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

3 FRANCESCA S. E. DAWSON PELL*, BEN J. HATCHWELL*, ALBA ORTEGA-SEGALERVA† and JUAN CARLOS
4 SENAR†

5 **Ecology and Evolutionary Biology, School of Biosciences, University of Sheffield, Sheffield, S10 2TN,*
6 *UK*

7 *†Museu de Ciències Naturals de Barcelona, Castell dels Tres Dragons, P^o Picasso s/n, 08003*
8 *Barcelona, Spain*

9

10 Corresponding author. Email: b.hatchwell@sheffield.ac.uk.

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12 *Running title:* Foraging parrots associate with neighbours

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

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

33

34

INTRODUCTION

35 Associations with conspecifics are often non-random in group-living species, with individuals associating
36 preferentially with certain group members (Whitehead, 2008; Farine *et al.*, 2015). The social
37 connections between individuals and the resulting network structure can have wide-ranging
38 implications for a variety of ecological and evolutionary processes (Gokcekus *et al.*, 2021). For example,
39 social structure can have consequences for sexual selection and mating strategies (Oh & Badyaev, 2010),
40 influence foraging behaviour (Firth *et al.*, 2015), determine how information spreads through a group or

41 population (Firth *et al.*, 2016) and, similarly, can determine the spread of disease or parasites through a
42 network of individuals (Sah *et al.*, 2018). Thus, variation among individuals in their social associations
43 can affect fitness (Royle *et al.*, 2012) by impacting survival (Stanton & Mann, 2012; Ellis *et al.*, 2017) or
44 reproductive success (Frère *et al.*, 2010; Riehl & Strong, 2018).

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

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

65 especially when multiple drivers of social association act together to determine social structure (Kurvers
66 *et al.*, 2013).

67 In this study, we examined the social associations of monk parakeets *Myiopsitta monachus* and
68 investigated two potential predictors of their affiliations. Monk parakeets are unique amongst parrots
69 because they build their own stick nests rather than breeding in natural cavities (Forshaw, 1989;
70 Eberhard, 1998). Their nests vary in size from single chambers to compound nests with multiple pairs or
71 groups using separate nest chambers within a shared nest structure. Nests are often aggregated within
72 a single tree or adjacent trees, forming loose colonies that are occupied throughout the year and may
73 persist for many years (Bucher *et al.*, 1990; Eberhard, 1998). A previous study revealed that monk
74 parakeets live in 'kin neighbourhoods' with relatives aggregated within both shared compound nests
75 and nesting trees (Dawson Pell *et al.*, 2021). Monk parakeets are also social away from the nest, foraging
76 in flocks throughout the year. There is some evidence from unmarked wild flocks and marked captive
77 individuals that pairs are the fundamental social unit in monk parakeets. Flocks of two individuals are
78 reportedly the most common both in captivity and in the wild (captive: 25.2-30.4%, wild 32.3% of total
79 flocks), although flocks of > 60 free-living individuals have been recorded in the wild (Hobson *et al.*,
80 2014). Captive birds also display a strong preference for associating with certain individuals, forming
81 strong bonds between pair members as well as between members within a small number of trios
82 (Hobson *et al.*, 2014). However, there has been no detailed investigation into social associations in
83 individually marked free-living monk parakeets. More generally, social structure and the drivers of social
84 associations are poorly known in the Psittacidae due to the methodological challenges of studying most
85 parrot species in the wild, with many species being canopy-dwelling and not amenable to observation.

86 The kin neighbourhood social system, aggregated nests and social foraging behaviour of the
87 monk parakeet make it an ideal species to examine the influence of kinship and familiarity through nest
88 proximity on the social associations of foraging birds. The aim of this study was to combine molecular
89 genetic techniques with field observations during the breeding season to first characterise the overall

90 pattern of social associations in the monk parakeet. We then investigated whether social associations
91 reflected either nest proximity or genetic relatedness. Finally, we examined whether members of pairs
92 and of breeding groups containing 3+ birds were close social associates away from the nest. Through
93 these investigations we aim to expand our understanding of sociality in this unusual parrot species and
94 add to the limited knowledge of parrot social systems.

95

96

MATERIAL AND METHODS

97

STUDY SITE AND SPECIES

98 The field study was conducted in the city of Barcelona, Spain (41.39°N 2.17°E) on the north-east
99 coast of the Iberian Peninsula. The metropolitan area of Barcelona is approximately 102 km² and
100 consists mainly of highly developed urban environment with numerous parks throughout the city.
101 The main study site encompassed Ciutadella Park (c. 30 ha), containing both native and exotic
102 vegetation, and smaller parks and streets with mature trees in the surrounding area up to
103 approximately 2 km away (for a list of survey locations see Supplementary Material S1).

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

110 Birds were individually marked after trapping them in the nest as nestlings or incubating
111 adults, or when foraging using a baited food trap or gas-propelled net. Birds have been captured
112 every year since 2002 in two six-week sampling periods in the winter and summer months (Conroy &
113 Senar, 2009). Captured birds are ringed with aluminium leg rings and marked with unique, light-
114 weight medals attached to neck collars (Senar *et al.*, 2012), which are visible through binoculars

115 from up to 30-40 m. Approximately 62-64% of the study population in Ciutadella Park are marked at
116 any time, based on the proportion of individuals marked in 10 mature pine trees subjected to
117 intensive monitoring during the breeding season. For birds first caught as adults, we use the year of
118 ringing to determine their minimum age.

119 COMPLIANCE WITH ETHICAL STANDARDS

120 Birds were handled and blood samples taken with special permission EPI 7/2015 (01529/1498/2015)
121 from Direcció General del Medi Natural i Biodiversitat, Generalitat de Catalunya, following Catalan
122 regional ethical guidelines for the handling of birds. JCS received special authorization (001501-
123 0402.2009) for the handling of animals in research from Servei de Protecció de la Fauna, Flora
124 i Animal de Companyia, according to Decree 214/1997/30.07. Handling times were kept to a
125 minimum.

126 IDENTIFYING GROUP MEMBERS

127 Ciutadella Park and the other parks visited during this study are public access parks and monk
128 parakeets are habituated to human presence near their nests and during foraging and other
129 activities. In 2018 and 2019, we recorded groups of individually-marked monk parakeets away from
130 the nest throughout the breeding season (March-September; Senar et al., 2019) in two contexts.
131 First, groups of monk parakeets were recorded opportunistically when encountered during surveys
132 of the field site. Groups were recorded engaging in various activities, often foraging, but also
133 drinking, bathing and resting. We used the 'gambit of the group', which assumes that all individuals
134 in a spatially and temporally clustered group are associated with one another (Whitehead & Dufault,
135 1999). Individuals were recorded as being in the same group if they were within c. 5 m of each other
136 and any individuals that joined the group within approximately 2 minutes of the observer
137 encountering the group were included as group members. GPS coordinates, date and time of each
138 group were recorded. Secondly, groups were recorded during observations made at a baited trap
139 (containing peanuts and sunflower seeds), situated on the roof of the Museu de Ciències Naturals

140 within Ciutadella Park. For observations at the trap an observer used binoculars to identify marked
141 birds in groups at the feeder. These observations were conducted for approximately three hours a
142 week throughout the breeding season. Marked birds present at the trap were recorded at 10 minute
143 intervals and, as during surveys of the park, any individuals that joined a group at the trap within
144 approximately 2 minutes of the observation starting were included in that flock. In both contexts, we
145 focused on recording marked individuals only because of the difficulty of recording accurately the
146 number of unmarked birds.

147 GENOTYPING AND RELATEDNESS

148 Blood samples (maximum 100 μ l) were taken from adults and nestlings for genetic sex-typing (monk
149 parakeets are sexually monomorphic (Forshaw, 1989)) and to assess genetic relatedness between
150 individuals. For details of blood sample storage, DNA extraction techniques, marker quality
151 assessment and PCR protocols see Dawson Pell *et al.* (2020) and Dawson Pell *et al.* (2021). Alleles
152 were scored blind to bird identity and sex and individuals were typed at 21 polymorphic
153 microsatellite loci: Mmon01, Mmon02, Mmon03, Mmon04, Mmon07, Mmon09, Mmon10, Mmon11,
154 Mmon13, Mmon14, Mmon15, Mmon16 (Dawson Pell *et al.*, 2020), MmGT060, MmGT046,
155 MmGT105, MmGT030, MmGT071, MmGT057 (Russello *et al.*, 2007), TG03-002 and TG05-046
156 (Dawson *et al.*, 2010), and CAM-20 (Dawson *et al.*, 2013). Individuals were sex-typed using the
157 sexing marker Z002B (Dawson, 2007). A previous estimate of genotyping error, based on the repeat
158 genotyping of 50 individuals with these markers in this study system is 3.1% (F. S. E. D. P.
159 unpublished data). We calculated pairwise genetic relatedness between individuals using Queller
160 and Goodnight's (1989) coefficient of relatedness (r_{QG}) in SPAGeDi version 1.5 (Hardy & Vekemans,
161 2002). We used the genotypes of all 142 unique individuals included in our social association dataset
162 to generate allele frequencies.

163 NEST LOCATIONS AND INTER-NEST DISTANCES

164 The nesting tree location of marked birds was determined in two ways. First, we conducted detailed
165 behavioural observations at 10 mature pine trees in Ciutadella Park throughout the breeding season
166 in 2018 (263 hours) and 2019 (124 hours). A total of 113 marked birds were located in these focal
167 trees in 2018 and 103 in 2019. Birds were never observed to enter a nest chamber they were not
168 using for breeding or roosting during our period of observation, so we are confident that birds
169 assigned as nest occupants were residents in that nest and nesting tree. Second, we conducted
170 surveys in the rest of Ciutadella Park and in likely nesting areas up to 6 km from the park in 2018 and
171 2019 (total = 380 hours). Once marked birds were assigned to a nest, we recorded the nest's GPS
172 coordinates; all birds in the same nesting tree were assigned the same GPS coordinates with a
173 distance of 0 m between their nests. GPS coordinates were converted to Cartesian coordinates
174 (UTM) for calculations of inter-nest distance in SPAGeDi version 1.5 (Hardy & Vekemans, 2002). We
175 calculated inter-nest distances separately for 2018 and 2019.

176 SOCIAL ASSOCIATIONS

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

$$182 \text{SRI}_{AB} = x / (x + y_{AB} + y_A + y_B)$$

183 in which the SRI between the individuals *A* and *B* is defined as the number of observations in which
184 the two co-occurred (*x*), divided by the number of observations in which they both occurred
185 together or individually, with y_{AB} representing the occasions the individuals were observed
186 simultaneously but apart and y_A indicating occasions that individual *A* was observed without
187 individual *B* and y_B indicating the reverse. To reduce bias in association indices caused by limited
188 sampling, we excluded birds observed on less than five occasions (2018: 171 out of 364 sighted

189 individuals excluded; 2019: 131/288 birds excluded). In addition, we excluded birds observed in their
190 fledging year because they were still fed by their parents and were therefore likely to be associated
191 with them away from the nest (2018: $N = 74$ fledglings excluded; 2019: $N = 46$ excluded).

192 SOCIAL ASSOCIATIONS, INTER-NEST DISTANCE AND PAIRWISE GENETIC RELATEDNESS

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

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

214 Following exclusions, in 2018 we had data on 821 social groups, comprising 110 individuals
215 (41 females, 69 males, 5995 dyads) with a mean number of observations per bird of 17.0 ± 7.8 SD,
216 females (13.9 ± 7.0 , median = 13) being observed less than males (18.8 ± 7.7 , median = 18; Wilcoxon
217 rank sum test: $Z = -3.28$, $p = 0.001$; Figure S2a). This dataset included birds aged from 1-12+ years old
218 based on year of ringing or fledging date. In 2019, we had data on 753 social groups that included 82
219 individuals (32 females, 50 males, 3403 dyads) that met the criteria for inclusion with ages ranging
220 from 1-13+ years old. The mean number of observations per bird in 2019 was 15.9 ± 7.8 SD and
221 males (18.7 ± 7.4 , median = 19) were again observed more than females (11.5 ± 6.4 , median 9.5; $Z =$
222 -4.33 , $P < 0.001$; Figure S2c).

223 We re-ran these analyses using a conservative dataset that excluded data collected at the
224 baited trap in case this large supplementary food source attracted birds from greater distances or
225 resulted in atypical aggregations. This smaller dataset included 656 social groups and 98 individuals
226 (33 females, 65 males) that met the inclusion criteria in 2018, and 680 social groups and 78
227 individuals (29 females, 49 males) in 2019. Age ranges were the same as above for both years. The
228 mean number of observations per bird was 12.5 ± 5.5 SD in 2018 and was 15.4 ± 7.4 SD in 2019, with
229 no difference between the number of observations per female (mean \pm SD = 11.5 ± 5.4 , median = 11)
230 and male (13.0 ± 5.5 , median = 13; $Z = -1.30$, $P = 0.19$; Figure S2b) in 2018, but with males ($17.7 \pm$
231 6.9 , median = 19) observed more than females in 2019 (11.4 ± 6.4 , median = 10; $Z = -3.91$, $P < 0.001$;
232 Figure S2d).

233 SAME-SEX AND OPPOSITE-SEX ASSOCIATIONS

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

239 ASSOCIATIONS BETWEEN MEMBERS OF SOCIAL PAIRS AND BREEDING GROUPS

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

250

251 RESULTS

252 CHARACTERISTICS OF MONK PARAKEET SOCIAL ASSOCIATIONS

253 Social association strengths between individuals were relatively sparse and weak in both years
254 (Figures 1 & 2). Mean SRI \pm SD was 0.02 ± 0.04 for 110 birds in 2018 ($N = 5995$ possible dyads), and
255 0.02 ± 0.04 for 82 birds in 2019 ($N = 3403$ possible dyads). In both years, distributions of associations
256 were right-skewed and included many birds without or with very weak associations (i.e. SRI of zero
257 or close to zero). However, maximum association strengths were around 0.5 in both years, and the
258 mean association strength between birds observed together on at least one occasion was $0.05 \pm$
259 0.04 in 2018 ($N = 2457$ associating dyads) and 0.06 ± 0.05 in 2019 ($N = 1038$ associating dyads).

260 FIGURE 1 HERE

261

262 EFFECTS OF RELATEDNESS AND INTER-NEST DISTANCES

263 Inter-nest distances ranged from 0 m (for birds nesting in the same tree) to 745 m (mean \pm SD 205 m
264 ± 153 in 2018, 214 m ± 157 in 2019). The mean pairwise coefficient of relatedness (r_{QG}) for dyads was

265 -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.
266 Inter-nest distance was negatively related to the strength of the social association between
267 individuals in both years (Figure 2a,c), birds nesting closer to each other having stronger social
268 associations when away from the nest (2018: posterior mean = -0.752, 95% credible intervals (CI) = -
269 0.792 to -0.712; 2019: posterior mean = -1.492, 95% CI = -1.572 to -1.412). In contrast, relatedness
270 was not a significant predictor of the strength of associations, with credible intervals overlapping 0 in
271 both years (Figure 2b,d; 2018: posterior mean = 0.023, 95% CI = -0.008 to 0.054; 2019: posterior
272 mean = 0.040, 95% CI = -0.002 to 0.083).

273 FIGURE 2 HERE

274

275 We found qualitatively the same results when excluding trap data (Figure S3); inter-nest
276 distance (2018: posterior mean = -1.151, 95% CI = -1.225 to -1.080; 2019: posterior mean = -1.394,
277 95% CI = -1.473 to -1.320), but not pairwise relatedness (2018: posterior mean = 0.024, 95% CI = -
278 0.023 to 0.070; 2019: posterior mean = 0.036, 95% CI = -0.008 to 0.079), was significantly related to
279 the strength of the observed associations in both years.

280 Kin are clustered within nesting trees in the monk parakeet (Dawson Pell *et al.*, 2021), so we
281 also examined whether pairwise relatedness of those birds nesting within the same tree predicted
282 their social association strength when away from the nest (for model details see Supplementary
283 Material S4). We found the same pattern as that revealed by the full data set, with relatedness
284 having negligible impact on the strength of social associations (posterior mean = -0.034, 95% CI = -
285 0.098 to 0.029).

286 When examining same and opposite-sex associations, we found qualitatively similar
287 patterns. Social association strength decreased with increasing inter-nest distance in female-female
288 (posterior mean = -0.523, 95% CI = -0.653 to -0.397), male-male (posterior mean = -0.793, 95% CI = -
289 0.849 to -0.736), and opposite-sex dyads (posterior mean = -0.747, 95% CI = -0.808 to -0.686), while

290 pairwise relatedness was unrelated to association strength in all cases (females: posterior mean =
291 0.003, 95% CI = -0.109 to 0.112; males: posterior mean = 0.025, 95% CI = -0.018 to 0.068; opposite-
292 sex: posterior mean = 0.031, 95% CI = -0.015 to 0.078).

293 ASSOCIATIONS BETWEEN SOCIAL PAIRS AND BREEDING GROUP MEMBERS

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

305 We observed nine separate breeding groups containing 32 birds (3-5 individuals per group;
306 mean = 3.6) in which all members of the group were also included in our social network. In 23/86
307 (27%) possible associations, the group member's closest social associate was another member of the
308 same breeding group, with 58/86 (67%) being in each other's top 10 closest associates (Figure 3b).
309 These results indicate that members of breeding groups are often close social associates when they
310 are away from the nest, but relationships with group members have lower precedence than those
311 between social pair members.

312 FIGURE 3 HERE

313

314 DISCUSSION

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

324 Social association with birds breeding in close proximity could result simply from shared
325 space use, birds living nearby being more likely to be seen together, without any active affiliation.
326 Alternatively, there may be a preference for association with familiar individuals. It seems unlikely
327 that this relationship is driven entirely by space use because monk parakeets are non-territorial and
328 foragers routinely travel distances that were beyond the inter-nest distances included in this study
329 so frequent interactions with birds from other nests would be expected. The mean inter-nest
330 distance of birds included in this study was approximately 200 m (range 0 – 745 m), and it is
331 estimated that adult monk parakeets regularly travel several hundred meters to forage, with home
332 ranges of c. 12 ha (Carrillo-Ortiz, 2009; Senar *et al.* 2021). Thus, despite the very extensive overlap of
333 home ranges, birds still preferentially associated with individuals from their own, or nearby trees
334 (Figure 2). Monk parakeets are relatively long-lived (Conroy & Senar, 2009) and exhibit high nest-site
335 fidelity (Dawson Pell *et al.*, 2021), which may facilitate long-term affiliations between individuals
336 breeding in close proximity. This association with familiar individuals could confer multiple fitness
337 benefits, including foraging benefits (Webster & Hart, 2007), enhanced predator avoidance (Griffiths
338 *et al.*, 2004), more stable dominance hierarchies (Höjesjö *et al.*, 1998), facilitation of social learning
339 (Guillette *et al.*, 2016), and reduced reproductive competition or increased reproductive
340 coordination (Kohn, 2017; Riehl & Strong, 2018). We have no direct evidence on what the benefits of

341 associating with familiar individuals might be in monk parakeets, but the fact that social ties are not
342 exclusive to breeding pairs or groups and do not differ between same-sex and opposite-sex dyads
343 suggests that any benefits are not exclusively related to reproduction. Research into long-term
344 associations would be worthwhile to understand the dynamics and potential fitness implications of
345 social bonds in this species.

346 In contrast to the relationship with nest proximity, we found that genetic relatedness did not
347 predict the strength of social associations away from the nest. This result is interesting because
348 relatives are clustered together in both compound nests and nesting trees (Dawson Pell *et al.*, 2021)
349 and yet these kin associations did not extend to movements away from the nest. Indeed, the
350 absence of a relationship between relatedness and foraging associations contrasts with many other
351 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
352 is almost inevitable (Gokcekus *et al.*, 2021). By contrast, in non-territorial species, or in group-living
353 species where interactions with kin and non-kin are frequent, evidence for preferential association
354 with kin is mixed (Hatchwell, 2010; Hirsch *et al.*, 2012; Arnberg *et al.*, 2015). A negligible relationship
355 between relatedness and social associations in monk parakeets might be expected given that the
356 closest social associate of an individual was their social mate in most (66%) cases and inbreeding is
357 rare or absent in our study population (Dawson Pell *et al.*, 2021). However, other social associations
358 that were sometimes stronger than that of the pair were observed so relatedness could still be a
359 predictor of associations if such a preference existed. It should also be noted that this study was
360 conducted in the breeding season, during which females spend extended periods in the nest
361 incubating eggs and brooding young chicks. Therefore, pair members may be observed separately
362 more often at this time and a different pattern may be expected if this study was repeated during
363 the non-breeding season. This difference in parental roles may also explain why males were
364 observed significantly more than females. As well as spending more time in the nest incubating and
365 brooding, incubating females are fed by males so their appearance outside the nest is reduced even
366

367 further (Eberhard, 1998). An alternative explanation is that females were observed less frequently
368 because they travel further from the nest to forage, but there is no evidence that females have
369 larger home ranges than males (Senar *et al.*, 2021).

370 Studies of parrot social structure in the wild are limited, presumably due to the practical
371 difficulties of observing a largely canopy-dwelling taxon often with high mobility. Our study
372 therefore adds to a limited but growing number of studies investigating patterns of social
373 associations in the Psittacidae, a family often discussed in the context of social evolution (Emery,
374 2006; Hobson *et al.*, 2014). Like other parrot species (Buhrman-Deever *et al.*, 2008), monk parakeets
375 exhibit short-term fission-fusion social dynamics (Hobson *et al.*, 2014), but this did not mask the
376 existence of consistent social ties away from the nest. Stable social relationships are present in
377 another parrot species adapted to living in the urban environment, the sulphur-crested cockatoo,
378 *Cacatua galerita*, that also has a fission-fusion social system (Aplin *et al.*, 2020). In the sulphur-
379 crested cockatoo it is mainly roost-site choice that drives social associations (Aplin *et al.*, 2020), a
380 pattern similar to that revealed here.

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

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

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409 DATA AVAILABILITY

410 All data will be made available via Dryad.

411 AUTHOR CONTRIBUTIONS

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

415

CONFLICT OF INTEREST

416 The authors have no conflict of interest to declare

417

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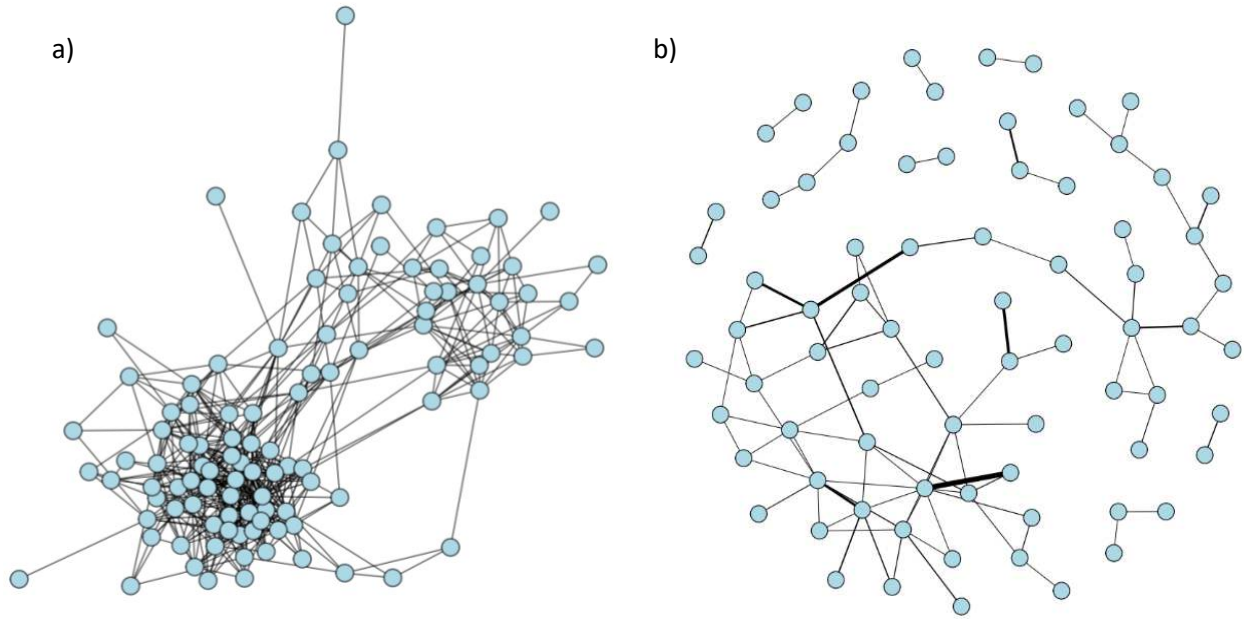
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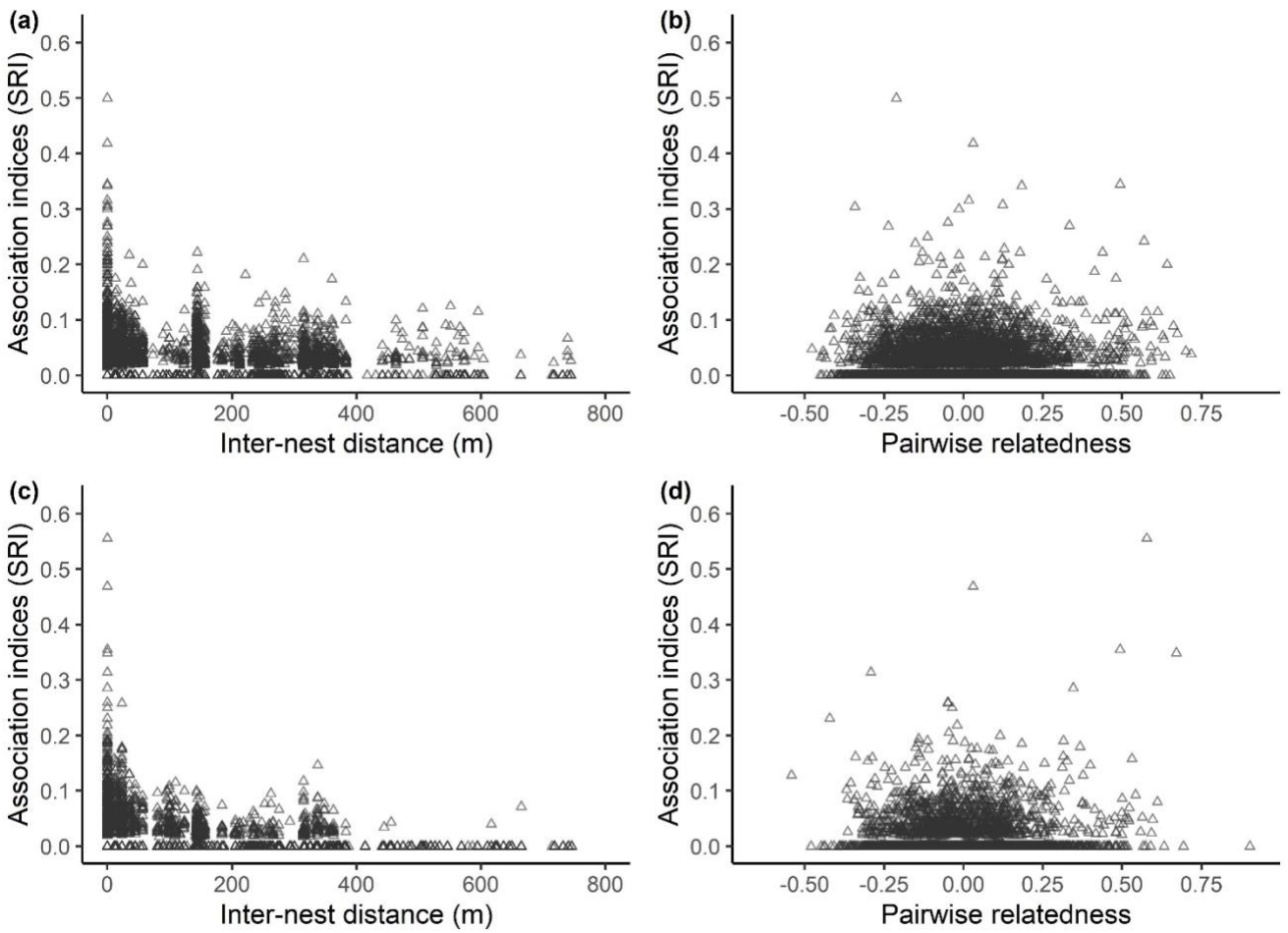
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628 **Figure 1.** Example networks using the full dataset from 2018. (a) Edges with association strengths
 629 (SRI) ≥ 0.07 (an arbitrary cut-off) shown with isolated individuals excluded; and (b) edges with
 630 association strengths (SRI) ≥ 0.13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

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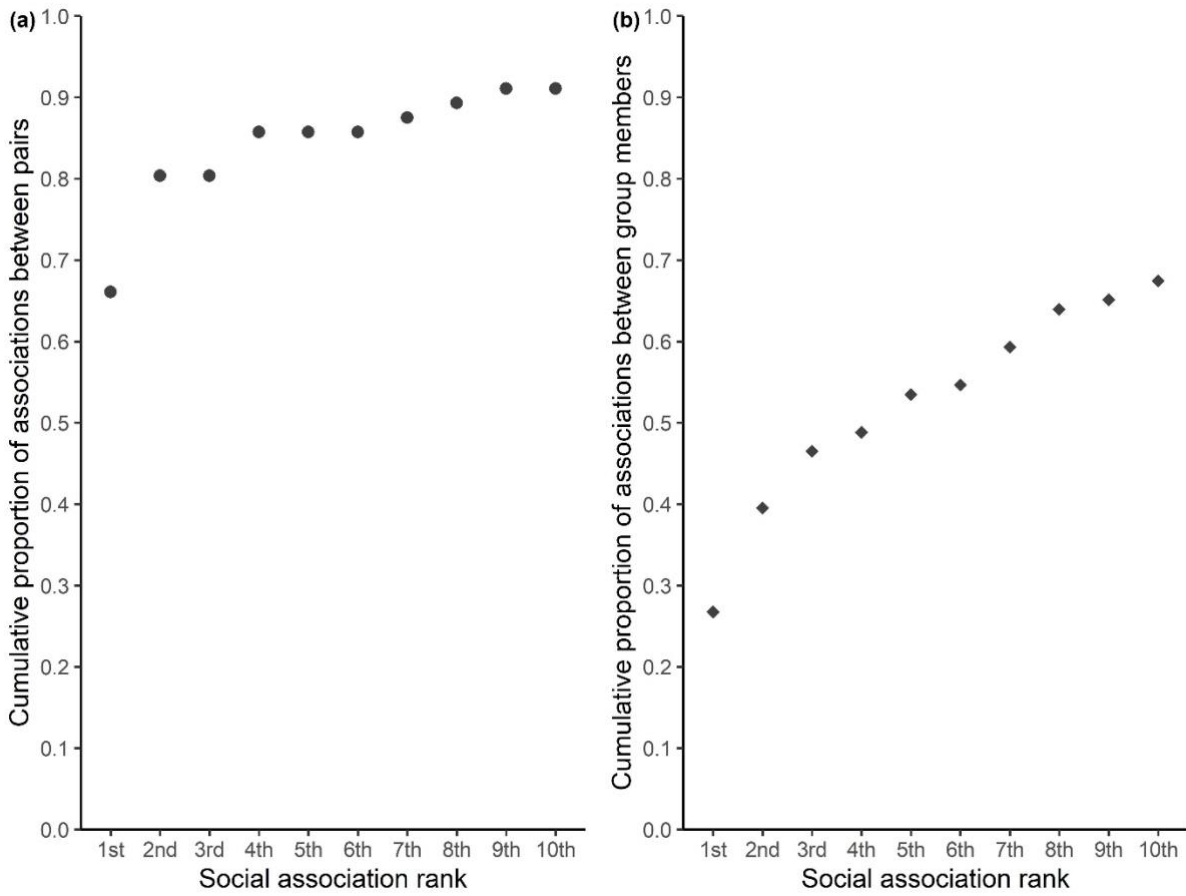
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635 **Figure 2.** The relationship between social association indices (SRI) and inter-nest distances (a, c), and
636 pairwise relatedness (b, d). Number of individuals as follows: 110 individuals in 2018 (a, b) and 82
637 individuals in 2019 (c, d).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

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642 **Figure 3.** Social association ranks from 1st (closest associate) to 10th between members of: (a) social
643 pairs ($N = 28$ pairs, 56 possible social association ranks); and (b) group members ($N = 32$ individuals,
644 86 possible social association ranks). Cumulative proportion of the total possible associations are
645 shown.

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648 **SUPPORTING INFORMATION**

649 **S1. Survey locations**

650 **S2. Social association strength and relatedness within nesting trees.**

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

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

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

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