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Variable social organization and breeding system of a social parrot revealed by genetic analysis

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Social organization and contributions to reproduction vary widely within and between species that breed in groups. Such variation often arises from the process of group formation, which drives patterns of relatedness and hence the degree of social conflict and co-operation between group members. Using field observations and molecular genetics, we investigated breeding behaviour in an urban population of the highly social Monk Parakeet *Myiopsitta monachus* to address two objectives. First, we investigated breeding-group frequency, composition and formation, finding that 19% of breeding units were co-operative groups, ranging in size from three to five birds, the remainder being pairs (81%). Group composition was variable with multi-male, multi-female and multi-male–female groups. Relatedness in breeding groups also varied with many containing kin, but some groups containing only non-kin. This variation reflected alternative routes to group formation, including offspring retention by pairs, sibling coalitions and aggregation of unrelated individuals. Secondly, we investigated productivity, reproductive investment and patterns of parentage in relation to the size of breeding units. Productivity did not differ significantly between pairs and groups. We detected extra-pair paternity in 27% of broods raised by pairs, and parentage shared among more than two members of most breeding groups, with joint-nesting by females detected in multi-female groups. In conclusion, the breeding system of the Monk Parakeet defies simple definition, instead showing variable reproductive roles, with potential for both indirect and direct fitness benefits.

Keywords: co-operative breeding, Monk Parakeet, *Myiopsitta monachus*, parentage, parrot.

Co-operative breeding, systems in which groups of three or more individuals contribute care to breeding attempts, occurs in c. 9% of bird species (Cockburn 2006). The social organization of such groups and individuals' contributions to reproduction vary widely both within and between species (Cockburn *et al.* 2017). The most frequent form of co-operative breeding involves a breeding pair with non-breeding 'helpers' that assist in raising offspring to which they are often related. However, the social groups of co-operative species may comprise multiple socially monogamous co-breeding pairs or include various systems of co-operative polygamy in which more than one male and/or female participate in breeding (Emlen 1991, Cockburn 1998, Koenig & Dickinson 2016, Cockburn *et al.* 2017). Among co-operative breeders, group-breeding is occasionally obligate (Heinsohn 1992), but it is typically facultative with pair- and group-breeding found in the same population, with multiple potential routes to breeding-group formation. For example, helper-at-the-nest systems typically form via offspring delaying natal dispersal and helping their parents to raise later broods (Koenig *et al.* 1992), while aggregations of multiple breeders typically arise via joint defence of a single territory and sharing of a single nest (Koenig & Dickinson 2016).

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Group composition can therefore be diverse and include only adults or a mixture of juveniles and adults (Preston *et al.* 2013, Barve *et al.* 2021). There may also be variable skew in reproduction, with either single or multiple breeders of each sex (Magrath *et al.* 2004), and supernumaries may be exclusively male (Mulder *et al.* 1994), mostly female (Komdeur 1996) or a mixture of both sexes (Green *et al.* 2016). Importantly, groups are often composed of relatives, although this is far from universal, with groups in some species composed entirely of unrelated individuals, or a mixture of kin and non-kin (Hatchwell 2009, Riehl 2013). This remarkable diversity in social organization has important consequences for the benefits that group members may derive, as well as for the intensity of co-operation and conflict between them. Breeding in groups can bring a variety of direct fitness benefits that enhance individuals' personal survival or their current or future reproductive success (Emlen 1991, Cockburn 1998). Group members may also accrue indirect—kin-selected—benefits via the increased fitness of non-descendant kin (Hamilton 1964, Dickinson & Hatchwell 2004). The widespread occurrence of familial social groups in birds (Drobniak *et al.* 2015) indicates the important role that such kin-selected benefits are likely to have played in the evolution of sociality in many species (Griesser *et al.* 2017). The overall aim of this study was to investigate group-living in the extraordinary social system of Monk Parakeets *Myiopsitta monachus*. Monk Parakeets are native to South America, but they have successfully established invasive populations outside the native range across South and North America, Europe and Asia (Forshaw 1989, Russello *et al.* 2008, Bush *et al.* 2014, Postigo *et al.* 2019). Unusually among parrots, Monk Parakeets are not cavity-nesters; instead, individuals use interlaced sticks to construct large, conspicuous nests that may contain a single nest chamber or multiple chambers in a compound structure (Fig. S1a; Eberhard 1998). Nests can vary widely in size and number of occupants. Single compound nests have been reported to contain up to 100 pairs of parakeets (Burger & Gochfeld 2005), but where the species is heavily managed, such as in urban areas in their invasive range, the number of chambers per nest is typically lower. For example, in Catalonia the majority of nests contain just one or two chambers, although nests with up to 36 chambers have been reported (Domènech *et al.* 2003). Nest structures are frequently aggregated, with large groups of nests occupying the same or neighbouring trees (Bucher *et al.* 1991, Eberhard 1998). Reports of co-operative breeding in the parrot family are scarce, with just 5% of parrots described as co-operative by Cockburn (2006), using a broad definition that included co-operative polyandry and polygynandry. Monk Parakeets have been reported to display characteristics indicative of co-operative breeding, including philopatry and delayed breeding, as well as some limited evidence for helpers assisting in breeding attempts (Bucher *et al.* 1991, 2016, Eberhard 1998). Relatives are clustered within compound nests and within shared nesting trees, resulting in 'kin-neighbourhoods' that form through limited and co-ordinated natal dispersal and high breeding-site fidelity (Dawson Pell *et al.* 2021). In addition, genetic evidence from a single breeding trio in the native range points towards a high degree of relatedness in groups sharing a single nest chamber, a male 'helper' being a full sibling of the breeding male (Bucher *et al.* 2016). However, this evidence is anecdotal and the breeding system of the Monk Parakeet remains very poorly known, with unanswered questions regarding the frequency of breeding in pairs and in groups, the composition of groups, and patterns of parentage, relatedness and (allo)parental investment. Here, we used field observations and molecular genetic analyses to investigate the social organization and breeding behaviour of an invasive urban population of Monk Parakeets. We addressed two objectives: first, we characterized the breeding system of individually marked birds by quantifying the social and genetic composition of breeding units and the process of group formation. Secondly, we examined patterns of parentage, productivity and reproductive investment in pairs and groups.

METHODS

Study system

We observed Monk Parakeets at nests in Ciutadella Park, Barcelona, Spain (41.39°N, 2.17°E). Ciutadella Park comprises c. 30 ha of native and exotic vegetation and contains a high density of Monk Parakeet nests; it is a public access park and Monk Parakeets are habituated to humans. Monk Parakeets in our study population were individually marked using leg rings and highly visible, unique neck collars (Fig. S1b) that enable individual identification at up to 40 m distance (Senar *et al.* 2012). We ringed birds either as nestlings or as adults, the latter being captured using either gas-propelled nets, a baited trap or in the nest during incubation; c. 64% of the breeding population was marked during this study. We used a cherry picker to access nests (Fig. S1c); no birds abandoned their nests following nest visits. We accurately recorded the age (in years) of birds that had been marked as nestlings, but individuals caught as adults were assigned a minimum age, assuming that they were 1-year-old in the year in which they were ringed; Monk Parakeets cannot be aged from morphometrics beyond 1 year of age.

DNA extraction and genotyping

Blood samples (maximum 100 μL) were extracted from the brachial or jugular vein for genetic analyses and sex determination. For details of blood sample storage and DNA extraction, see Dawson Pell *et al.* (2020). Male and female Monk Parakeets are indistinguishable in the field, so marked birds were sexed using the sexing marker Z002B (Dawson 2007). We genotyped samples at 21 microsatellite loci: Mmon01, Mmon02, Mmon03, Mmon04, Mmon07, Mmon09, Mmon10, Mmon11, Mmon13, Mmon14, Mmon15 and Mmon16 (Dawson Pell *et al.* 2020); MmGT060, MmGT046, MmGT105, MmGT030, MmGT071 and MmGT057 (Russello *et al.* 2007); TG03-002 and TG05-046 (Dawson *et al.* 2010); and CAM-20 (Dawson *et al.* 2013). For further details of multiplexes and marker quality assessment, see Dawson Pell *et al.* (2021). PCR and allele-scoring protocols followed Dawson Pell *et al.* (2020), and all alleles were scored blind to the identity and sex of the bird.

Behavioural observations

Observations were conducted during the breeding season from April to July 2018 and 2019 at nests in 10 mature pine trees, *Pinus halepensis*, in Ciutadella Park. Initially, we surveyed trees and individually labelled each nest chamber with a numbered tag visible from the ground; no nests were deserted as a consequence of this disturbance. Each nest was observed for 1 h every 2–7 days in 2018 and for 1 h every 2–11 days in 2019. Multiple nests in a single nesting tree were observed simultaneously by the observer (FSEDP) from the ground using binoculars. Observations at each nest alternated between the morning and afternoon, and between early and late morning/afternoon, so that the range of available daylight hours was covered. A total of 390 h of observation were conducted across 2 years (2018: 263 h, 22 h per chamber; 2019: 127 h, 14–15 h per chamber).

In the 10 focal pine trees there were 72 nests containing 149 separate nest chambers by the end of observations in 2018. Of these, 112 chambers were occupied and 74 were used in breeding attempts by 113 marked birds and at least 64 unmarked birds. In 2019, there were 81 nests containing 98 chambers, 92 of which were occupied, 76 being used in breeding attempts by 103 marked birds and at least 64 unmarked birds. There were fewer compound nests and fewer unoccupied chambers in 2019 owing to the removal (as a control measure) of all the Monk Parakeet nests in pine trees in July 2018, so there were no older nests, which are more likely to have multiple chambers (see Results). The age of observed birds ranged from 1-year-old to at least 13-years-old.

Breeding-group composition and formation

We characterized breeding unit composition by determining the number of birds attending a nest chamber to identify pairs and groups engaged in breeding attempts. If one or more unringed birds were present, we recorded the maximum number of unringed birds seen attending at the same time. The genetic relatedness and sexes of marked members of breeding groups were determined subsequently. Dyadic genetic relatedness between individuals in breeding pairs and groups was estimated in SPAGeDi v.1.5 (Hardy & Vekemans 2002) using Queller and Goodnight's (1989) coefficient of relatedness. We used the genotypes of all adults nesting in the 10 focal trees in 2018 and 2019 (n = 134) to generate allele frequencies for estimating genetic relatedness. For breeding pairs in which both individuals were genotyped, we calculated dyadic relatedness and compared the mean relatedness of all pairs to zero using a one-sample t-test. For breeding groups, we calculated all dyadic relatedness values among individuals within each group and mean dyadic relatedness values per group. We compared relatedness estimates between same-sex and opposite-sex group members using *t*-tests. Each dyad was included only once in calculations of genetic relatedness, even if that particular dyad persisted across years.

We also used the social pedigree to explore routes to breeding-group formation. Our social pedigree began in 2017 with a large ringing effort for offspring fledged in that year. Nestlings were also ringed in 2018 and 2019, with social parents assigned to them from nest observations. The social pedigree is incomplete but informative because it is likely to be the information about relatedness that birds have access to if kin recognition relies on learned associations.

Productivity, reproductive investment and parentage

Productivity of pairs and breeding groups

Productivity was determined by checking the contents of nest chambers, accessed by a cherry picker, at approximately 2-week intervals from April to July in 2018 and 2019. This interval between nest checks was short relative to Monk Parakeet incubation (c. 24 days) and nestling (c. 40 days) periods, permitting accurate recording of key events. We compared clutch sizes produced by pairs and breeding groups using a Poisson generalized linear model (GLM), with year as an additional explanatory factor. We examined whether breeding groups or pairs were more likely to fledge any offspring (Y/N) using a binary logistic regression GLM with a logit-link function, including year as an explanatory factor. Then, using only pairs and groups that fledged at least one chick, we compared the number of chicks attaining ringing age of >21 days old (a proxy for fledgling number; the last of two to three nest visits per breeding attempt was timed to coincide with ringing age) using a Poisson GLM, again including year as an explanatory factor. We also compared clutch sizes for multi-female breeding groups and multi-male breeding groups using a Wilcoxon rank sum test. All data were for first broods, which represent the main annual reproductive investment in the study population (Senar *et al.* 2019). These and all later statistical tests were performed in R v.3.5.0 (R Core Team 2018), with a significance level of $P = 0.05$.

Investment by group members

We investigated provisioning of offspring in two ways. First, we observed nest visits in observation periods during the nestling phase, recording when an individual entered a nest chamber but excluding any visits when it was carrying or manipulating nest material. Nestling provisioning by Monk Parakeets cannot be observed directly because feeding is by regurgitation within the nest chamber, so we assumed any bird entering the nest chamber provisioned nestlings, although we could not confirm that such visits always resulted in nestlings being fed. Secondly, we recorded instances of fledglings being fed by identifiable adults outside the nest, either in the natal tree during nest observation periods or opportunistically during surveys of the field site.

Copulations and parentage

To determine the mating patterns of Monk Parakeets, we recorded all copulations seen during nest observation periods and during surveys of the field site, noting whether either or both individuals were marked. We determined parentage of 27 broods (17 in 2017 and 10 in 2018) where all social parents and all chicks were marked and genotyped. In 2017, nest occupants were identified in surveys of Ciutadella Park and surrounding areas, with 73 trees observed for c. 2 h each (total of c. 146 h). In 2018, social parents were identified during dedicated nest observations totalling 263 h. Therefore, while we are confident that social parents were correctly assigned for all broods in 2018, we assess parentage in 2017 more cautiously.

Blood samples were collected when nestlings were ringed, so genotypes were obtained only for nestlings that reached >21 days old. DNA samples were not collected from unhatched eggs, nor from nestlings that died before 21 days old but whose bodies were still present in the nest. We performed parentage analyses using the maximum-likelihood approach applied in Cervus v.3.0.7 (Kalinowski *et al.* 2007). We estimated allele frequencies for all sampled birds from 2017 and 2018 ($n = 249$) at the 21 loci detailed above. However, during initial parentage analyses we noted that a large proportion of mismatches between offspring and their social mother occurred at one locus (*Mmon07*), all involving a single base-pair difference and so probably caused by scoring error. Therefore, we excluded this locus for parentage analyses.

We performed separate parentage simulations and analyses for broods attended by pairs and breeding groups, and also for broods in 2017 and 2018 owing to the different numbers of marked candidate parents in each year, and to prevent individuals being included in both offspring and parent analyses. For broods attended by pairs, we assigned the social mother as the known parent and then ran paternity simulations and analyses. For broods attended by groups we conducted parent-pair simulations and analyses, because we could not be certain of the identity of the putative mother, particularly when more than one female was present at the nest. In each year we included all genotyped adults as potential parents; in 2018 we included 66 possible candidate fathers (in pair and group analyses) and 46 possible candidate mothers (in pair analyses only), and in 2017 we included 42 possible fathers (in both analyses) and 29 possible mothers (pair analyses). We also took account of relatives in the population during simulations, because relatives of both sexes live in close proximity in shared compound nests and/or nesting trees (Dawson Pell *et al.* 2021), which may influence parentage analyses. To assess the number of relatives within the pool of candidate mothers and fathers we used maximum-likelihood relationship estimations in ML-RELATE (Kalinowski *et al.* 2006), and quantified the proportion of individuals assigned as having either a parent–offspring or full-sibling relationship with another individual in 2018. This estimate was 3% between candidate mothers and 2% between candidate fathers, and these values were applied in parentage simulations in both years. To estimate the proportion of sampled candidate parents, we used the numbers of marked and unmarked birds within the 10 focal trees in 2018 because these numbers were the result of the most extensive observations. In 2018, we estimated that 113 birds in focal trees were marked and 64 were unmarked, so we assumed that 64% (113/177) of potential parents were sampled in both years. Both simulations used 100 000 offspring, an estimated genotyping error rate of 3.1% (based on previous estimates; see Dawson Pell *et al.* 2021), 64% of candidate parents sampled, a minimum of 10 loci typed, 2% of males having first-order relatives (both analyses), 3% of females having first-order relatives (parent pair simulation only) and 97% of loci being successfully typed (calculated during allele frequency analysis). We examined all mismatches with assigned parents thoroughly and accepted those with just one or fewer mismatches between offspring and a likely parent. One offspring had two mismatches with both the putative mother and father, but as these were the social parents and the trio (offspring, mother and father) was assigned with 95% confidence we accepted this assignment.

To corroborate the results of parentage analyses we used SPAGeDI (Hardy & Vekemans 2002) to estimate pairwise relatedness within broods using Queller and Goodnight's (1989) coefficient of relatedness. First, we compared pairwise relatedness within broods produced by apparently sexually monogamous parents to the relatedness values in broods with evidence of either extra-pair paternity or mixed parentage (i.e. co-breeding), using a linear mixed model, with extra-pair paternity/mixed parentage (Y/N) as a fixed effect and brood ID as a random effect. We also compared the mean relatedness for broods having evidence of extra-pair paternity/mixed parentage and those with no such evidence using a Wilcoxon rank sum test. Maximum-likelihood estimates of relatedness between social siblings in ML-RELATE (Kalinowski *et al.* 2006) were also used to assign relationships as full-sibling, half-sibling and unrelated individuals. Finally, we visually assessed the relationship estimates from ML-RELATE against the relatedness estimates from SPAGeDI to see whether similar patterns were detected using these different approaches.

RESULTS

Breeding-group composition and formation

Most nest chambers used for breeding were occupied by a pair (81%), but 19% (18% in 2018, 20% in 2019) were occupied by groups of three to five individuals (Fig. 1a). Most groups occupied a single nest chamber, in which they bred, but a minority of groups (6/27 across both years) also occupied a second chamber that was used either for roosting ($n = 5$) or breeding ($n = 1$). A further two chambers were occupied by non-breeding groups, one containing three birds and the other four. The estimated frequency of breeding groups was potentially conservative because not all the birds attending a nest were necessarily marked, but our intensive observations suggest that any misclassifications were minimal. The mean size of

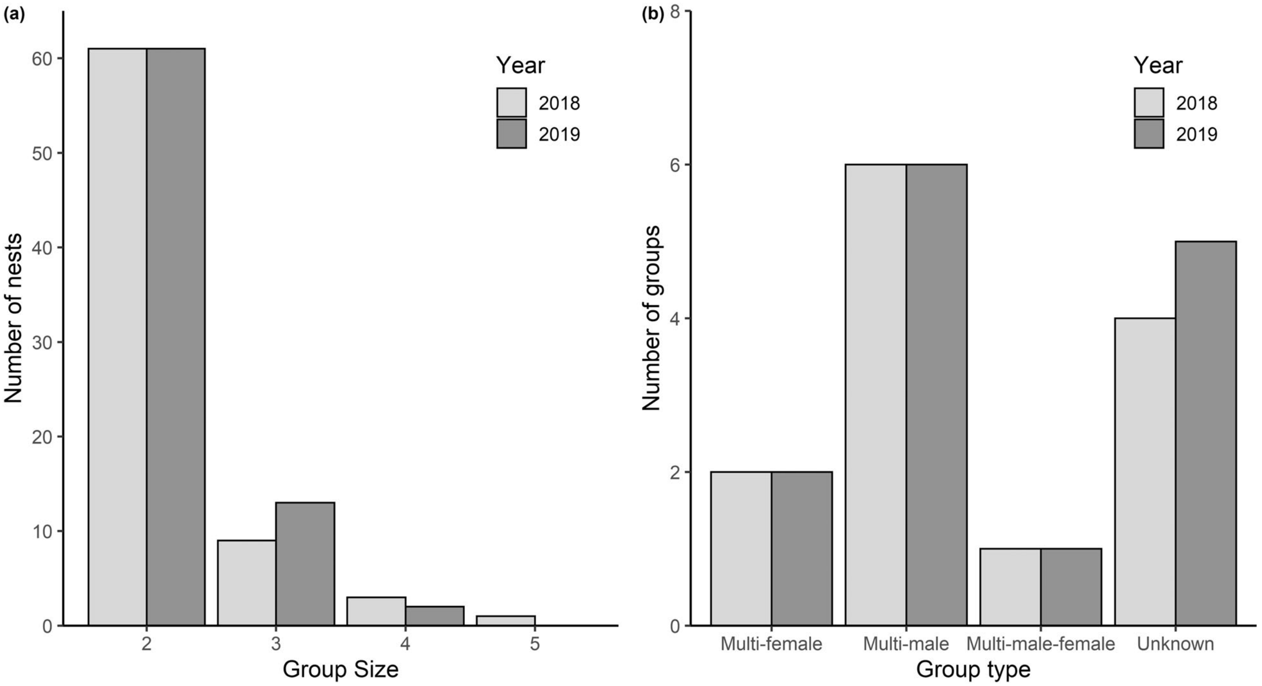

Figure 1. (a) Number of nest chambers attended by pairs (group size 2) and breeding groups (group size 3–5) of Monk Parakeets in 2018 (*n* = 74 nest chambers) and 2019 (*n* = 76 nest chambers). (b) Number of each group type: multi-female, multi-male and multi-male–female in 2018 and 2019 (*n* = 27 groups). Groups shown here all engaged in breeding attempts.

breeding groups (excluding pairs) was 3.3 ± 0.5 sd (*n* = 27).

We ringed, sexed and genotyped all birds in 13 out of 27 groups and deduced the sexes of unmarked birds from observations in a further five groups, revealing variable group composition. Groups contained either one female and more than one male ('multi-male' groups, 46% across both years), one male and more than one female (' multi-female' groups, 15%), two or more of each sex ('multi-male–female' groups, 8%) or were of unknown composition (31%; Fig. 1b). All groups of unknown sex composition could only have been multi-male or multi-female, as each contained three birds.

We identified the routes to group formation for a minority of groups (*n* = 12) using social pedigrees. Eight (30%) of the 27 breeding groups contained only 1-year-old birds, and in seven cases these included social siblings (six male duos and one male trio); the other group contained three 1-year-old birds, all from different nest chambers. In four groups (15%), offspring (three females, two males) remained with either one or both parents to form a group. These cases indicate that groups may form either through delayed dispersal of offspring, through male sibling coalitions pairing with a female, or by unrelated birds breeding together.

Genetic pedigrees provided more extensive information on group formation (*n* = 22 groups). Dyadic relatedness values between group members ranged from unrelated individuals to that expected for first-order kin when including all groups (Fig. 2a,b); similar patterns were observed when including only those groups with all members marked (*n* = 12 groups; Fig. 2c,d). These results indicate that some groups contained multiple close relatives (which could have resulted from delayed dispersal or through sibling coalitions), while others contained only unrelated individuals, as suggested by pedigree relationships. Collectively, our findings show that routes to group formation in the Monk Parakeet are variable.

Our conclusion of heterogeneous group origins is supported by the age profile of birds in breeding groups, which ranged from 1-year-old to at least 6-years-old (mean 2.1 ± 1.6 sd, *n* = 68, including 31 birds ringed as nestlings and 37 with minimum ages assigned as adults). Some groups contained a mix of young (1-year-olds) and older birds up to

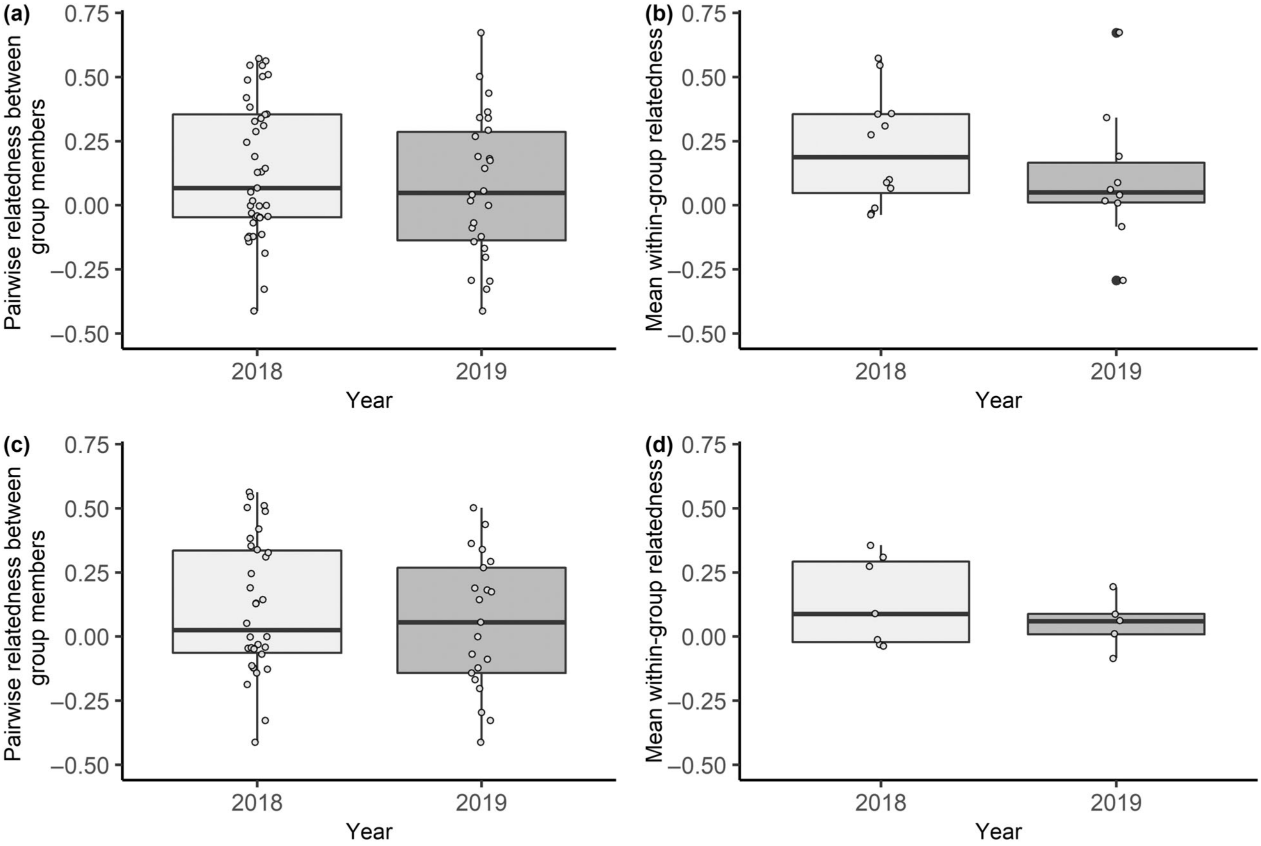

Figure 2. (a) Pairwise Queller and Goodnight relatedness estimates between members of breeding groups of Monk Parakeets in 2018 (n = 41 pairwise comparisons) and 2019 (n = 26) including all individuals; and (b) mean within-group relatedness values for breeding groups in 2018 (n = 12 groups) and 2019 (n = 10 groups) when all groups with at least one comparison were included. (c) Pairwise relatedness between breeding group members in 2018 (n = 34 pairwise comparisons) and 2019 (n = 21) only including birds for which the whole group was genotyped; and (d) mean within-group relatedness values for breeding groups in 2018 (n = 7 groups) and 2019 (n = 5 groups) only including groups in which all birds were genotyped. Boxplots indicate the interquartile range (box upper and lower limits), median (thick lines within boxes), maximum values excluding outliers (lines extending from boxes) and outliers (filled dots).

6-years-old, as would be expected if offspring are retained. Other groups contained only 1-year-olds, as expected when coalitions of yearling siblings joined with unrelated yearlings, while others contained only birds that were at least 2-years-old.

A substantial proportion of dyadic comparisons within breeding groups would involve mates. Pair members are unlikely to be related because mean male–female relatedness in 27 pairs (−0.02 ± 0.17 sd, range −0.34 to 0.33) was not significantly different from 0 ($t_{26} = 0.481$, $P = 0.634$), as would be expected in this outbred population (Dawson Pell *et al.* 2021). This suggests that, within groups, relatedness should be higher in same-sex dyads than in opposite-sex dyads. This expectation held when we included dyads from all groups, some with unmarked birds ($t_{56} = 2.259$, $P = 0.028$; Fig. 3a), and approached statistical significance when we included only dyads from groups with all birds marked and genotyped ($t_{45} = 1.998$, $P = 0.053$; Fig. 3b). These results are again consistent with the formation of some groups via same-sex sibling coalitions and/or offspring retention.

Productivity and reproductive investment

Productivity of pairs and breeding groups

Clutch sizes did not differ significantly between pairs (mean = 6.2 ± 1.9 sd, range 1–16, n = 101) and groups (mean = 6.6 ± 3.3 sd, range 2–14,

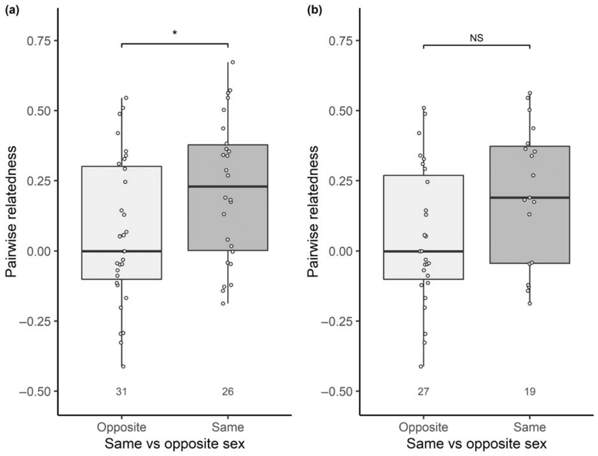

Figure 3. Pairwise Queller and Goodnight relatedness estimates for dyads from breeding groups of Monk Parakeets comparing opposite-sex and same-sex dyads for: (a) all breeding groups including some with unmarked birds; and (b) breeding groups containing only marked birds. Boxplots indicate the interquartile range (box upper and lower limits), median (thick lines within boxes), maximum values excluding outliers (lines extending from boxes) and outliers (filled dots). Sample sizes are given above the *x*-axis. *, $P < 0.05$.

$n = 27$; Table 1a), although it should be noted that, in both cases, some clutches were extremely large and unlikely to have been laid by a single female. Nor was there any significant difference between pairs and groups in either the probability of fledging young (Table 1b) or the number of fledglings produced (pairs: mean = 2.7 ± 1.3 sd, range 1–6; groups: mean = 3.0 ± 1.5 sd, range 1–5; Table 1c). Comparing among groups, the clutch sizes of multi-female groups ($n = 6$, range 3–14) tended to be larger than those of multi-male groups ($n = 12$, range 2–8; $Z = -1.89$, $P = 0.059$) suggesting joint-nesting in multi-female groups.

Investment by group members

We assessed provisioning indirectly by assuming that birds without nest material entering nest chambers containing nestlings provisioned young. More males than females were observed provisioning, perhaps because females spent more time brooding younger chicks (2018: $n = 46$ females and 58 males, mean = 5.9 ± 4.8 sd visits per bird, range 1–31; 2019: $n = 32$ females and 42 males, mean = 2.5 ± 1.5 sd; range 1–7). At nine out of 14 (64%) group nests with at least three marked members, three or more birds were observed entering nests and were assumed to feed nestlings. We also recorded 47 instances of fledglings being fed by adults outside the nest, but just 12 feeds were by adults from a group rather than a pair and we did not observe fledglings being fed by more than two marked members of the group, so we were unable to confirm that fledglings from groups were fed by all group members.

Copulations and parentage

All copulations observed between marked birds ($n = 9$) were within pairs, and no definite cases of extra-pair copulation or mating with multiple partners within groups were recorded in the remaining nine observed copulations. Nevertheless, when we examined the parentage of 76 chicks in 22 broods raised by social pairs, and of 23 chicks in five broods raised by groups (mean = 3.7 chicks ± 1.8 sd, range 1–9, $n = 27$ broods), multiple paternity was evident. In 2018, two out of 23 (9%) chicks in two out of eight (25%) broods raised by pairs

Table 1. Effects of breeding-unit size and year on clutch sizes, fledging success and the number of fledglings in Monk Parakeets.

Model	Parameter	Estimate ± se	*t*	*P*
Clutch size (*n* = 101 pair nests, *n* = 27 group nests)	(Intercept)	−1.877 ± 0.052	36.205	<0.001
	Breeding group	0.067 ± 0.085	0.785	0.432
	Year	−0.103 ± 0.071	−1.457	0.145
Fledging success (*n* = 101 pair nests, *n* = 27 group nests)	(Intercept)	0.1650 ± 0.267	0.618	0.536
	Breeding group	−0.506 ± 0.447	−1.132	0.258
	Year	−0.374 ± 0.358	−1.045	0.296
Number of fledglings (*n* = 50 pair nests, *n* = 10 group nests)	(Intercept)	1.157 ± 0.102	11.294	<0.001
	Breeding group	0.121 ± 0.202	0.601	0.548
	Year	−0.374 ± 0.358	−1.045	0.014

Clutch size and number of fledglings analysed using Poisson GLMs; fledging success analysed using a binary logistic regression GLM.

were likely to be the result of extra-pair paternity, the remainder being assigned to the social male. In 2017, 13 out of 53 (25%) chicks in four out of 14 (29%) pair broods were identified as the result of extra-pair paternity, while in one brood (7%) there was evidence that one nestling resulted from intraspecific brood parasitism. The remaining 40 (75%) chicks were assigned to their putative mother and father. Observations were less intensive in 2017, so group members could have been overlooked and cases of extra-pair paternity or intraspecific brood parasitism could potentially have been offspring from an unidentified group member. Overall, across both years our analyses indicate genetic monogamy in 68% of broods raised by pairs, at least one chick resulting from extra-pair paternity in 27% of broods, and one case (5% of broods) of possible intraspecific brood parasitism.

We assessed parentage for just five broods raised by groups. In one group a single male and single female were assigned parentage of a brood, whereas in the other four groups we detected either co-breeding pairs, more than one male breeding with a single female, and two breeding females with either more than one male or unsampled parents.

Examining relatedness among nestlings that shared a nest, mean pairwise relatedness within all broods was 0.417 ± 0.192 sd ($n = 187$ dyads, 27 broods; range – 0.191 to 0.809; Fig. 4a and Fig. S2), indicating a mixture of potentially unrelated individuals, half-siblings and full siblings, as would be expected given the results from the parentage analysis and the occurrence of siblings in breeding groups. Mean relatedness among all chicks within broods ranged from 0.163 to 0.640, again indicating a range of relationships between nestlings (Fig. 4b). Unsurprisingly, pairwise relatedness was significantly higher among nestlings in broods that showed no evidence of extra-pair paternity or mixed parentage compared to those broods with at least one extra-pair offspring or evidence of mixed parentage ($P < 0.001$; Fig. 4a; Table S1), although the difference was non-significant for mean brood relatedness ($Z = -1.680$, $P = 0.093$; Fig. 4b); note that in both cases mean relatedness is close to that expected among full siblings ($r = 0.5$) for apparently monogamous broods. Our results were further corroborated by maximum-likelihood relationship estimations from ML-RELATE; with 65% (121 dyads) assigned as full-siblings or parent–offspring relationships (all comparisons were within broods, so parent–offspring is not possible, but this assignment indicates close relatedness, as expected, between full-siblings). A further 28% (53 dyads) were assigned as half-siblings and 7% (13 dyads) were determined to be unrelated individuals. In sum, these patterns of relatedness among nestlings closely match those found in parentage analyses.

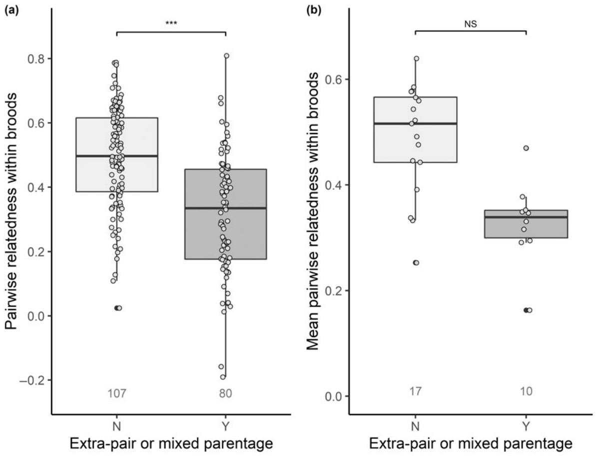

Figure 4. (a) Pairwise relatedness in dyads of Monk Parakeet nestlings within broods that showed extra-pair paternity or mixed parentage (Y) or indicated monogamous parents (N); and (b) mean pairwise relatedness within broods indicated as monogamous (N), and those that indicated an alternative parentage pattern (Y). Boxplots indicate the interquartile range (box upper and lower limits), median (thick lines within boxes), maximum values excluding outliers (lines extending from boxes) and outliers (filled dots). Sample sizes are indicated above the *x*-axis. ***, $P < 0.001$.

DISCUSSION

In our study population, c. 20% of Monk Parakeet breeding attempts involved groups of three or more birds. These breeding groups varied in size, sex-composition, age, relatedness and the route taken to formation, with evidence of groups forming through offspring retention, sibling coalitions and unrelated individuals aggregating to breed. This diversity of breeding organization points to multiple drivers of breeding associations, with the potential for both indirect and direct benefits of co-operative breeding. In the groups that contained kin—that retained offspring or where sibling coalitions raised offspring together—birds could accrue indirect fitness benefits by increasing the production of related offspring (Hamilton 1964), but that does not necessarily mean that the benefits of co-operation are indirect only. Indeed, we also found evidence of unrelated birds associating in breeding groups, where only direct fitness could be accrued.

First, we consider the potential effects of group-breeding on productivity. We observed multiple members of breeding groups of both sexes entering nest chambers, so it is likely that helpers or co-breeders shared provisioning duties with breeders, as suggested in earlier studies (Bucher *et al.* 1991, 2016, Eberhard 1998). We were unable to directly observe food items being fed to chicks and it is possible that birds entered their nests for other reasons. However, in an earlier study of nest-building conducted throughout the breeding season, birds were never observed to enter a nest chamber that was not their own, even though they stole nest material from the exterior of neighbouring nests (Dawson Pell *et al.* 2024). Therefore, while we cannot conclude unequivocally that all group members contributed to provisioning of nestlings, circumstantial evidence indicates that this was the case. Higher provisioning rates in groups could have a short-term impact on offspring condition (te Marvelde *et al.* 2009, Bolopo *et al.* 2019) that ultimately causes higher recruitment (Hatchwell *et al.* 2004, Preston *et al.* 2016), but we had insufficient data to test for such effects.

Interestingly, we found no significant differences between the clutch sizes of breeding pairs and groups, although our results suggested that multi-female groups tended to have larger clutch sizes than multi-male groups. This indication of co-breeding by multiple females in a single nest was corroborated by our parentage analyses, which found that groups can have more than one female, as well as more than one male, contributing genetically to the breeding attempt. Co-breeding is routine in other co-operative species with multi-female groups, such as the Acorn Woodpecker *Melanerpes formicivorus* (Mumme *et al.* 1988) and the Greater Ani *Crotophaga major* (Riehl 2011). Among parrots, joint-nesting has been reported in Horned Parakeets *Eunymphicus cornutus*, although at a single nest only (Theuerkauf *et al.* 2009). It should also be noted that just one very large clutch was recorded in a pair nest (16 eggs), which is unlikely to have been laid by a single female and could have resulted from an undetected second female, or via intraspecific brood parasitism. Indeed, our parentage analysis indicated that the latter occurs, albeit rarely. Colonial nesting facilitates intraspecific brood parasitism in Monk Parakeets, as suggested by Martínez *et al.* (2013), but our results show the need for caution in interpreting multiple maternity within a nest because multiple females in a breeding group may lay eggs, potentially leading to offspring that are unrelated within the same brood. This demonstrates the importance of combining molecular genetic analyses with detailed behavioural observations to describe and understand complex breeding systems.

Parentage analyses and estimation of relatedness within broods also revealed multiple paternity of broods raised by pairs and groups. We detected extra-pair paternity in 9–25% of chicks in 25–29% of broods attended by social pairs at our study site, a lower overall estimate than that obtained in the native range (40% of chambers), although that estimate was not made in conjunction with nest observations (Martínez *et al.* 2013). Mating patterns frequently vary among populations of the same species, and other differences in breeding behaviour are known to exist between native and invasive populations of Monk Parakeets. Most notably, in Barcelona the reproductive capacity of Monk Parakeets is higher than in the native range, with double the fledging success, three times more pairs attempting a second brood, and 55% of 1-year-old birds breeding compared to zero (Senar *et al.* 2019). These demographic differences may have profound impacts on breeding; for example, a smaller number of non-breeding yearlings could reduce the frequency of co-breeding and helping behaviour in our population relative to the native range.

We have previously shown that kin of both sexes aggregate within nesting trees at our study site as a result of limited and co-ordinated dispersal (Dawson Pell *et al.* 2021). This kin structure generates an opportunity for the kin-directed co-operation that we have reported here, but it also creates a risk of inbreeding. However, very few breeding pairs had relatedness estimates exceeding that expected for second-order kin, supporting the earlier conclusion of no significant inbreeding at this study site (Dawson Pell *et al.* 2021). Together, our findings of kin affiliation in breeding groups and inbreeding avoidance suggest an effective mechanism for the recognition of at least first-order kin. Signatures of individual identity have been detected in Monk Parakeet vocalizations (Smith-Vidaurre *et al.* 2020, 2021, Smeele *et al.* 2023) and could facilitate such kin recognition, although we have no direct evidence for how such discrimination is achieved from our observations.

The diversity of the Monk Parakeet breeding system revealed here precludes a simple definition; we have presented evidence of social monogamy, extra-pair paternity and intraspecific brood parasitism, co-breeding and helping. Most parrots are socially monogamous (Forshaw 1989, Cockburn 2006), although that does not necessarily equate to genetic monogamy (Saunders *et al.* 2018). Co-operative breeding is correspondingly rare among parrots, and indeed among frugivores more generally (Arnold & Owens 1998). However, in a small minority of parrot species, a broad range of breeding systems has been reported. For example, co-operative breeding with helpers occurs in the El Oro Parakeet *Pyrrhura orcesi* (Klauke *et al.* 2013), and female promiscuity with multiple males provisioning breeding females has been described in the Greater Vasa Parrot *Coracopsis vasa* (Ekstrom *et al.* 2007), the Seychelles Black Parrot *Coracopsis barklyi* (Reuleaux *et al.* 2014) and the Papuan Eclectus Parrot *Eclectus polychloros* (Heinsohn *et al.* 2007). Other systems involve joint-nesting by potentially monogamous pairs in the Horned Parakeet (Theuerkauf *et al.* 2009), and lek mating in the Kakapo *Strigops habroptilus* (Merton *et al.* 1984). At present, we are unable to characterize the Monk Parakeet breeding system definitively within this spectrum of social systems, but we have demonstrated an unusual diversity of breeding behaviour in one population, and our results add to our understanding of the breadth of the different breeding systems within the Psittacidae.

CONCLUSIONS

We have revealed diverse and variable breeding behaviour in the Monk Parakeet. Although most breeding attempts in our study population were made by social pairs, around 20% of breeding attempts were made by groups. Groups were diverse in sex ratios, ages and genetic relatedness, and we found two clear routes to breeding group formation (retained offspring and sibling coalitions), although high relatedness between group members was not apparent in all groups. Productivity did not differ between groups and pairs, but evidence from clutch sizes and patterns of genetic relatedness indicated joint nesting by some females. Besides adding to knowledge of parrot breeding behaviour, our description of the Monk Parakeet breeding system has shown that they are potentially an ideal system for investigation of the causes and evolutionary consequences of various routes to co-operation.

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AUTHOR CONTRIBUTIONS

Francesca S. E. Dawson Pell: Conceptualization; methodology; data curation; investigation; validation; formal analysis; visualization; writing – original draft. **Juan Carlos Senar:** Conceptualization; investigation; methodology; supervision; resources; funding acquisition; project administration; writing – review and editing. **Alba Ortega-Segalerva:** Methodology; investigation; writing – review and editing. **Terry Burke:** Methodology; validation; project administration; resources; writing – review and editing. **Ben J. Hatchwell:** Conceptualization; methodology; supervision; funding acquisition; project administration; resources; writing – review and editing.

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CONFLICT OF INTEREST

There are no conflicts of interest.

ETHICAL NOTE

J.C.S. 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. 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.

DATA AVAILABILITY STATEMENT

Data associated with this paper are available via DRYAD at http://doi.org/10.5061/dryad.5qfttdzkf.

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SUPPORTING INFORMATION

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

Figure S1. (a) Compound nest of Monk Parakeet in Ciutadella Park, Barcelona; (b) Monk Parakeet fitted with neck collar; (c) cherry-picker being used to access nests in Ciutadella Park. Photo credits: Ben Hatchwell.

Figure S2. Maximum likelihood relationships estimated in ML-RELATE (Kalinowski *et al.* 2006) compared to pairwise relatedness estimates made in SPAGeDI (Hardy & Vekemans 2002).

Table S1. Linear mixed model examining factors affecting the relatedness between nest-mates.