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Fine-scale genetic structure reflects limited and coordinated dispersal in the colonial monk parakeet, *Myiopsitta monachus*

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Abstract

The genetic structure of animal populations has considerable behavioural, ecological and evolutionary implications and may arise from various demographic traits. Here, we use observational field data and molecular genetics to determine the genetic structure of an invasive population of monk parakeets, *Myiopsitta monachus*, at a range of spatial scales, and investigate the demographic processes that generate the observed structure. Monk parakeets construct large nests that can house several pairs occupying separate chambers; these nests are often aggregated within nesting trees. We determined patterns of relatedness within compound nests, within nesting trees and between trees. Spatial autocorrelation analyses of pairwise genetic relatedness revealed fine-scale genetic structure with relatives of both sexes spatially clustered within, but not beyond, nesting trees. In addition, males were more related to males sharing their compound nests than to other males occupying the same nesting tree. By contrast, males and females within compound nests were not significantly more closely related than elsewhere in the same tree, and we found no evidence for inbreeding. Adults showed high breeding site fidelity between years despite considerable disturbance of nest sites. Natal dispersal was female-biased, but dispersal distances were relatively short with some natal philopatry observed in both sexes. Sibling coalitions, typically of males, were observed amongst both philopatric and dispersing birds. Our results show significant clustering of kin within compound nests and nesting trees resulting from limited and coordinated natal dispersal, with subsequent breeding site fidelity. The resulting genetic structure has implications for social behaviour in this unusual parrot species.

KEYWORDS
dispersal, monk parakeet, *Myiopsitta monachus*, philopatry, population genetic structure, site fidelity

1 | INTRODUCTION

Population genetic structure, that is the distribution and frequency of alleles and genotypes within and between populations, is a crucial demographic attribute that can have diverse behavioural, ecological and evolutionary implications. Genetic structure has consequences at a range of spatial scales; for instance, at fine scales, it can influence mate choice (Lee, Simeoni, et al., 2010), cooperation (Leedale et al., 2018) and kin competition (West et al., 2002), whereas at broad spatial scales, it can result in local adaptation and even speciation (Papadopulos et al., 2014; Winker et al., 2013). Limited dispersal due to geographical distance (isolation by distance), or physical barriers such as roads and rivers, can result in significant genetic structure (Garnier et al., 2004; Hayes & Sewlal, 2004; Riley et al., 2006; Wright, 1943). However, physical barriers or large distances are not prerequisites for genetic differentiation; behavioural and life history traits can also generate genetic structure, for example through natal philopatry (Leedale et al., 2018; MacColl et al., 2000; Solmsen et al., 2011), site or group fidelity (Adams et al., 2006; Lee, Simeoni, et al., 2010), and small effective population sizes (Beckerman et al., 2011; Lehmann & Rousset, 2010).

Gene flow is ordinarily expected to be high in very mobile animals such as birds, such that genetic differentiation may be expected to be observed only at large spatial scales (Avise, 1996; Crochet, 2000). However, fine-scale genetic structure of adults following natal dispersal has been demonstrated across a variety of both cooperative and noncooperative avian species, often driven by characteristic patterns of behaviour (e.g., Double et al., 2005; Lee et al., 2009; Temple et al., 2006; van Dijk et al., 2015). For example, fine-scale kin structure in the colonial sociable weaver, *Philetairus socius*, is driven by natal philopatry and limited female-biased dispersal (van Dijk et al., 2015) whereas male-biased dispersal leads to significantly stronger genetic structure amongst females in the white-browed sparrow-weaver, *Plocepasser mahali*, (Harrison et al., 2014) and in some species of waterfowl (e.g., McKinnon et al., 2006). Despite the potential for dispersal to disrupt kin-structured populations, there is also growing evidence from several species that dispersal in coalitions of relatives can maintain kinship ties and opportunities for kin-selected cooperation post-dispersal (e.g., Bradley et al., 2007; Sharp et al., 2008; Williams & Rabenold, 2005). However, investigations of the occurrence of dispersal in kin coalitions are limited despite the implications for population genetic structure and cooperative behaviour (Sharp et al., 2008; Williams & Rabenold, 2005).

The spatial clustering of relatives has implications for the evolution of sociality, allowing cooperative behaviours to be directed towards kin resulting in kin-selected fitness benefits (Hamilton, 1964). For example, in vinous-throated parrotbills, *Paradoxornis webbianus*, clusters of male relatives in the breeding population result in increases in juvenile recruitment (Lee et al., 2009) and in the long-tailed tit, *Aegithalos caudatus*, genetic structuring in kin neighbourhoods provides opportunities for indirect fitness benefits through helping at relatives' nests (Leedale et al., 2018). However, such spatial aggregations of relatives may also increase kin competition (Moore et al., 2006; Platt & Bever, 2009; West et al., 2002) and the risk of inbreeding (Brouwer et al., 2011; Lukas & Clutton-Brock, 2011; Nelson-Flower et al., 2012).

A limited number of studies have combined investigations of fine-scale genetic structure among post-dispersal adults with a detailed examination of the potential mechanisms driving the observed structure. Therefore, the processes generating structure and its behavioural, ecological and evolutionary implications require further investigation. This is particularly true of dispersal, which is inherently challenging to study (Koenig et al., 1996). Investigations combining behavioural field data and molecular genetics can provide detailed insights into the genetic structure of populations and reveal the demographic mechanisms driving it. Here we investigate fine-scale population genetic structure in a worldwide invasive parrot species, the monk parakeet (*Myiopsitta monachus*), and examine key demographic characteristics behind the observed structure. The monk parakeet is a sexually monomorphic species native to South America (Forshaw, 1989) that thrives in the urban environment and has become established throughout the world through escapes from the pet trade (Bush et al., 2014; Lever, 2005; Russello et al., 2008).

Monk parakeets are unique amongst parrots in their nest building behaviour, using interlaced sticks to construct large nest structures that are used year round for roosting and breeding (Eberhard, 1998; Forshaw, 1989; Spreyer & Bucher, 1998). Nest structures vary in size from those containing a single nest chamber to compound nests containing up to 100 pairs, each occupying a separate nest chamber (Naumberg, 1930). However, numbers are typically lower; for instance, in Catalonia, the majority of nest structures contained only one or two chambers in 2001, although nests with up to 36 chambers were detected (Domènech et al., 2003). Nests containing more than one chamber are referred to hereafter as compound nests. Nest chambers are occupied most commonly by pairs of birds, although the occurrence of trios occupying nest chambers has been reported (Bucher et al., 1990; Eberhard, 1998). Nests are often spatially clustered in groups occupying the same or neighbouring trees; these aggregations have been referred to as colonies (Bucher et al., 1990; Eberhard, 1998); however, due to a lack of clear delimitations between monk parakeet colonies we conduct analyses at the level of compound nests, within nesting trees and between trees. There have been no previous investigations into the genetic structure of monk parakeets at these fine spatial scales.

Using a combination of field observations and molecular genetics we first assessed whether there was significant inbreeding or outbreeding at our study site. Second, we investigated the fine-scale spatial genetic structure of adult monk parakeets to determine whether relatives were spatially clustered within nesting trees and whether any genetic structure extended beyond the nesting tree. We then investigated whether relatives were clustered in compound nests within nesting trees. Finally, we examined the demographic mechanisms generating kin structure in the monk parakeet including: adult breeding site fidelity, natal dispersal and philopatry, and the coordinated dispersal of sibling coalitions.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted in Barcelona, Spain (41.39°N, 2.17°E), on the northeast coast of the Iberian Peninsula. We conducted surveys across the city of Barcelona with the majority of fieldwork conducted in Ciutadella Park, a large (~30 ha) central park in the city that contains the city's zoological gardens and a large public access area of highly managed native and exotic vegetation. Ciutadella Park is the site of the first record of monk parakeet nests in Barcelona (Batllori & Nos, 1985) and now contains a high density of monk parakeet nests.

2.2 | Sample collection

For ringing, monk parakeets were either caught in a baited trap controlled remotely, using gas-propelled nets, or in nest chambers either prior to fledging or as incubating adults. A cherry picker was used for nest access in these cases. No birds abandoned their nests as a result of disturbance caused by nest checks or by ringing. Each bird was ringed with an aluminium leg ring and also marked with a unique neck collar for visual identification in the field at distances of up to 30–40 m (Senar et al., 2012) allowing behavioural observations and the identification of nesting locations. During ringing, blood samples (maximum 100 µl) were collected for genetic analyses and sex determination.

2.3 | Compliance with ethical standards

Birds were handled and blood samples taken with special permission EPI 7/2015 (01529/1498/2015) from Direcció General del Medi Natural i Biodiversitat, Generalitat de Catalunya, following Catalan regional ethical guidelines for the handling of birds. J.C. Senar received special authorization (001501-0402.2009) for the handling of animals in research from Servei de Protecció de la Fauna, Flora i Animal de Companyia, according to Decree 214/1997/30.07.

2.4 | Nest observations

To determine nesting locations of adult monk parakeets during the breeding season, we conducted detailed behavioural observations between April and July 2018 at 10 large, mature pine trees in Ciutadella Park that contained monk parakeet nests. During the breeding season, marked individuals were never observed to enter a chamber that they did not use as their roosting or breeding chamber (F. S. E. Dawson Pell, unpublished observations), so we are confident that individuals recorded entering or leaving chambers were the occupants of that chamber. We conducted 263 hr of behavioural observations at a total of 72 nests that contained 149 individual nest chambers. These nests were occupied by 113 marked individuals and at least 64 unmarked individuals during the period of observation. Blood samples were available for genetic analysis from 112 of the marked birds. GPS coordinates of each nesting tree were recorded; all monk parakeets with nests in the same tree were assigned the same spatial coordinates. Distances between nesting trees were calculated from GPS locations and used to inform distance bands in the spatial analysis of genetic relatedness (see *Spatial genetic structure*).

2.5 | DNA extraction and genotyping

For details of blood sample storage and DNA extraction see Dawson Pell et al. (2020). We used 26 microsatellite markers optimized in six multiplexes (for details see Table S1). These markers were: Mmon01, Mmon02, Mmon03, Mmon04, Mmon05, Mmon06, Mmon07, Mmon09, Mmon10, Mmon11, Mmon13, Mmon14, Mmon15, Mmon16 (Dawson Pell et al., 2020), MmGT012, MmGT090, MmGT054, MmGT060, MmGT046, MmGT105, MmGT030, MmGT071, MmGT057 (Russello et al., 2007), TG03-002 and TG05-046 (Dawson et al., 2010), and CAM-20 (Dawson et al., 2013). PCR (polymerase chain reaction) and allele scoring protocols were the same as those followed in Dawson Pell et al. (2020). Alleles were scored blind to bird identity. Allele scoring error was examined for these markers for a concurrent study of monk parakeet behaviour; based on repeat genotyping of 50 individuals, scoring error was estimated at 3.1% (F. S. E. Dawson Pell, unpublished data). Monk parakeets are sexually monomorphic in the field (Forshaw, 1989), so individuals were sex-typed using a sexing marker, Z002B (Dawson, 2007).

2.6 | Assessing marker quality

Estimated null allele frequencies were calculated using CERVUS version 3.0.7 (Kalinowski et al., 2007). One locus (MmGT054) possessed high estimated null allele frequencies (>10%) and was excluded from further analyses. Both linkage disequilibrium and departures from Hardy–Weinberg equilibrium were assessed using GENEPOP web version 4.2, using 100 batches of 1000 iterations (Rousset, 2008). A false discovery rate control (FDR; Verhoeven et al., 2005) was applied to *p*-values obtained for both tests to correct for multiple testing. Following FDR control, departures from Hardy–Weinberg equilibrium were detected for four loci (Mmon05, Mmon06, MmGT090, MmGT012) so these loci were not included in any further analyses. The presence of relatives was assessed using ML-RELATE (Kalinowski et al., 2006) and close relatives were removed before analyses of linkage disequilibrium, resulting in 45 individuals being used in linkage assessment. No significant linkage disequilibrium was found between loci. Heterozygotes were observed for both males and females at each of the remaining 21 loci, indicating these markers are located on the autosomes in monk parakeets. We therefore used 21 polymorphic microsatellite loci in all further analyses.

2.7 | Spatial genetic structure

To investigate the overall population genetic structure of adult monk parakeets and assess whether mating occurs randomly within our study population we used two measures. First, we used R_{IS}, a microsatellite allele size-based genetic differentiation estimate (Rousset, 1996; Slatkin, 1995); second, we used F_{IS}, Weir and Cockerham's (1984) inbreeding coefficient. Both measures were calculated in SPAGEDI version 1.5 (Hardy & Vekemans, 2002); alleles were permuted among individuals 20,000 times and multilocus estimates were jackknifed over loci in order to calculate estimates of differentiation and approximate standard error of genetic relatedness.

To investigate fine-scale genetic structure in our population of monk parakeets, we conducted spatial autocorrelation analyses of pairwise genetic relatedness (r_{QG}; Queller & Goodnight, 1989) between individuals as a function of the geographical distance between their nesting tree locations. Some nests are built in trees in close proximity to each other, but in the absence of clear and objective delimitation between monk parakeet "colonies," we use nesting tree as the level of analysis. We used a Cartesian coordinate system (UTM) to determine geographical distances between nesting trees in these analyses. Spatial analyses were conducted in SPAGEDI version 1.5 (Hardy & Vekemans, 2002) over six distance bands: 0 m for analyses of birds within the same nesting tree, from >0 to 25 m, from 25 to 100 m, then increments of 100 m to a maximum of 400 m distance between nesting trees. Observed distances between nesting trees ranged from 5 to 382 m and the chosen distance bands generated sufficiently large sample sizes to ensure meaningful analyses whilst making sure statistics computed for each distance interval were not based on small fractions of the available individuals (see Figure 1 for the number of pairwise comparisons per distance band). We conducted these analyses separately for: (a) all individuals, (b) males, (c) females and (d) between males and females. Mean observed r_{QG} values calculated for each distance band in our population were compared to distributions of r_{QG} values generated using 20,000 random permutations of individual nest locations and all tests were two-tailed. For all analyses, we considered the observed r_{QG} to be statistically significant if it fell outside of the 95% confidence interval of the random distribution generated by data permutations.

2.8 | Relatedness within compound nests

To investigate relatedness within compound nests, we first determined the number of compound nests in our study site and identified their occupants; we excluded any nests with more than one chamber where all the chambers were used by the same individuals, as these individuals could be considered one pair/group sharing multiple chambers, rather than separate pairs/groups with individual nest chambers. To examine whether males sharing a compound nest were more closely related to each other than to other males nesting in the same tree, we constructed a multimembership GLMM with the MCMCGLMM package (Hadfield, 2010) using default priors. We included nesting tree as a random intercept to account for repeated measures, and the identities of the individuals within relatedness dyads were included as multilevel random effects because relatedness is an undirected relationship. MCMCGLMM automatically adds a random intercept at the level of the dyad. We ran the default number of Markov chain Monte Carlo (MCMC) iterations and used the default burnin, with a thinning interval of 10. We then randomly permuted relatedness between dyads within nesting trees and refitted the model 999 times, and then compared the effect size from the original model to those from models fitted to the permutations to calculate *p*-values for a one-tailed test. Statistical tests were carried out in R 3.5.0 (R Core Team, 2018). For these analyses, the genetic relatedness between dyads was estimated using Queller and Goodnight's (1989) r_{QG} coefficient of relatedness in SPAGEDI version 1.5 (Hardy & Vekemans, 2002). Data sets included relatedness values for males that share compound nests and relatedness values between the males that occupied compound nests and the other males occupying different nests in the same nesting tree. We repeated the same analysis on two more conservative data sets. First, we excluded from the data set the relatedness values of male dyads that shared the same nest chamber. This analysis removed within-chamber comparisons that could bias the results if close kin share breeding chambers. Second, we randomly selected a single bird from multimale chambers and included only the relatedness values between this bird and other males sharing its compound nest in the data set because again closely related males sharing a nest chamber could bias the relatedness values within a compound nest. This analysis also excluded relatedness values for males sharing the same nest chamber, as described above.

To examine whether males were more related to females sharing their compound nest than to other females in the same nesting tree, we repeated the process described for males. For this analysis we excluded relatedness values of known pairs. We corrected for multiple comparisons using the Bonferroni correction in each of the above analyses, resulting in $\alpha = 0.0125$. Relatively few females in compound nests were marked, so we were unable to conduct equivalent analyses comparing female relatedness in compound nests and nesting trees.

Ideally we would also have examined whether compound nest associations between individuals persist over time in order to examine long-term cooperative associations between individuals. However, all nests were removed in 2018 so we were unable to examine such associations. Nest removal is used as an invasive species management strategy for monk parakeets in Barcelona as it is elsewhere in both the native and invasive range (Pruett-Jones et al., 2007).

2.9 | Breeding site fidelity

We examined breeding site fidelity of adult birds by comparing occupation of nesting trees during the breeding season (March–September; Senar et al., 2019) across years. Individually marked birds were located in the 10 pine trees in Ciutadella Park during censuses undertaken in 2017. In 2018 and 2019 marked birds were then located in the 10 pine trees by detailed behavioural observations totalling 387 hr. Beyond the focal 10 trees, marked birds were located during surveys of nests in Ciutadella Park or in surveys of monk parakeet nest sites across Barcelona up to 6 km from Ciutadella Park. Over 380 hr were spent surveying colonies across Barcelona for marked individuals in 2018 and 2019. Birds were recorded as the nest occupants only if they were observed either in a nest chamber or bringing nest material to a nest; birds that were only observed perched in a tree that contained a nest were not recorded as nest occupants. We determined the number of marked birds that bred in the same or different trees between years and across all 3 years to assess site fidelity. We used previously calculated survival estimates for monk parakeets in our study location to approximate survival between years (Conroy & Senar, 2009). We used the GPS coordinates of nesting trees to calculate breeding dispersal distances for birds that were detected in a different nesting location between years in R using the distGeo function from the GEOSPHERE package (Hijmans et al., 2019). We tested for sex differences in breeding dispersal distances using a Wilcoxon rank sum test.

In addition, we used data from a concurrent study into social associations of monk parakeets (F. S. E. Dawson Pell, unpublished data) to search for marked target birds not identified at a nest to corroborate our calculations of the number of putative survivors. These data were collected opportunistically on encountering marked birds away from nests (F. S. E. Dawson Pell unpublished data). We examined social groups recorded over the breeding seasons (March–September) in 2018 and 2019 for sightings of target birds not located at nests, enabling calculation of the total number of surviving birds seen either at nests or elsewhere.

2.10 | Natal philopatry and dispersal

To investigate natal dispersal in the monk parakeet, we ringed nestlings during the breeding seasons (March–August) in 2017 and 2018, using a cherry picker to access nests. In 2017, we ringed nestlings in Ciutadella Park, Passeig de Lluís Companys and Plaça de Tetuan; in 2018 nests were accessed only in Ciutadella Park and Passeig de Lluís Companys. Nestlings more than ~21 days old were removed briefly from nest chambers and marked with aluminium leg rings and unique medals attached to neck collars, as detailed in *Sample collection*. Blood samples were also taken for sex determination and genetic analyses as above.

We followed classical definitions of natal dispersal (e.g., Greenwood & Harvey, 1982) and determined the distance between natal nests and the nests occupied during each individual's first breeding season post-fledging. In a previous investigation into the breeding activity of 1-year-old birds at our study site, 55% were engaged in a breeding attempt as a member of a pair, and a further 18% were part of a trio, although it was not confirmed whether 1-year-olds in trios were parents to any offspring (Senar et al., 2019). Thus, 1-year-old monk parakeets are sexually mature, although not all individuals engage in breeding attempts in their first year post-fledging. We recorded the GPS coordinates of natal trees and the nesting trees of marked birds located during the breeding season in their first year post-fledging (2018 or 2019) in the surveys detailed in *Breeding site fidelity*. Natal dispersal distances were calculated for each bird in R with the distGeo function (Hijmans et al., 2019) using the GPS coordinates of their natal and first-year nesting trees. Finally, we tested for a sex difference in natal dispersal distances using a Wilcoxon rank sum test.

3 | RESULTS

3.1 | Genotypes and estimation of inbreeding

Marked adults (total genotyped =112; 46 females, 66 males; age range 1–12+ years) recorded nesting in the 10 focal pine trees in 2018 were genotyped at 21 microsatellite loci (multilocus averages across all individuals: individual inbreeding coefficient $F_I = -0.006$, mean allele number per locus =7.33, allelic richness =6.60, effective alleles =4.06 (Nielsen et al., 2003), observed heterozygosity =0.66 and gene diversity corrected for sample size =0.65). A total of 154 unique alleles were detected in our population (range of allele numbers per locus =2–17). For the distribution of allele number by locus, observed and expected heterozygosity and observed allele size ranges see Table S2. We detected no significant outbreeding or inbreeding in our study population; the average genetic variation among individuals did not differ significantly from random (based on 20,000 permutations, microsatellite-specific genetic differentiation estimate $R_{IS} = -0.003 \pm 0.027$ *SE*, $p = .93$; population inbreeding coefficient $F_{IS} = -0.007 \pm 0.015$ *SE*, $p = .56$).

3.2 | Spatial genetic structure

Spatial autocorrelation analyses revealed significant fine-scale genetic structure in our study population (Figure 1). Mean ± *SE* relatedness within nesting trees was 0.027 ± 0.01 for all individuals, 0.028 ± 0.01 for males, 0.013 ± 0.01 for females and 0.021 ± 0.01 between males and females, with *SE* calculated by jackknifing over loci. In all cases, pairwise relatedness within nesting trees was higher than expected by chance (all $p < .02$; Figure 1; based on 20,000 data permutations), indicating that relatives are clustered in nesting trees. Significant genetic structuring was not found beyond the level of the nesting tree, even between trees <25 m away, until the 300–400 m distance band that indicated individuals separated by this distance were less related to each other than expected by chance for all individuals ($p = .011$) and between the sexes ($p = .004$); no significant structure was found at this distance for either males ($p = .19$) or females ($p = .39$).

3.3 | Relatedness within compound nests

Thirteen (18.1%) of the 72 observed nests housed more than one pair of birds using separate chambers. The relatively small overall

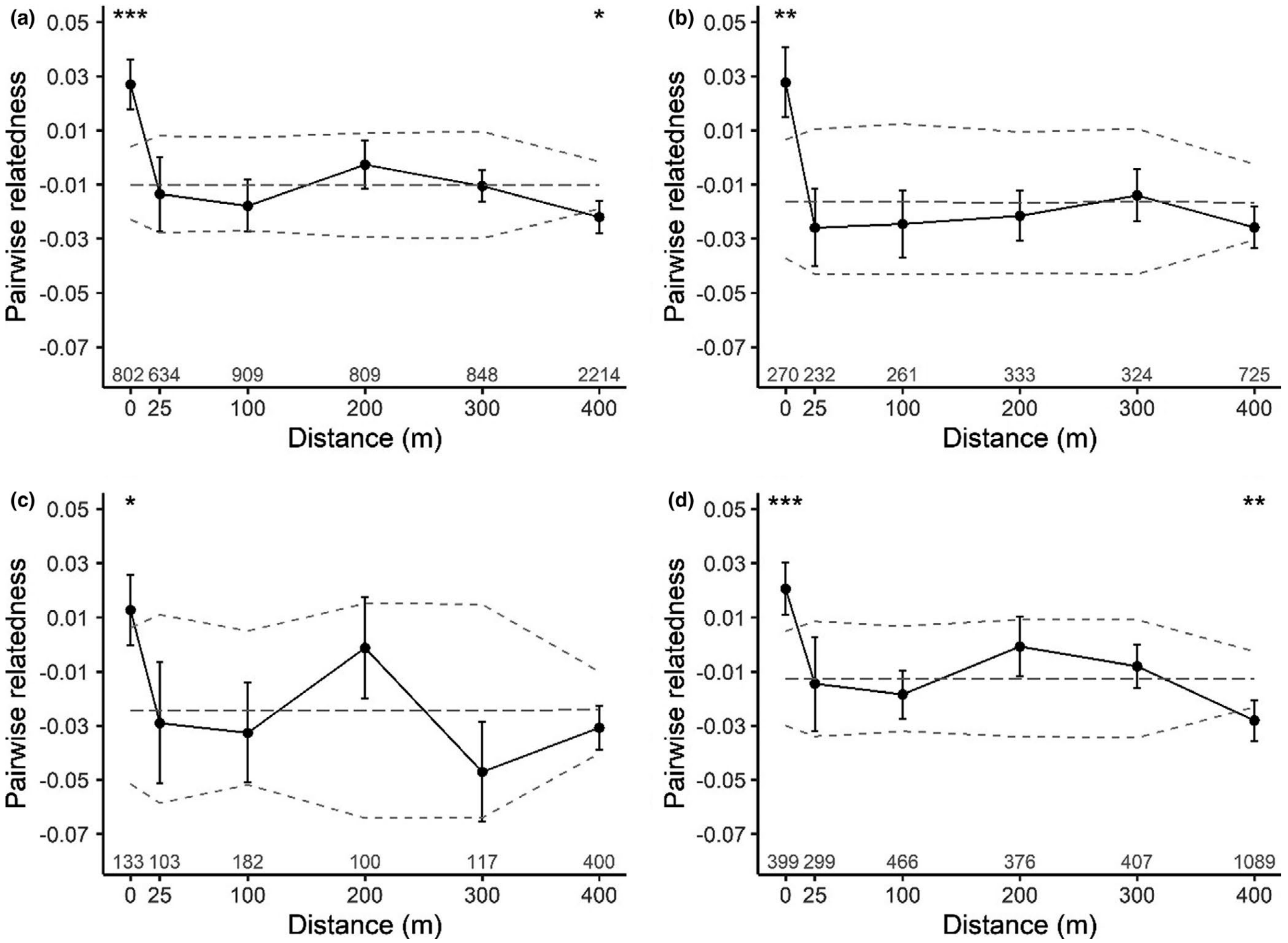

FIGURE 1 Mean pairwise relatedness ± *SE* within nesting trees (0 m distance) and over five further distance bands of inter-tree distances: (a) among all individuals, (b) among males, (c) among females and (d) between males and females. Error bars were generated by jackknifing over loci to approximate *SE*. Null mean pairwise relatedness and 95% CI generated through 20,000 data permutations are indicated by dashed lines. The number of pairwise comparisons is indicated above the *x*-axis for each distance band. $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$

number of compound nests in our population may be due to management practices at our study location that regularly involve nest removal. For analysis of relatedness of males within compound nests, we excluded any compound nests with just one marked male, leaving 24 suitable males from nine compound nests in five separate nesting trees to include in analyses. Seven of these compound nests housed two separate groups of monk parakeets and two nests had three separate groups occupying different nest chambers. Relatedness between males sharing a compound nest was on average 0.199 higher than relatedness of those males to the other males in the same nesting tree when including relatedness values for all male dyads in a compound nest (posterior mean =0.199, 95% credible interval =0.127–0.276, $p < .001$; Figure 2a). More conservative analyses gave qualitatively similar results: when within-chamber comparisons were excluded from the data set (posterior mean =0.183, 95% credible interval =0.100–0.271, $p < .001$; Figure 2b), and when a single male from multimale chambers was randomly selected for comparison with other males in the same compound nest combined with within-chamber exclusion (posterior mean =0.183, 95% credible interval =0.109–0.269, $p < .001$; Figure 2c).

We also compared the relatedness between males and the females that shared their compound nest to the relatedness between those males and all other females in the same nesting tree for 14 males from eight compound nests located in five different nesting trees. These compound nests comprised six nests occupied by two separate groups of monk parakeets and two nests containing three groups occupying separate nest chambers. In contrast to our findings for male–male relatedness, there was no significant difference between the relatedness of males to females that share a compound nest compared to the females occupying the rest of the same nesting tree with the credible interval overlapping zero (posterior mean =0.079, 95% credible intervals = −0.038 to 0.200, $p = .114$; Figure 2d).

The clustering of male relatives within compound nests could potentially drive the significant spatial genetic structure observed for males and for all birds within nesting trees, as described in the previous section. Therefore, we conducted additional spatial autocorrelation analyses for males and for all birds using the same distance bands as described previously, but randomly selected one male only from each compound nest to be included in analyses (for additional details see Supporting Information S3). Our results were

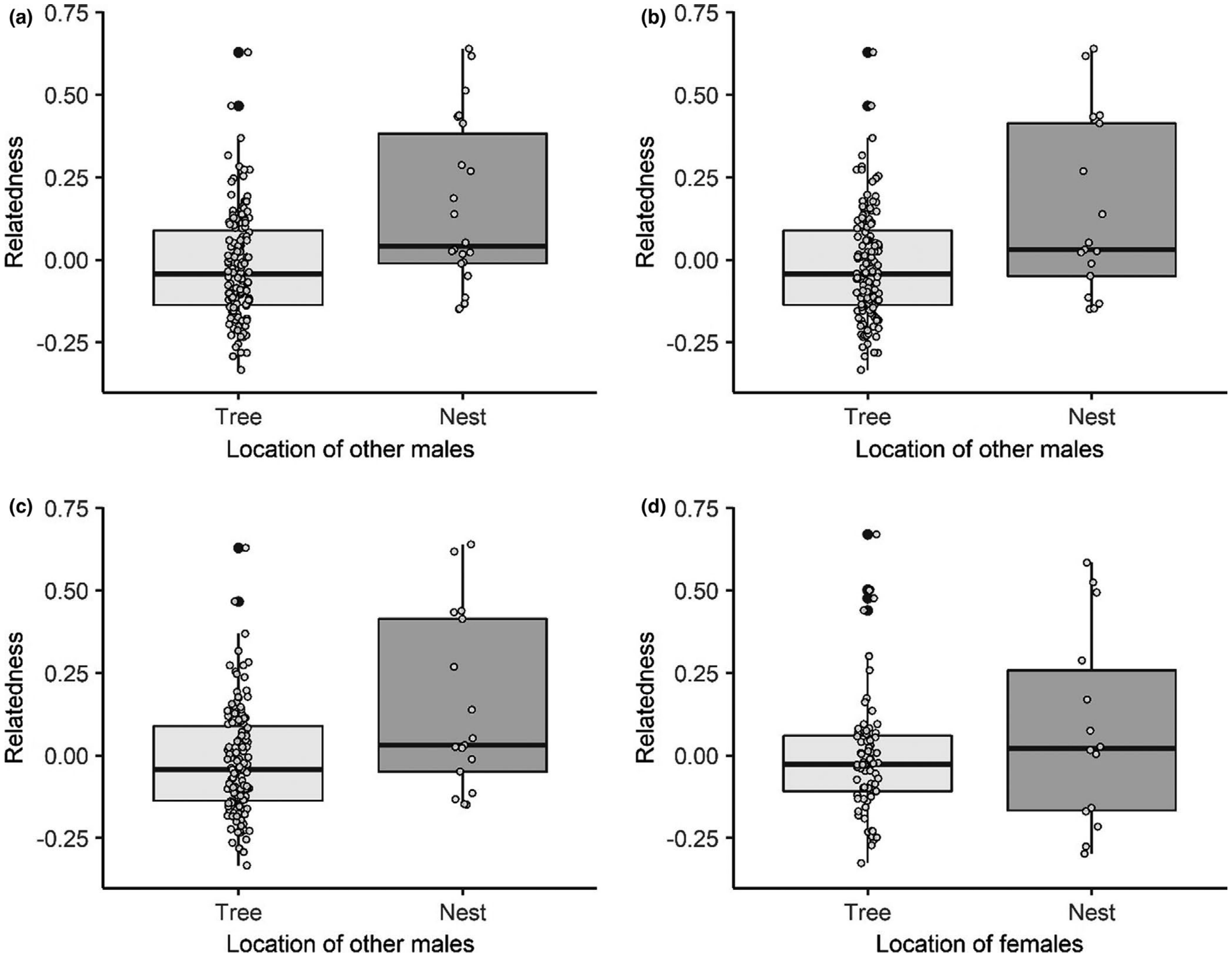

FIGURE 2 Dyadic genetic relatedness of individuals from compound nests to birds sharing the same compound nest and to birds occupying other nests in the same nesting tree for: (a) males compared to all other males sharing their compound nests and to males occupying other nests in the same nesting tree ($p < .001$); (b) males compared to other males sharing the same compound nest, excluding within-chamber comparisons, and to males occupying other nests in the same nesting tree ($p < .001$); (c) males compared to other males sharing the same compound nest with random selection of males from multimale chambers and excluding within-chamber comparisons, and to males occupying other nests in the same nesting tree ($p < .001$); and (d) males compared to females in the same compound nest, excluding mate comparisons, and to other females occupying other nests in the same nesting tree ($p = .114$). Boxplots indicate: the interquartile range (box upper and lower limits), median relatedness values (thick lines within boxes), minimum and maximum values excluding outliers (lines extending from boxes) and outliers (filled dots)

qualitatively similar to those we obtained when all males in compound nests were included in the analyses (Supporting Information S3; Figure S1), demonstrating that the significant spatial genetic structure of males and of all birds within nesting trees was not simply a function of kin being clustered in compound nests, but must also result from kin being clustered within trees.

3.4 | Breeding site fidelity

In the 2017 breeding season, we located 72 marked adults (23 female, 38 male, 11 unknown sex) in the 10 focal pine trees; 46 (64%; 16 female, 30 male) bred in the same tree in 2018 and 25 (54%; nine female, 16 male) of these bred in the same location for a third consecutive year in 2019. In 2018, a total of 113 marked birds (46 female, 66 male, one unknown sex, including the 46 still present from 2017) were located in the 10 focal pine trees and 51 (45%; 21 female, 30 male) remained in the same nesting tree in 2019. Thus, estimated annual site-fidelity ranged from 45% to 64%, although this disregards the fact that some of the birds not located again were likely to have died between breeding seasons.

The estimated annual survival rate for monk parakeets in our study site is 0.82 (Conroy & Senar, 2009). Therefore, of the 72 birds alive in 2017 we would expect 59 to have survived to 2018; 46 (78%) of these 59 putative survivors were observed to be faithful to their breeding site. Of the 112 birds alive in 2018 (one bird found dead in their nest during the 2018 breeding season was excluded from the total), 92 were likely to have survived to 2019, but just 51 (55%) of these putative survivors remained in the same nesting tree. However, it is important to note that in July 2018, all nests in the 10 focal nesting trees were removed by park authorities due to the risk they posed to the public. The apparently lower site fidelity in 2018–2019 relative to 2017–2018 may have been a consequence of this nest destruction.

In addition, we recorded 23 breeding dispersal events that involved adult birds moving between our 10 focal trees. During more extensive surveys in the rest of Ciutadella Park and across Barcelona to detect breeding dispersers, we located the nests of 92 marked adult birds, only two of which had dispersed from one of the focal trees. In total therefore, we recorded 25 breeding dispersal events by 24 birds (11 female, 13 male), 21 (84%) of which occurred following nest destruction in 2018. The median breeding dispersal distance for all dispersers was 37 m (range =5–464 m, mean =87 m ± 103 *SD*, *N* = 25 dispersal events), and there was no significant difference between the breeding dispersal distances of males and females (Z = −0.30, *p* = .76, *N* = 25; Figure 3).

Using data collected for a concurrent study of monk parakeet social associations (F. S. E. Dawson Pell, unpublished data), we identified 12 birds in 2018 and six birds in 2019 that had survived from the previous breeding season but whose nest locations were unknown. Taken together, we therefore sighted 62 birds (86%) in 2018 out of the 72 that nested in the 10 focal pine trees in 2017, and a total of 78 birds (70%) in 2019 out of the 112 that nested in the 10 trees in 2018. Therefore, the total numbers of survivors observed were similar to those expected to survive (82%) given typical survival rates for this species in Barcelona.

3.5 | Natal philopatry and dispersal

The nests of 83 birds ringed as nestlings were located over the course of the study. Seven birds were first located during their second breeding season and were excluded because we could not be certain that their observed nest location was necessarily their first nest following dispersal. This left 76 birds for the study of natal dispersal and philopatry, 74 of which were sexed.

Thirty-one birds (41%) were philopatric to their natal tree, males (*N* = 24) being more likely to remain than females (*N* = 7). Six of these (three males, three females) remained in the same chamber as at least one of their parents for the whole, or part of their first breeding season. Two males left their parents' nest chamber part way through their first breeding season, in both cases after being chased from the nest by parents during nest building and maintenance activities (one bird was observed being chased twice, the other bird was observed being chased four times). A further six males remained in the same nest as their parents, although they built their own nest chambers on to their parent's nest to form compound nests and made separate breeding attempts to their parents. These birds consisted of one trio of brothers, one dyad of brothers (see below) and an individual male. Four philopatric birds did not have marked parents, so we could confirm only that they were not sharing a nest chamber with individuals that could have been their parents (as these philopatric individuals were not sharing nest chambers with any unmarked birds). The remaining 15 birds built their own nests within their natal nesting trees entirely separate from their parents' nests. Forty-five of the 76 marked birds (59%; 17 females, 26 males and two unknown sex) dispersed to other nesting trees for their first breeding season.

Nineteen birds nested with a sibling (eight dyads of siblings and one trio) in their first year. For all but two of the dyads, we were able to confirm that the siblings nested with another bird, forming six trios and one group of four birds. The trio and four of the dyads of siblings were philopatric, nesting in their natal tree in their first breeding season; two of these groups used separate chambers in the same compound nest as their parents and the remaining four sibling

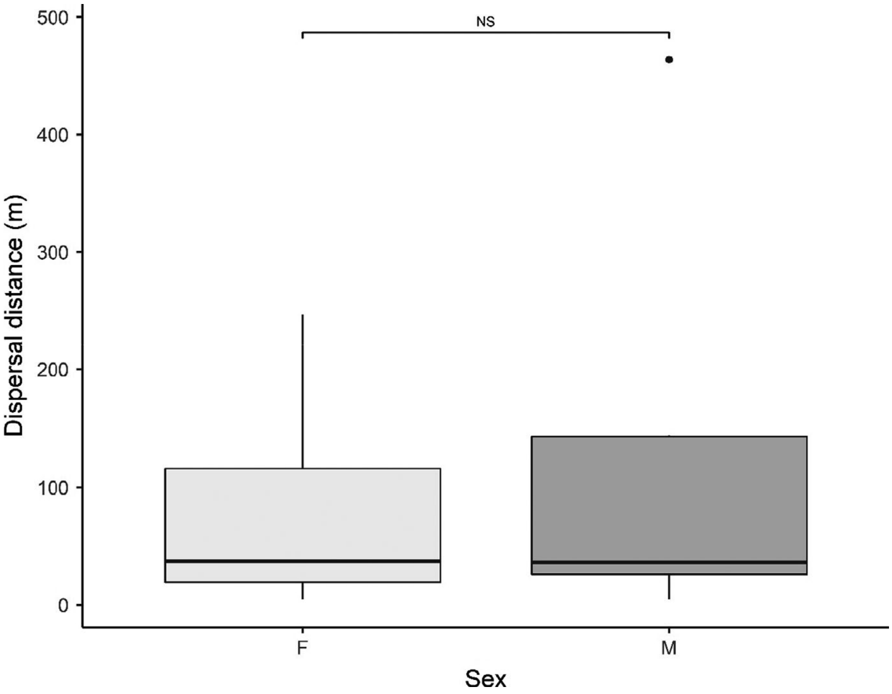

FIGURE 3 Breeding dispersal distances for monk parakeet: females (F; *N* = 11 dispersal events) and males (M; *N* = 14 dispersal events). Boxplots indicate: the interquartile range (box upper and lower limits), median dispersal distances (thick lines within boxes), minimum and maximum values excluding outliers (lines extending from boxes) and outliers (filled dots)

dyads had dispersed to another tree as coalitions. The trio and seven of the dyads of siblings were all males, and the remaining dyad was a male–female coalition and was one of the dyads that dispersed.

For all individuals, including philopatric birds and all members of sibling coalitions, median natal dispersal distance was 45 m (range =0–1795 m, mean =158 m ± 310 *SD*, *N* = 76). The natal dispersal distance of females (median 144 m) was significantly further than that of males (median 15 m) when including all members of sibling coalitions (Z = −2.44, *N* = 74, *p* = .015; Figure 4a). We also examined natal dispersal distances after removing one individual at random from each sibling pair and two individuals from the trio of siblings because these individuals (all males) were unlikely to have made independent choices on dispersal distance. In this more conservative data set, median natal dispersal for all birds was 48 m (range =0–1795 m, mean =145 m ± 258 *SD*, *N* = 66) and again the dispersal distance of females (median =144 m) was significantly further than that of males (median =16 m; Z = −2.44, *N* = 64, *p* = .015; Figure 4b). Removing the female from the male–female sibling pair rather than the male did not qualitatively change these results.

4 | DISCUSSION

Monk parakeets are unusual amongst parrot species in that they build their own stick nests that they use year-round for roosting and breeding (Eberhard, 1998; Forshaw, 1989; Spreyer & Bucher, 1998). Their nests can contain a single nest chamber or several individual nest chambers used by different pairs or groups. Nests are often loosely aggregated in the same and neighbouring trees. Here, we used a combination of population genetic analyses and detailed field observations to examine genetic structure in the monk parakeet and determine the demographic mechanisms driving the observed kin structure in this highly unusual social system. Our results revealed significant fine-scale genetic structure in our study population, with positive spatial autocorrelation of pairwise relatedness estimates among birds occupying the same nesting tree. Relatedness was higher than expected for all birds, among males, among females and between the sexes, indicating that relatives of both sexes are spatially clustered within nesting trees. This pattern was observed among adult birds after the period of natal dispersal and was therefore not the result of recently fledged individuals causing a temporary increase in spatial genetic structure (Scribner & Chesser, 1993).

We also showed that male monk parakeets are more related to other males sharing the same compound nest than to the males occupying the rest of the same nesting tree. This result held when we removed both within-chamber comparisons and when randomly selecting a bird from a multimale chamber for comparisons with other birds in the compound nest. There was no significant difference between the relatedness of focal males to females sharing the same compound nest when compared to the females in the rest of the tree. This result may indicate individuals avoid sharing compound nests with close relatives of the opposite sex. The pattern of clustering of relatives found here in monk parakeet nesting trees and compound nests echoes that found in a wide variety of taxa, from the large communal nests of sociable weavers (van Dijk et al., 2015) and the coteries of bell miners, *Manorina melanophrys* (Painter et al., 2000), to the communal nests of mound-building mice, *Mus spicilegus* (Garza et al., 1997), and the nests and colonies of a wide variety of social insects (e.g., Bono & Crespi, 2008; Pirk et al., 2001).

Such clustering of relatives can have diverse ecological, behavioural and evolutionary implications. Living or breeding near kin can result in fitness benefits in the absence of obvious cooperative behaviours, for example through increased reproductive success (Fowler, 2005; Pasenhu et al., 1998) or offspring survival (Brown & Brown, 1993). The fine-scale relatedness revealed by our analyses also creates an opportunity for kin-selected cooperation to operate

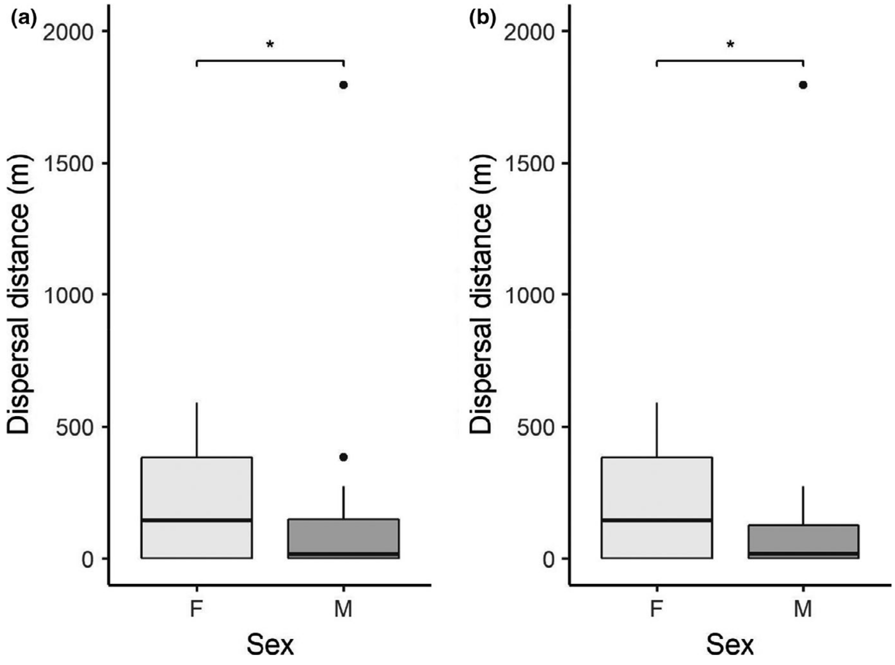

FIGURE 4 Natal dispersal distances for male and female monk parakeets including philopatric individuals: (a) all sexed individuals (males (M) *N* = 50, females (F) *N* = 24); (b) all sexed individuals excluding one/two birds from sibling coalitions (males *N* = 40, females *N* = 24). **p* < .05. Boxplots indicate the interquartile range (box upper and lower limits), median dispersal distances (thick lines within boxes), maximum values excluding outliers (lines extending from boxes) and outliers (filled dots)

in the monk parakeet. Monk parakeets exhibit a range of apparently cooperative behaviours that may have been influenced by aggregations of kin: for example, cooperative breeding (Bucher et al., 1990), the use of alarm calls in predator defence (F. S. E. Dawson Pell pers. obs.) and potentially other more "cryptic" kin-directed behaviours, such as foraging or breeding associations (Hatchwell, 2010). Moreover, associating with kin in compound nests may allow for a variety of additional kin-selected benefits in monk parakeets. For instance, nest building is energetically expensive (Mainwaring & Hartley, 2013), and monk parakeets use and maintain nests year-round (Bucher et al., 1990), so the nest may represent a significant energetic investment. Initiating a new chamber on a pre-existing nest may be less energetically and temporally expensive than constructing a new nest with less structural support (Martín & Bucher, 1993). In addition, the nest structures themselves may help to reduce energy expenditure. Like the nests of sociable weavers (van Dijk et al., 2013), monk parakeet nests act as buffers against fluctuations in external temperature, and are particularly effective at thermoregulation in high temperatures (Viana et al., 2016). This could reduce energy expenditure by both nestlings and adults to maintain body temperature within optimal limits (Viana et al., 2016). If larger, compound nests are more effective at thermoregulation, then allowing relatives to build new chambers onto existing nests may result in energetic benefits for both parties. A further benefit of sharing compound nests may come from a reduction in the time and energy costs of nest maintenance or defence due to the greater number of birds occupying the nest. There are, therefore, a variety of avenues for both direct and indirect benefits of sharing compound nests with relatives, so the benefits of philopatry may be highest when new chambers are built on to the existing parental nest.

In many social birds, particularly those that breed cooperatively, prolonged associations of relatives and hence genetic structure arises through delayed or limited dispersal (Ekman et al., 2004; Woxvold et al., 2006). In such cases, members of one sex tend to disperse before breeding occurs so inbreeding risk is relatively low (Koenig & Haydock, 2004). In species with "kin neighbourhood" social systems (e.g., Dickinson & Hatchwell, 2004; Koenig & Haydock, 2004; Preston et al., 2013), genetic structure exists among adults even after the period of natal dispersal, leading to a risk of inbreeding (Dickinson et al., 2016; Lee, Simeoni, et al., 2010; Leedale et al., 2018; Lukas & Clutton-Brock, 2011) and an increased chance of kin competition (Moore et al., 2006; Platt & Bever, 2009). We found that adult male and female monk parakeets live in kin neighbourhoods, with adults within nesting trees significantly more related than expected by chance. However, despite this close nesting proximity of relatives of opposite sexes, opposite sex relatives did not commonly share nests and we did not detect significant inbreeding in our population. A similar situation exists in sociable weavers, where natal philopatry to the colony is high, but individuals disperse within the colony, effectively dispersing from the family group whilst remaining in the natal colony, a strategy that may help to mitigate the risk of inbreeding (van Dijk et al., 2015). This is similar to what we observed in monk parakeets, where despite observations of natal philopatry in both sexes, the majority (62%) of philopatric birds disperse from the natal nest to build a new nest within the same nesting tree but independent of parental nests (see below).

A passive mechanism of inbreeding avoidance, such as sex-biased natal dispersal, may substantially reduce the risk of inbreeding (Johnson & Gaines, 1990). However, we still detected significant genetic structuring between the sexes within nesting trees, indicating that such passive processes may be insufficient to remove the risk of inbreeding completely. In such cases, if inbreeding is sufficiently costly there may be selection for active mechanisms of kin discrimination, such as via kin-recognition or avoidance of familiar individuals as mates (Leedale, Li, et al., 2020; Sherman et al., 1997). The monk parakeet has extensive vocal learning capabilities (Forshaw, 1989), and signatures of individual identity have been detected (Smith-Vidaurre et al., 2020) that may allow discrimination between familiar and unfamiliar individuals, or kin and nonkin. Recognition and association of close kin using vocal cues has been demonstrated in a variety of cooperatively breeding species (e.g., Crane et al., 2015; McDonald & Wright, 2011; Sharp et al. 2005), and it has been suggested that the same mechanism may also be used for active avoidance of close inbreeding in the long-tailed tit (Leedale, Simeoni, et al., 2020). Further study of vocal recognition in the monk parakeet in the contexts of both cooperation and inbreeding avoidance would be worthwhile alongside a detailed study into relatedness of monk parakeet pairs.

Our investigation of the demographic processes generating the observed genetic structure at the level of the compound nest and nesting tree revealed three mechanisms: high nest site fidelity of adults, limited natal dispersal, and coordinated dispersal and nesting of siblings. First, we found high breeding site fidelity in adult monk parakeets, with 55%–78% of birds remaining in the same nesting tree between years when taking annual survival probabilities into account. In July 2018, all nests were removed in our study site as part of an invasive species management strategy, which probably explains the lower site fidelity between 2018 and 2019. However, high breeding site fidelity (55%) was still observed after nest removal, showing that individuals remained faithful to nest sites despite significant disturbance. Incidentally, routine nest removal may also limit the size of compound nests at our study site; nests containing 60 chambers are seen in parts of the native range of monk parakeets (Burger & Gochfeld, 2005), but not in Barcelona. Larger compound nests develop over time, so regular nest removal is likely to limit the number of such nests. Site fidelity in this species was expected to be high because nests are used year round and maintaining the same nest is presumably less costly than constructing a new nest elsewhere. On the other hand, long-term occupancy of older or larger nests may incur the potential cost of increased parasite load (e.g., Brown et al., 2017; Spottiswoode, 2007). The parasite load of monk parakeet nests during the breeding season is high (F. S. E. Dawson Pell pers. obs.), and the number of parasites on adult monk parakeets increases with increasing population density (Mori et al., 2019), although no comparison of parasite density in relation to nest size has yet been conducted.

High site fidelity by breeding adults alone does not explain the existence of kin-structured populations. Rather, it must operate in combination with other traits that ensure prolonged association of relatives, such as limited and/or coordinated natal dispersal, both of which we observed here. Natal dispersal distances were short (median distances of 16 m for males and 144 m for females) despite survey areas covering 6 km from the natal ringing locations. Our natal dispersal distances are considerably shorter than those reported in the native range (median 1230 m), but that estimate was based on just four individuals (Martín & Bucher, 1993). Long-distance dispersal over 100 km has also been detected in the invasive range using genetic data (Gonçalves da Silva et al., 2010). Despite female-biased dispersal, we found significant genetic structure both within and between sexes at the level of the nesting tree. This reflects a degree of natal philopatry in both sexes, with some 1-year-old birds remaining either in the same nest or nesting tree as their parents. Building a separate nesting chamber on to the nest of parents is one mechanism for the formation of compound nests, and explains why males in compound nests are more related to each other than to males in the rest of the nesting tree. Taken together, limited natal dispersal combined with high breeding site fidelity by adults provides a mechanism for the formation of kin structure in this species that is widespread among social animals (Rubenstein & Abbot, 2017).

Finally, we also detected coordinated dispersal of sibling coalitions. These were composed predominantly of male siblings, but also involved one male–female sibling dyad, showing that while male coalitions are the most common coalition type in monk parakeets, mixed-sex coalitions do also occur. Four of these coalitions dispersed to a different nesting tree, but five remained in their natal tree. Dispersal of sibling coalitions has been observed in a number of bird species, including the vinous-throated parrotbill (Lee, Lee et al., 2010), brown jay, *Cyanocorax morio* (Williams & Rabenold, 2005), and Arabian babbler, *Turdoides squamiceps* (Ridley, 2012). The majority of such studies involve single-sex coalitions, for example all male coalitions in the brown jay (Williams & Rabenold, 2005), but mixed-sex coalitions have also been reported in a number of species (Lee, Lee, et al., 2010; Sharp et al., 2008). These observations contrast with the general expectation that dispersal dilutes kin structure and precludes opportunities for kin cooperation; instead, dispersing in kin coalitions presents opportunities for kin-selected cooperation and additional benefits of associating with kin post-dispersal. For example, in the long-tailed tit dispersal in kin coalitions allows helpers to direct their assistance towards relatives even after dispersal (Sharp et al., 2008). Our results indicate that dispersal does not preclude opportunities for kin-selected cooperative behaviour in the monk parakeet and that dispersal of sibling coalitions may maintain kin-structure without requiring natal philopatry.

In conclusion, we have presented evidence of fine-scale genetic structure in an invasive population of monk parakeets, with relatives of both sexes clustered within nesting trees and male relatives aggregated in compound nests. Such spatial aggregations of relatives provide an opportunity for fitness benefits through kin-directed cooperation in a variety of behaviours, but also increase the risk of kin competition and inbreeding, although we found no evidence that inbreeding actually occurs. We also identified the key demographic characteristics that lead to kin-structured populations. Our study is the first to define fine-scale population genetic structure in this highly unusual social system and has implications for the evolution of social behaviour, colony formation and cooperation in this species.

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AUTHOR CONTRIBUTIONS

F.S.E.D.P., B.J.H. and J.C.S. designed the study. F.S.E.D.P. and J.C.S. conducted the fieldwork, F.S.E.D.P. conducted laboratory work and F.S.E.D.P. and D.W.F. analysed the data. F.S.E.D.P. wrote the paper with input from co-authors. All authors read and approved the final manuscript.

DATA AVAILABILITY STATEMENT

Microsatellite genotypes, nest locations, relatedness and dispersal data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.ffbg79csb.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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