fig. 2d). While genetic structure was slightly lower for females (mean $F_{ST}^{WC} = 0.010 \pm 0.004$, Fig. 2e) than for males (mean $F_{ST}^{WC} = 0.011 \pm 0.002$, Fig. 2f), this difference was not statistically significant ($t = -0.005$, $P = 0.14$).

Isolation-by-distance

There was no evidence for isolation-by-distance based on the Mantel tests of F_{ST}^{WC} between compound nests, considering all individuals together or the sexes separately (Fig. 2d–f). Across all individuals, there was no association between geographical distance and genetic differentiation (Mantel's $r = -0.04$, $P = 0.67$, 95% CI = −0.18 to 0.10; Fig. 2d), nor were associations statistically significant when the sexes were tested separately (females: Mantel's $r = -0.07$, $P = 0.85$, 95% CI = −0.21 to 0.06; Fig. 2e; males: Mantel's $r = -0.09$, $P = 0.90$, 95% CI = −0.24 to 0.05; Fig. 2f). Isolation-by-distance results based on the AMOVA F_{ST} estimates were, similarly, non-significant for all groups (Fig. S6).

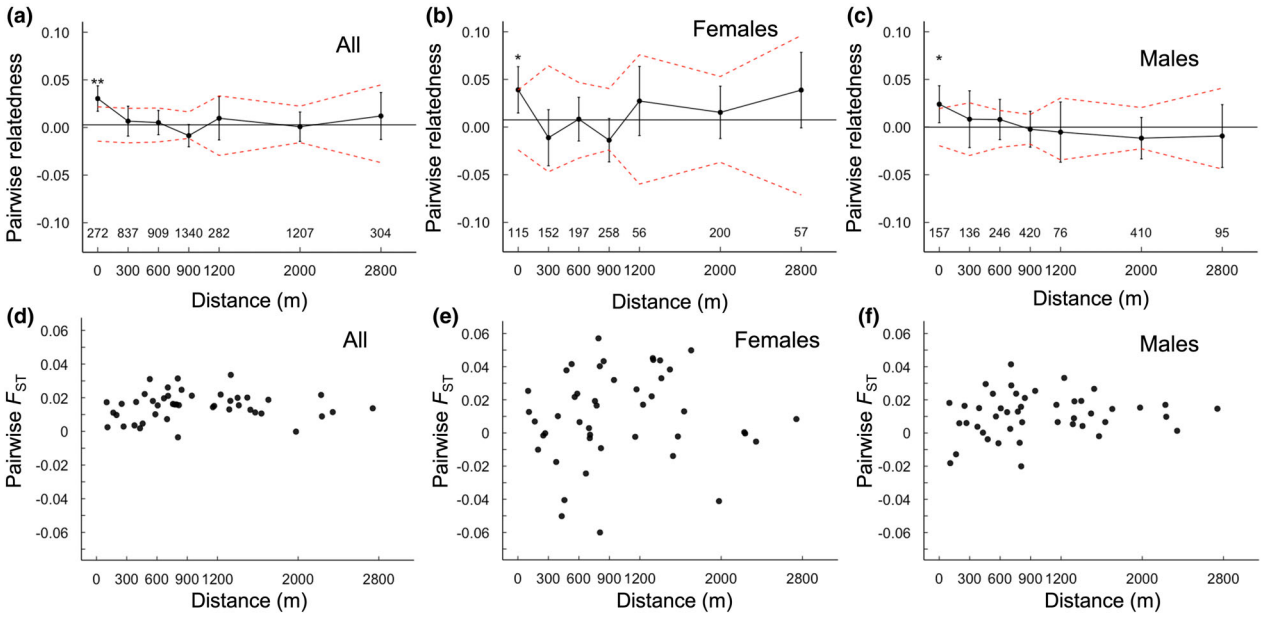

Figure 2. Correlograms of mean pairwise relatedness among different dyads (a–c) and isolation by distance plots of pairwise F_{ST} (d–f). Mean pairwise relatedness values are for (a) all dyads, (b) female–female dyads and (c) male–male dyads. Points are mean relatedness estimates at seven distance bands, error bars represent 95% confidence intervals (CI) and red-dotted lines represent 95% CI for the null expectation generated through 1000 data permutations. Numbers above the *x*-axes indicate the number of pairwise comparisons for each distance band. Solid black horizontal lines represent the mean relatedness values for the respective category of dyads. $*P < 0.05$; $**P < 0.01$. Pairwise F_{ST} by distance plots use the Weir and Cockerham estimate of F_{ST} and are between compound nests among (d) all individuals and between compound nests, but only (e) among female or (f) among male Palmchats captured at focal compound nests.

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DISCUSSION

Our population genomic analysis of birds associated with compound nests sheds new light on kin relationships within Palmchat social groups. Analysis of both genetic relatedness and kinship classification indicated that compound nesting groups contained at least some first- and/or second-order kin, and spatial autocorrelation analyses indicated that genetic relatedness was low but generally higher within than among compound nests for all sex pairings of dyads. Nesting groups also contained many dyads of low relatedness. Together, these results suggest that Palmchat nesting groups are likely to comprise a heterogeneous mix of kin and non-kin, raising the possibility that both direct and indirect fitness benefits are involved in compound nesting for this species.

Genetic relatedness and kinship classification analyses suggest that some nesting group members are close relatives. In particular, the presence of first-order kin relationships involving both males and females is consistent with natal philopatry of both sexes. Putative full- and half-sibling relationships were also consistent with this interpretation, being more likely within compound nests than between. While male-biased natal philopatry and female-biased natal dispersal is a common pattern in birds (Greenwood & Harvey 1982), philopatry of female offspring is less common (e.g. Langen 1996). Another possibility is that same-sex first- and/or second-order kin dyads occupying the same compound nest occur through dispersal of coalitions (Barve *et al.* 2019). However, it is important to note that we were unable to assign age or behavioural roles (e.g. breeder, non-dispersed offspring or non-breeding helper) to individuals, so it is not clear which dispersal or demographic processes gave rise to these patterns. Furthermore, we assumed that all birds captured at focal nests were indeed associated with that nest, but it is unknown whether (or to what extent) adults may move between compound nests or associate with multiple nests. It is possible that that some birds sampled at one compound nest were actually 'visiting', perhaps to prospect or to visit a former family group (e.g. Leedale *et al.* 2018, Smith *et al.* 2020). However, capture of some individuals at the same site days later (Table S1) is consistent with our interpretation of nesting group membership. Future work with Palmchats would benefit from multi-year mark–recapture studies, including colour-banding and sampling of both nestlings and adults, which will be necessary to detect natal philopatry and characterize the degree of fission-fusion of Palmchat societies.

Our analyses were conducted at the level of the compound nest; we were unable to describe the composition of breeding units within nests. Like other species with compound nests, Palmchats exhibit co-operative brood care, with three to five individuals feeding young in the same nest (Keys 1991), but the relatedness of helpers to the brood is not known. In both Sociable Weavers (Van Dijk *et al.* 2015) and Monk Parakeets (Dawson Pell *et al.* 2021), helpers and/or co-breeding adults are often first-order kin (either offspring delaying dispersal or siblings that disperse as coalitions), but breeding adults are typically unrelated to opposite-sex breeders. Our findings of potential first- and second-order kin within compound nests raises the possibility that Palmchat helpers might be philopatric kin, but further field observations are needed to confirm this. Similarly, description of the Palmchat's genetic mating system would further our understanding of the Palmchat's population genetics (Ross 2001). For example, extra-pair mating and conspecific brood parasitism would lower relatedness within, and genetic structuring among, compound nests, if extra-pair sires or brood parasites originated from outside the nesting group. Extra-pair parentage is common among passerines (Brouwer & Griffith 2019, Valcu *et al.* 2021) and so might be expected in Palmchats. Delineating the Palmchat's genetic mating system will thus be necessary for understanding its unique social system.

Consistent with the analyses of relatedness and kinship, the analyses of genetic structuring and isolation-by-distance suggest appreciable gene flow between compound nests. While the population exhibited weak, yet statistically significant, genetic structuring associated with compound nesting groups, none of the isolation-by-distance relationships were significant. Genetic differentiation among individuals from different compound nests was only slightly higher for males than for females, but this difference was not significant. This lack of a spatial pattern and difference between sexes suggests that Palmchats disperse over a range of distances sufficiently large to encompass our field site. The median and maximum distances between sampled compound nests were 793 and 2740 m,

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respectively, so greater distances between sampled nests might be necessary to detect spatial structuring. Despite the limited scale of sampling, it is important to note that our study area encompassed a high density of Palmchat compound nests, not all of which were sampled. Given that other studies of compound-nesting birds have detected significant kin structuring over much smaller distances (e.g. within compound nests and nesting trees; Dawson Pell *et al.* 2021), the absence of significant genetic structuring at this spatial scale is likely to be biologically relevant.

Together, our findings of mixed kinship in compound nesting groups, overall weak genetic structure and no evidence of isolation-by-distance suggest that social nesting in Palmchats may involve both direct and indirect fitness benefits. The Palmchat's social organization—multiple pairs and/or breeding groups join together to form compound nesting groups which themselves can be spatially clustered in neighbourhoods of compound nests—also appears to represent a multilevel society, which has recently been described in a small number of social birds (Papageorgiou *et al.* 2019, Camerlenghi *et al.* 2022, 2023). More detailed studies are needed to understand the fitness consequences and functions of this unusually complex social structure, which will shed light on the selective pressures favouring sociality more broadly.

We thank the Cornell Laboratory of Ornithology and Princeton University for support for this project. We also thank R. Ortíz, J. Goetz, and the Muséo Nacional de Historía Natural in Santo Domingo for assistance with local permitting. The following people provided invaluable assistance in the field: M. Angelucci, C. Cerrilla, A. Diaz, L. Emerson, N. Gilbert, A. Janik, K. Kauffman, A. Lascher-Posner, M. Larrieu, K. Larsen, A. Occhialini and P. Werner. We thank SUNY Buffalo State College for support during this project. We thank an anonymous reviewer and G. Voelker for constructive comments on an earlier version of the manuscript that helped us improve the final version. Finally, we thank Wei Wang and the staff of the Princeton University Genomics Core Facility for assistance with library preparation and sequencing. Finally, J.B.L. dedicates this manuscript to the memory of Simón Guerrero Suriñach (1946–2024), who graciously and freely shared his knowledge of Hispaniolan birds and inspired countless individuals to further Caribbean ornithology and conservation.

FUNDING

J.B.L. was supported by a Charles Walcott Graduate Fellowship, a Linda and Samuel Kramer Graduate Student Fellowship and an Eleanore Stuart Graduate Fellowship from the Cornell Lab of Ornithology for fieldwork activities. Additional funding was provided by the National Science Foundation (IOS-1755279 to C.R.; BIO-1523748 to G.M.L.).

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

ETHICAL NOTE

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.

AUTHOR CONTRIBUTIONS

Joshua B. LaPergola: Conceptualization; investigation; writing – original draft; writing – review and editing; visualization; methodology; formal analysis; project administration; data curation; validation. **Gavin M. Leighton:** Writing – original draft; writing – review and editing; conceptualization; investigation; funding acquisition; methodology. **Christina Riehl:** Conceptualization; writing – original draft; writing – review and editing; funding acquisition; project administration; resources; supervision.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Open Science Framework at https://osf.io/yha2q/overview or https://doi.org/10.17605/OSF.IO/YHA2Q (LaPergola *et al.* 2025).

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Received 16 December 2023;
Revision 9 December 2025;
revision accepted 20 February 2026.
Associate Editor: Sandi Willows-Munro.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Map of sampled Palmchat compound nest locations near Jarabacoa, La Vega province, Dominican Republic. Large circles indicate sampled compound nests, solid black lines indicate major paved roads and dashed black lines indicate primary dirt roads. Letters denote compound nest IDs corresponding to those in Table S1.

Table S1. Descriptive details for Palmchat compound nests sampled for the present study.

Figure S2. Scatterplot of pairwise relatedness of Palmchat dyads as calculated using either a panel of 779 SNPs or 3068 SNPs.

Figure S3. Pairwise relatedness of individual Palmchats across all distances recorded in the study. Points represent Palmchat dyads. Blue lines represent LOESS curves (span = 0.5) as plotted with the geom_smooth argument in ggplot. The titles correspond to different filter settings. For example, the SNP panels differed in whether a Hardy–Weinberg Equilibrium (HWE) filter was applied.

Table S2. Results of pairwise comparisons of Palmchat relatedness based on the interaction between nest of origin (same vs. different) and sex pairings (among females, among males or between sexes). Significant contrasts are bolded and italicized. Significant contrasts were determined using Tukey's HSD method.

Table S3. Generalized linear mixed-effects model results of kinship. The response variable was the binary of whether dyads were kin (1) or non-kin (0). Fixed effects included the compound nest of origin (same vs. between) for pairs, sex pairing of dyads (among males, among females or between sexes), and the interaction of these two terms. The IDs of the first and second individuals in dyads were included as random effects. Significant terms are bolded and italicized.

Figure S4. Palmchat compound nest groups show extensive overlap based on a principal components analysis of 779 SNPs. The first two principal components (PC1 and PC2) explained relatively little of the overall variance (2.7% and 2.3%, respectively). Points represent individual Palmchat samples. Colour and shapes of points correspond to the 10 unique compound nests sampled.

Table S4. Spearman rank correlations between principal components 1 and 2 (PC1 and PC2) and UTM northing and easting. We conducted the principal component analysis using the 779 loci SNP panel and the 102 Palmchat individuals sampled. Each cell contains the Spearman's ρ value followed by the *P*-value in parentheses.

Figure S5. Map of PC1 based on 779 SNPs overlaid on the field site and locations of the 10 Palmchat compound nests. Points represent individual Palmchats coloured by PC1 values. Solid black lines represent paved roads and dashed lines represent major dirt roads.

Figure S6. Isolation by distance plots of pairwise F_{ST} and distance (m) between compound nests among (A) all individuals, (B) among female Palmchats and (c) among male Palmchats captured at focal compound nests. Each point represents a dyad of compound nesting groups. F_{ST} was calculated in STACKS using the analysis of molecular variance F_{ST} calculation based on Weir (Weir 1996).

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