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Social associations are predicted by nest proximity but not kinship in a free-living social parrot

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Running title: Foraging parrots associate with neighbours

Social associations among conspecifics are typically non-random, often being a function of relatedness, familiarity or of spatial distributions. The aim of this study was to combine field observations with molecular genetic techniques and social network analysis to investigate the predictors of social associations in free-living monk parakeets *Myiopsitta monachus*. Monk parakeets are non-territorial parrots whose nests are often aggregated, with relatives clustered in kin neighbourhoods and within cooperatively breeding groups. First, we characterised social associations when away from the nest, showing that individuals typically had a few, strong social ties. Secondly, we investigated whether these social associations were related to nest proximity or genetic relatedness. Association strength decreased with increasing inter-nest distance, but there was negligible influence of relatedness on the strength of associations. These patterns did not differ between same-sex and opposite-sex dyads. Finally, we investigated whether members of breeding pairs were close social associates, finding that in most cases an individual's closest associate was their mate, although social bonds also existed outside of the pair; members of breeding groups also associated closely when foraging. Social associations are poorly known in parrots due to methodological challenges, so our results add to the limited knowledge of sociality in this taxon.

ADDITIONAL KEYWORDS: colony – genetic relatedness – kin structure – kinship – monk parakeet – *Myiopsitta monachus* – parrots – Psittacidae

INTRODUCTION

Associations with conspecifics are often non-random in group-living species, with individuals associating preferentially with certain group members (Whitehead, 2008; Farine *et al*., 2015). The social connections between individuals and the resulting network structure can have wide-ranging implications for a variety of ecological and evolutionary processes (Gokcekus *et al*., 2021). For example, social structure can have consequences for sexual selection and mating strategies (Oh & Badyaev, 2010), influence foraging behaviour (Firth *et al*., 2015), determine how information spreads through a group or population (Firth *et al*., 2016) and, similarly, can determine the spread of disease or parasites through a network of individuals (Sah *et al*., 2018). Thus, variation among individuals in their social associations can affect fitness (Royle *et al*., 2012) by impacting survival (Stanton & Mann, 2012; Ellis *et al*., 2017) or reproductive success (Frère *et al*., 2010; Riehl & Strong, 2018).

Several factors may affect an individual's choice of social affiliations from among potential associates. One such factor is kinship, preferential association with kin having been demonstrated in a wide range of taxa (Fraser *et al*., 2005; Gaspari *et al*., 2007; Kurvers *et al*., 2013). Inclusive fitness theory predicts that by associating with kin, individuals can accrue indirect fitness benefits if they enhance their relatives' fitness (Hamilton, 1964) and such benefits may be accrued in multiple ways (Hatchwell, 2010). For example, preferential association with kin could allow sharing of ecologically relevant knowledge leading to reduced foraging interference (Jarman, 1991), increase territory sharing and reduce time for food patch acquisition (Griffiths & Armstrong, 2002), nepotistic alarm calling (Sherman, 1977), and assistance in rearing offspring (Hatchwell *et al*., 2014). However, despite the presence of kin in close proximity within populations, preferential association with kin within social networks is not universal (Arnberg *et al*., 2015; Baden *et al*., 2020), presumably because direct rather than indirect benefits are acquired from stable associations with a subset of conspecifics.

Associations within social networks may also be influenced by familiarity. Individuals may become familiar simply from shared use of space, as in eastern grey kangaroos *Macropus giganteus* (Best *et al*., 2014), or it may refer to association at a specific life history stage, often as juveniles, as in Trinidadian guppies *Poecilia reticulata* (Griffiths & Magurran, 1999). Association with familiar individuals may confer a range of fitness benefits, including increased reproductive coordination and reduced competition (Riehl & Strong, 2018), and enhanced predator avoidance (Griffiths *et al*., 2004). However, the concept of familiarity is a more complex one than is often appreciated and, problematically, familiarity may co-vary with kinship, making the two hard to disentangle (Leedale *et al*., 2020), especially when multiple drivers of social association act together to determine social structure (Kurvers *et al*., 2013).

In this study, we examined the social associations of monk parakeets *Myiopsitta monachus* and investigated two potential predictors of their affiliations. Monk parakeets are unique amongst parrots because they build their own stick nests rather than breeding in natural cavities (Forshaw, 1989; Eberhard, 1998). Their nests vary in size from single chambers to compound nests with multiple pairs or groups using separate nest chambers within a shared nest structure. Nests are often aggregated within a single tree or adjacent trees, forming loose colonies that are occupied throughout the year and may persist for many years (Bucher *et al*., 1990; Eberhard, 1998). A previous study revealed that monk parakeets live in 'kin neighbourhoods' with relatives aggregated within both shared compound nests and nesting trees (Dawson Pell *et al*., 2021). Monk parakeets are also social away from the nest, foraging in flocks throughout the year. There is some evidence from unmarked wild flocks and marked captive individuals that pairs are the fundamental social unit in monk parakeets. Flocks of two individuals are reportedly the most common both in captivity and in the wild (captive: 25.2-30.4%, wild 32.3% of total flocks), although flocks of > 60 free-living individuals have been recorded in the wild (Hobson *et al*., 2014). Captive birds also display a strong preference for associating with certain individuals, forming strong bonds between pair members as well as between members within a small number of trios (Hobson *et al*., 2014). However, there has been no detailed investigation into social associations in individually marked free-living monk parakeets. More generally, social structure and the drivers of social associations are poorly known in the Psittacidae due to the methodological challenges of studying most parrot species in the wild, with many species being canopy-dwelling and not amenable to observation.

The kin neighbourhood social system, aggregated nests and social foraging behaviour of the monk parakeet make it an ideal species to examine the influence of kinship and familiarity through nest proximity on the social associations of foraging birds. The aim of this study was to combine molecular genetic techniques with field observations during the breeding season to first characterise the overall pattern of social associations in the monk parakeet. We then investigated whether social associations reflected either nest proximity or genetic relatedness. Finally, we examined whether members of pairs and of breeding groups containing 3+ birds were close social associates away from the nest. Through these investigations we aim to expand our understanding of sociality in this unusual parrot species and add to the limited knowledge of parrot social systems.

MATERIAL AND METHODS

STUDY SITE AND SPECIES

The field study was conducted in the city of Barcelona, Spain (41.39°N 2.17°E) on the north-east coast of the Iberian Peninsula. The metropolitan area of Barcelona is approximately 102 km^2 and consists mainly of highly developed urban environment with numerous parks throughout the city. The main study site encompassed Ciutadella Park (c. 30 ha), containing both native and exotic vegetation, and smaller parks and streets with mature trees in the surrounding area up to approximately 2 km away (for a list of survey locations see Supplementary Material S1).

The monk parakeet is a medium-sized parrot (c. 100-150g) native to South America that has become an invasive species around the world (Forshaw, 1989; Russello *et al*., 2008). Monk parakeets were first reported breeding in Barcelona in 1975 (Batllori & Nos, 1985) and now exist at one of the highest densities found in Europe, with a population estimate of c. 5000 individuals in 2015 (Molina *et al*., 2016; Senar *et al*., 2017). As a generalist forager, monk parakeets feed in trees and on the ground (Bucher & Aramburú 2014; Borray-Escalante *et al*., 2020) where they are readily observed.

Birds were individually marked after trapping them in the nest as nestlings or incubating adults, or when foraging using a baited food trap or gas-propelled net. Birds have been captured every year since 2002 in two six-week sampling periods in the winter and summer months (Conroy & Senar, 2009). Captured birds are ringed with aluminium leg rings and marked with unique, light-weight medals attached to neck collars (Senar *et al*., 2012), which are visible through binoculars from up to 30-40 m. Approximately 62-64% of the study population in Ciutadella Park are marked at any time, based on the proportion of individuals marked in 10 mature pine trees subjected to intensive monitoring during the breeding season. For birds first caught as adults, we use the year of ringing to determine their minimum age.

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. JCS 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. Handling times were kept to a minimum.

IDENTIFYING GROUP MEMBERS

Ciutadella Park and the other parks visited during this study are public access parks and monk parakeets are habituated to human presence near their nests and during foraging and other activities. In 2018 and 2019, we recorded groups of individually-marked monk parakeets away from the nest throughout the breeding season (March-September; Senar et al., 2019) in two contexts. First, groups of monk parakeets were recorded opportunistically when encountered during surveys of the field site. Groups were recorded engaging in various activities, often foraging, but also drinking, bathing and resting. We used the ‘gambit of the group’, which assumes that all individuals in a spatially and temporally clustered group are associated with one another (Whitehead & Dufault, 1999). Individuals were recorded as being in the same group if they were within c. 5 m of each other and any individuals that joined the group within approximately 2 minutes of the observer encountering the group were included as group members. GPS coordinates, date and time of each group were recorded. Secondly, groups were recorded during observations made at a baited trap (containing peanuts and sunflower seeds), situated on the roof of the Museu de Ciències Naturals within Ciutadella Park. For observations at the trap an observer used binoculars to identify marked birds in groups at the feeder. These observations were conducted for approximately three hours a week throughout the breeding season. Marked birds present at the trap were recorded at 10 minute intervals and, as during surveys of the park, any individuals that joined a group at the trap within approximately 2 minutes of the observation starting were included in that flock. In both contexts, we focused on recording marked individuals only because of the difficulty of recording accurately the number of unmarked birds.

GENOTYPING AND RELATEDNESS

Blood samples (maximum 100 µl) were taken from adults and nestlings for genetic sex-typing (monk parakeets are sexually monomorphic (Forshaw, 1989)) and to assess genetic relatedness between individuals. For details of blood sample storage, DNA extraction techniques, marker quality assessment and PCR protocols see Dawson Pell *et al*. (2020) and Dawson Pell *et al.* (2021). Alleles were scored blind to bird identity and sex and individuals were typed at 21 polymorphic microsatellite loci: Mmon01, Mmon02, Mmon03, Mmon04, Mmon07, Mmon09, Mmon10, Mmon11, Mmon13, Mmon14, Mmon15, Mmon16 (Dawson Pell *et al*., 2020), 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). Individuals were sex-typed using the sexing marker Z002B (Dawson, 2007). A previous estimate of genotyping error, based on the repeat genotyping of 50 individuals with these markers in this study system is 3.1% (F. S. E. D. P. unpublished data). We calculated pairwise genetic relatedness between individuals using Queller and Goodnight's (1989) coefficient of relatedness (r_{QG}) in SPAGeDi version 1.5 (Hardy & Vekemans, 2002). We used the genotypes of all 142 unique individuals included in our social association dataset to generate allele frequencies.

NEST LOCATIONS AND INTER-NEST DISTANCES

The nesting tree location of marked birds was determined in two ways. First, we conducted detailed behavioural observations at 10 mature pine trees in Ciutadella Park throughout the breeding season in 2018 (263 hours) and 2019 (124 hours). A total of 113 marked birds were located in these focal trees in 2018 and 103 in 2019. Birds were never observed to enter a nest chamber they were not using for breeding or roosting during our period of observation, so we are confident that birds assigned as nest occupants were residents in that nest and nesting tree. Second, we conducted surveys in the rest of Ciutadella Park and in likely nesting areas up to 6 km from the park in 2018 and 2019 (total = 380 hours). Once marked birds were assigned to a nest, we recorded the nest's GPS coordinates; all birds in the same nesting tree were assigned the same GPS coordinates with a distance of 0 m between their nests. GPS coordinates were converted to Cartesian coordinates (UTM) for calculations of inter-nest distance in SPAGeDi version 1.5 (Hardy & Vekemans, 2002). We calculated inter-nest distances separately for 2018 and 2019.

SOCIAL ASSOCIATIONS

Using flock co-membership, we calculated association indices using the simple ratio index (SRI; Cairns & Schwager, 1986) in R version 4.1.1 (R Core Team, 2018). The simple ratio index is used to estimate the strength of a social association between individuals and varies between 0 and 1, with 1 indicating that individuals are always observed together and 0 indicating two individuals have never been observed associating. The simple ratio index is calculated using the following equation:

$$\mathrm{SRI}_{AB} = x / (x + y_{AB} + y_A + y_B)$$

in which the SRI between the individuals *A* and *B* is defined as the number of observations in which the two co-occurred (x), divided by the number of observations in which they both occurred together or individually, with y_{AB} representing the occasions the individuals were observed simultaneously but apart and y_A indicating occasions that individual *A* was observed without individual *B* and y_B indicating the reverse. To reduce bias in association indices caused by limited sampling, we excluded birds observed on less than five occasions (2018: 171 out of 364 sighted individuals excluded; 2019: 131/288 birds excluded). In addition, we excluded birds observed in their fledging year because they were still fed by their parents and were therefore likely to be associated with them away from the nest (2018: *N* = 74 fledglings excluded; 2019: *N* = 46 excluded).

SOCIAL ASSOCIATIONS, INTER-NEST DISTANCE AND PAIRWISE GENETIC RELATEDNESS

Following recent developments in the field, we used multi-membership models without permutations for our dyadic analysis (Franks *et al*., 2021; Hart *et al*., 2021; Weiss *et al*. 2021). To investigate whether social association strengths reflected inter-nest distance or pairwise genetic relatedness we fitted Bayesian multi-membership regression models in Stan (Stan Development Team, 2020a) via RStan (Stan Development Team, 2020b) using the brms package (Bürkner, 2017) in R version 4.1.1. We included the dyads as multi-membership terms to account for undirected dependencies in allowing the dyad to be a member of both nodes. For this model, we used a binomial likelihood with association strength (SRI) as the response, and the predictor variables of pairwise genetic relatedness and inter-nest distance. Both predictor variables were transformed to z scores before being used in the model. We applied weakly regularizing priors in these models. Our models were fit over four independent chains with a warmup of 3000 followed by 6000 iterations of sampling. We ran models separately for the data collected in each of the 2018 and 2019 breeding seasons.

Some dyads had data for inter-nest distance only, or relatedness only; these birds were removed before the brms analyses. Using data collected in 2018, including data collected at the food trap, we checked for any bias in those dyads removed for missing data through data visualisation. We plotted dyads with only one data point for either relatedness or inter-nest distance against SRI, and also plotted the full dataset that included no individuals with missing data to determine whether there was any bias in those removed (Figure S1). We could not visually detect any bias in removed dyads, indicating that data was missing at random, so we proceeded with the dataset that included only dyads with complete data.

Following exclusions, in 2018 we had data on 821 social groups, comprising 110 individuals (41 females, 69 males, 5995 dyads) with a mean number of observations per bird of 17.0 ± 7.8 SD, females (13.9 ± 7.0, median = 13) being observed less than males (18.8 ± 7.7, median = 18; Wilcoxon rank sum test: Z = -3.28, p = 0.001; Figure S2a). This dataset included birds aged from 1-12+ years old based on year of ringing or fledging date. In 2019, we had data on 753 social groups that included 82 individuals (32 females, 50 males, 3403 dyads) that met the criteria for inclusion with ages ranging from 1-13+ years old. The mean number of observations per bird in 2019 was 15.9 ± 7.8 SD and males (18.7 ± 7.4, median = 19) were again observed more than females (11.5 ± 6.4, median 9.5; Z = - 4.33, *P* < 0.001; Figure S2c).

We re-ran these analyses using a conservative dataset that excluded data collected at the baited trap in case this large supplementary food source attracted birds from greater distances or resulted in atypical aggregations. This smaller dataset included 656 social groups and 98 individuals (33 females, 65 males) that met the inclusion criteria in 2018, and 680 social groups and 78 individuals (29 females, 49 males) in 2019. Age ranges were the same as above for both years. The mean number of observations per bird was 12.5 ± 5.5 SD in 2018 and was 15.4 ± 7.4 SD in 2019, with no difference between the number of observations per female (mean ± SD = 11.5 ± 5.4, median = 11) and male (13.0 ± 5.5, median = 13; Z = -1.30, *P* = 0.19; Figure S2b) in 2018, but with males (17.7 ± 6.9, median = 19) observed more than females in 2019 (11.4 ± 6.4, median = 10; Z = - 3.91, *P* < 0.001; Figure S2d).

SAME-SEX AND OPPOSITE-SEX ASSOCIATIONS

Using 2018 data and including observations recorded at the food trap, we ran the same model described above separately for female-female (*N* = 820 dyads), male-male (*N* = 2346 dyads), and opposite-sex (*N* = 2829) associations to investigate whether the drivers of social associations were similar for same-sex and opposite-sex dyads. The 2019 dataset had too few female-female dyads to repeat this analysis.

ASSOCIATIONS BETWEEN MEMBERS OF SOCIAL PAIRS AND BREEDING GROUPS

We assessed whether members of social pairs were each other's closest social associates when away from the nest using the full datasets from 2018 and 2019. In addition, c. 20% of the breeding attempts made by monk parakeets at our study site involve groups of three or more birds (Dawson Pell unpublished data), so we also examined whether breeding group members were close associates when away from the nest. Pairs and groups were identified during 387 hours of behavioural observations at 10 focal pine trees across the 2018 and 2019 breeding seasons. We included only those groups in which all members were marked and that met the inclusion criteria described above. For members of pairs and groups we determined their top 10 social associates, ranked by social association strength (SRI) to assess whether members of pairs and social groups preferentially associated with each other away from the nest.

RESULTS

CHARACTERISTICS OF MONK PARAKEET SOCIAL ASSOCIATIONS

Social association strengths between individuals were relatively sparse and weak in both years (Figures 1 & 2). Mean SRI ± SD was 0.02 ± 0.04 for 110 birds in 2018 (*N* = 5995 possible dyads), and 0.02 ± 0.04 for 82 birds in 2019 (*N* = 3403 possible dyads). In both years, distributions of associations were right-skewed and included many birds without or with very weak associations (i.e. SRI of zero or close to zero). However, maximum association strengths were around 0.5 in both years, and the mean association strength between birds observed together on at least one occasion was 0.05 ± 0.04 in 2018 (*N* = 2457 associating dyads) and 0.06 ± 0.05 in 2019 (*N* = 1038 associating dyads).

FIGURE 1 HERE

EFFECTS OF RELATEDNESS AND INTER-NEST DISTANCES

Inter-nest distances ranged from 0 m (for birds nesting in the same tree) to 745 m (mean ± SD 205 m ± 153 in 2018, 214 m ± 157 in 2019). The mean pairwise coefficient of relatedness (r_{QG}) for dyads was

-0.005 ± 0.167 (range: -0.478 to 0.718) in 2018 and 0.00 ± 0.163 (range: -0.542 to 0.903) in 2019. Inter-nest distance was negatively related to the strength of the social association between individuals in both years (Figure 2a,c), birds nesting closer to each other having stronger social associations when away from the nest (2018: posterior mean = -0.752, 95% credible intervals (CI) = -0.792 to -0.712; 2019: posterior mean = -1.492, 95% CI = -1.572 to -1.412). In contrast, relatedness was not a significant predictor of the strength of associations, with credible intervals overlapping 0 in both years (Figure 2b,d; 2018: posterior mean = 0.023, 95% CI = -0.008 to 0.054; 2019: posterior mean = 0.040, 95% CI = -0.002 to 0.083).

FIGURE 2 HERE

We found qualitatively the same results when excluding trap data (Figure S3); inter-nest distance (2018: posterior mean = -1.151, 95% CI = -1.225 to -1.080; 2019: posterior mean = -1.394, 95% CI = -1.473 to -1.320), but not pairwise relatedness (2018: posterior mean = 0.024, 95% CI = -0.023 to 0.070; 2019: posterior mean = 0.036, 95% CI = -0.008 to 0.079), was significantly related to the strength of the observed associations in both years.

Kin are clustered within nesting trees in the monk parakeet (Dawson Pell *et al*., 2021), so we also examined whether pairwise relatedness of those birds nesting within the same tree predicted their social association strength when away from the nest (for model details see Supplementary Material S4). We found the same pattern as that revealed by the full data set, with relatedness having negligible impact on the strength of social associations (posterior mean = -0.034, 95% CI = -0.098 to 0.029).

When examining same and opposite-sex associations, we found qualitatively similar patterns. Social association strength decreased with increasing inter-nest distance in female-female (posterior mean = -0.523, 95% CI = -0.653 to -0.397), male-male (posterior mean = -0.793, 95% CI = -0.849 to -0.736), and opposite-sex dyads (posterior mean = -0.747, 95% CI = -0.808 to -0.686), while pairwise relatedness was unrelated to association strength in all cases (females: posterior mean = 0.003, 95% CI = -0.109 to 0.112; males: posterior mean = 0.025, 95% CI = -0.018 to 0.068; opposite-sex: posterior mean = 0.031, 95% CI = -0.015 to 0.078).

ASSOCIATIONS BETWEEN SOCIAL PAIRS AND BREEDING GROUP MEMBERS

Data were available from 28 social pairs in which both sexes were marked (2018: 16 pairs; 2019: 12 pairs; note that three pairs featured in both years, but analyses were conducted on years separately, so no pairs appear more than once in any analyses). For 15/28 (54%) pairs, partners were each others' closest associate, i.e. had the highest association strength. For seven (25%) pairs, one bird's closest associate was their social mate whereas for the other member of the pair their social mate ranged from second closest associate to 18th. Thus, 37/56 (66%) of possible associations were closest for social pair members when away from the nest. However, this was not always the case and monk parakeets consistently associated with non-partners. Overall, 51/56 (91%) associations between social pair members are within their top 10 closest associates (Figure 3a). Only one pair was not observed together away from the nest despite the pair members being observed with 49 and 28 other individuals respectively.

We observed nine separate breeding groups containing 32 birds (3-5 individuals per group; mean = 3.6) in which all members of the group were also included in our social network. In 23/86 (27%) possible associations, the group member's closest social associate was another member of the same breeding group, with 58/86 (67%) being in each other's top 10 closest associates (Figure 3b). These results indicate that members of breeding groups are often close social associates when they are away from the nest, but relationships with group members have lower precedence than those between social pair members.

FIGURE 3 HERE

DISCUSSION

We combined detailed field observations with molecular genetic techniques to investigate the influence of inter-nest distance and pairwise genetic relatedness on social associations during the breeding season in free-living monk parakeets. Overall, social associations away from the nest were generally weak, with small numbers of stronger associations. Birds that nested closer together associated more strongly when away from the nest, but pairwise relatedness did not predict social associations despite the role of kinship in determining nest locations in this species (Dawson Pell *et al*., 2021). These results were qualitatively similar in both years of the study, when we repeated analyses without the data collected at the artificial food source, and when we conducted the analyses on same-sex and opposite-sex associations separately.

Social association with birds breeding in close proximity could result simply from shared space use, birds living nearby being more likely to be seen together, without any active affiliation. Alternatively, there may be a preference for association with familiar individuals. It seems unlikely that this relationship is driven entirely by space use because monk parakeets are non-territorial and foragers routinely travel distances that were beyond the inter-nest distances included in this study so frequent interactions with birds from other nests would be expected. The mean inter-nest distance of birds included in this study was approximately 200 m (range 0 – 745 m), and it is estimated that adult monk parakeets regularly travel several hundred meters to forage, with home ranges of c. 12 ha (Carrillo-Ortiz, 2009; Senar *et al*. 2021). Thus, despite the very extensive overlap of home ranges, birds still preferentially associated with individuals from their own, or nearby trees (Figure 2). Monk parakeets are relatively long-lived (Conroy & Senar, 2009) and exhibit high nest-site fidelity (Dawson Pell *et al*., 2021), which may facilitate long-term affiliations between individuals breeding in close proximity. This association with familiar individuals could confer multiple fitness benefits, including foraging benefits (Webster & Hart, 2007), enhanced predator avoidance (Griffiths et al., 2004), more stable dominance hierarchies (Höjesjö *et al*., 1998), facilitation of social learning (Guillette *et al.*, 2016), and reduced reproductive competition or increased reproductive coordination (Kohn, 2017; Riehl & Strong, 2018). We have no direct evidence on what the benefits of associating with familiar individuals might be in monk parakeets, but the fact that social ties are not exclusive to breeding pairs or groups and do not differ between same-sex and opposite-sex dyads suggests that any benefits are not exclusively related to reproduction. Research into long-term associations would be worthwhile to understand the dynamics and potential fitness implications of social bonds in this species.

In contrast to the relationship with nest proximity, we found that genetic relatedness did not predict the strength of social associations away from the nest. This result is interesting because relatives are clustered together in both compound nests and nesting trees (Dawson Pell *et al*., 2021) and yet these kin associations did not extend to movements away from the nest. Indeed, the absence of a relationship between relatedness and foraging associations contrasts with many other social species in which kinship plays a key role in shaping spatial and social distributions (Drobniak *et al*., 2015). Such kin-based groups often live on exclusive territories where social association with kin is almost inevitable (Gokcekus *et al*., 2021). By contrast, in non-territorial species, or in group-living species where interactions with kin and non-kin are frequent, evidence for preferential association with kin is mixed (Hatchwell, 2010; Hirsch *et al*., 2012; Arnberg *et al*., 2015). A negligible relationship between relatedness and social associations in monk parakeets might be expected given that the closest social associate of an individual was their social mate in most (66%) cases and inbreeding is rare or absent in our study population (Dawson Pell *et al*., 2021). However, other social associations that were sometimes stronger than that of the pair were observed so relatedness could still be a predictor of associations if such a preference existed. It should also be noted that this study was conducted in the breeding season, during which females spend extended periods in the nest incubating eggs and brooding young chicks. Therefore, pair members may be observed separately more often at this time and a different pattern may be expected if this study was repeated during the non-breeding season. This difference in parental roles may also explain why males were observed significantly more than females. As well as spending more time in the nest incubating and brooding, incubating females are fed by males so their appearance outside the nest is reduced even further (Eberhard, 1998). An alternative explanation is that females were observed less frequently because they travel further from the nest to forage, but there is no evidence that females have larger home ranges than males (Senar *et al*., 2021).

Studies of parrot social structure in the wild are limited, presumably due to the practical difficulties of observing a largely canopy-dwelling taxon often with high mobility. Our study therefore adds to a limited but growing number of studies investigating patterns of social associations in the Psittacidae, a family often discussed in the context of social evolution (Emery, 2006; Hobson *et al*., 2014). Like other parrot species (Buhrman-Deever *et al*., 2008), monk parakeets exhibit short-term fission-fusion social dynamics (Hobson *et al*., 2014), but this did not mask the existence of consistent social ties away from the nest. Stable social relationships are present in another parrot species adapted to living in the urban environment, the sulphur-crested cockatoo, *Cacatua galerita*, that also has a fission-fusion social system (Aplin *et al*., 2020). In the sulphur-crested cockatoo it is mainly roost-site choice that drives social associations (Aplin *et al*., 2020), a pattern similar to that revealed here.

The mechanism through which social associations are maintained in the monk parakeet is unknown, although their individual vocal signatures (Smith-Vidaurre *et al*., 2020, 2021, 2023; Smeele *et al*., 2023), could facilitate interactions with familiar individuals away from the nest through social learning. Indeed, studies on captive populations indicate that monk parakeets may be able to discriminate social associates through contact calls (Hobson *et al*., 2015). However, unlike other parrot species that have been shown to produce contact calls that are specific to certain roost sites (Wright, 1996; Wright & Dahlin, 2017), there is no evidence of ‘higher-level’ vocal signatures in monk parakeets beyond the level of the individual, such as at the level of the nest-site (Smith-Vidaurre *et al*., 2020, 2021, 2023), that could facilitate associations between individuals that share a nesting tree when they are away from the nest.

In conclusion, we studied the social structure and the factors underlying social associations in free-living monk parakeets. This system is highly tractable for assessing social associations as flocks are often highly visible and the study population has a large number of uniquely identifiable individuals. We demonstrated that social associations of monk parakeets away from the nest are relatively weak, although some strong connections between individuals were detected. The strength of social associations is driven by inter-nest distance rather than kinship. This result may be explained by preferential association with familiar individuals, perhaps in combination with shared space use. Our results add to the limited knowledge of affiliative behaviours in the social systems of parrots and in other taxa with fission-fusion societies.

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DATA AVAILABILITY

All data will be made available via Dryad.

AUTHOR CONTRIBUTIONS

FSEDP, JCS and BJH designed the study. FSEDP, JCS and AS-O conducted fieldwork, FSEDP conducted labwork and analysed the data. FSEDP wrote the paper with input from co-authors. All authors read and approved the final manuscript.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare

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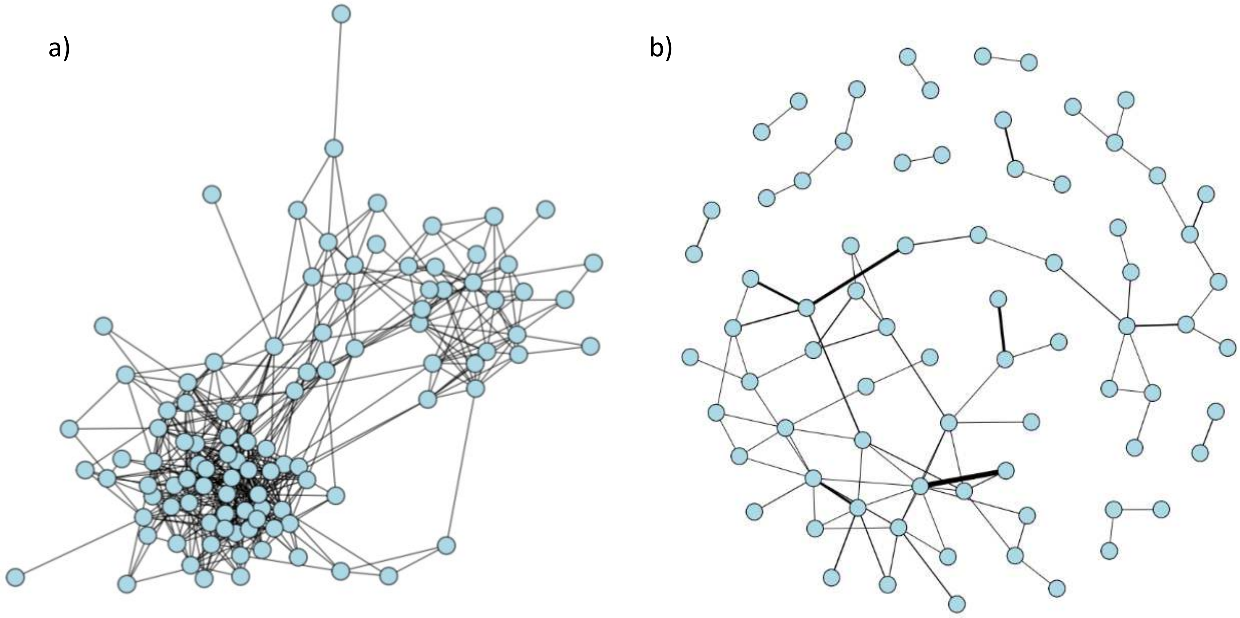

Figure 1. Example networks using the full dataset from 2018. (a) Edges with association strengths (SRI) ≥ 0.07 (an arbitrary cut-off) shown with isolated individuals excluded; and (b) edges with association strengths (SRI) ≥ 0.13 (an arbitrary cut-off) shown, edge thickness weighted by SRI (range: 0.13 to 0.5) and isolated individuals excluded.

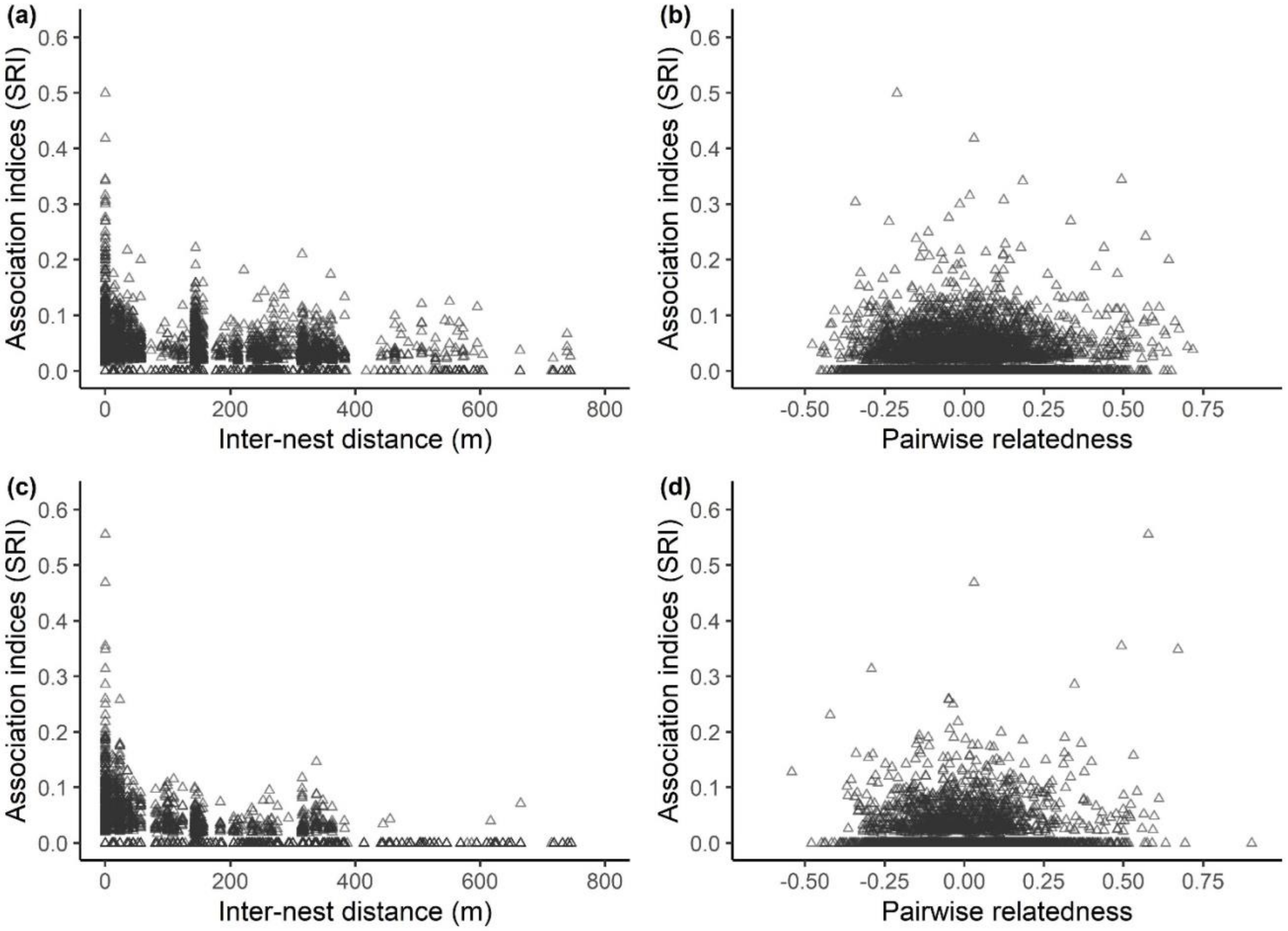

Figure 2. The relationship between social association indices (SRI) and inter-nest distances (a, c), and pairwise relatedness (b, d). Number of individuals as follows: 110 individuals in 2018 (a, b) and 82 individuals in 2019 (c, d). Including data collected at a baited food trap.

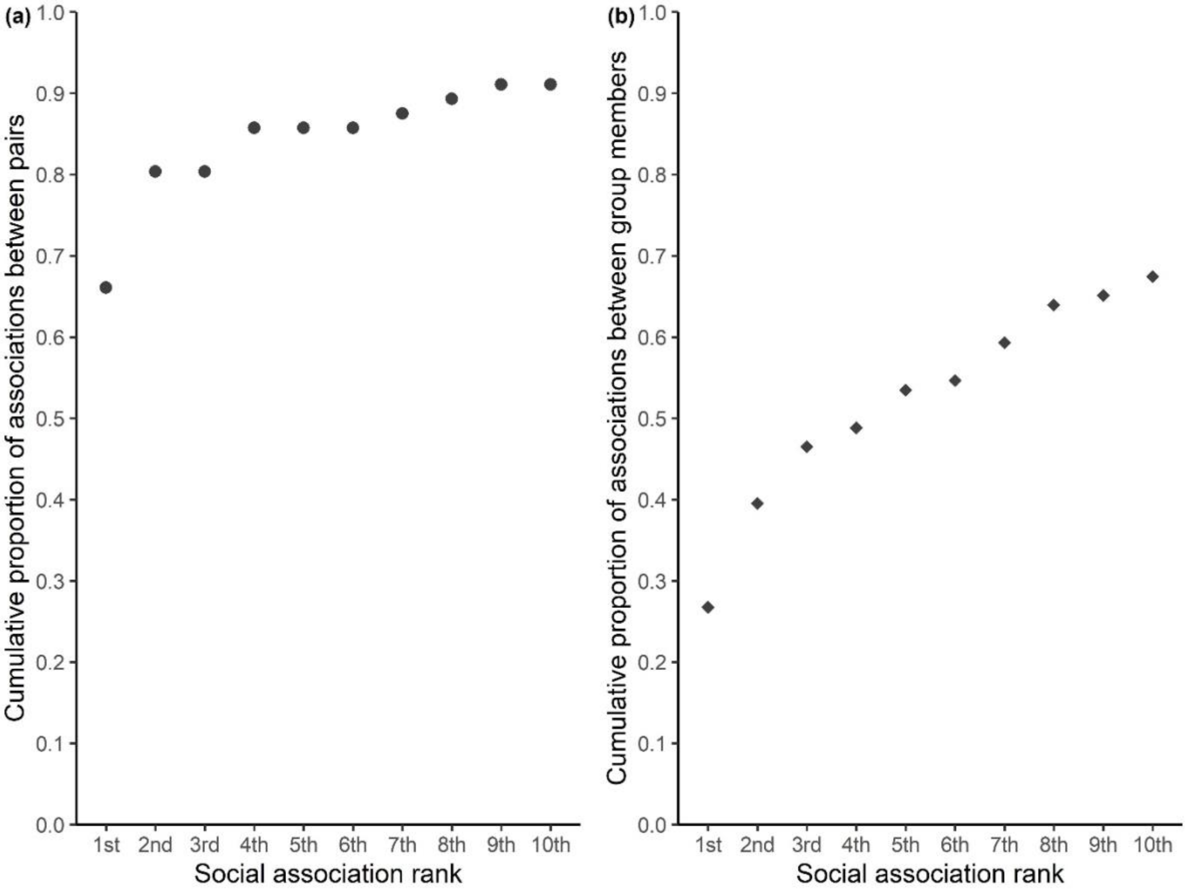

Figure 3. Social association ranks from 1st (closest associate) to 10th between members of: (a) social pairs (*N* = 28 pairs, 56 possible social association ranks); and (b) group members (*N* = 32 individuals, 86 possible social association ranks). Cumulative proportion of the total possible associations are shown.

SUPPORTING INFORMATION

S1. Survey locations

S2. Social association strength and relatedness within nesting trees.

Figure S1. The relationship between social association indices and pairwise relatedness and inter-nest distances, including all data.

Figure S2. The number of observations of males and females in 2018 and 2019, with data from the artificial food source included and excluded.

Figure S3. The relationship between social association indices and inter-nest distances and pairwise relatedness, when data collected at an artificial food source was excluded.