Multi-network analysis reveals context-dependent kin relationships in wild sulphur-crested cockatoos, *Cacatua galerita*.

Penndorf, J.[a], Ewart, K. M. [b,c], Klump, B. C. [a], Martin, J. M. [c,d,*], Aplin, L. M.[a, e,f,*]

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[a] Cognitive and Cultural Ecology Research Group, Max Planck Institute of Animal Behavior, Radolfzell, Germany.

[b] Australian Museum Research Institute, Sydney, NSW, Australia.

[c] School of Life and Environmental Sciences, The University of Sydney, Camperdown, NSW, Australia.

[d] Institute of Science and Learning, Taronga Conservation Society Australia, Mosman, NSW, Australia.

[e] Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany.

[f] Division of Ecology and Evolution, Research School of Biology, Australian National University, Canberra, Australia.

[*] Co-senior authors

Abstract

1. A preference to associate with kin facilitates inclusive fitness benefits, and increased tolerance or cooperation between kin may be an added benefit of group living. Many species exhibit preferred associations with kin, however it is often hard to disentangle active preferences from passive overlap, for example caused by limited dispersal or inheritance of social position.

2. Parrots are often thought to exhibit social complexity, and many species appear to show a multi-level society consisting of pair-bonded individuals moving between fission-fusion foraging groups, within larger communal roosts. Previous work has shown that, despite these fission-fusion dynamics, individuals can exhibit long-term preferred foraging associations outside their pair-bonds. Yet the underlying drivers of these social preferences remain largely unknown.

3. In this study, we use a multi-layered social network approach to examine the influence of kinship on social associations and interactions in wild sulphur-crested cockatoos, *Cacatua galerita*. We recorded roost co-membership, social associations, and affiliative and aggressive interactions in 561 individually marked birds across three neighbouring roosts. We then collected genetic samples from 205 cockatoos, and conducted a relationship analysis to construct a kinship network. Finally, we tested correlations between kinship and four social networks: spatial proximity, affiliative, low-intensity aggression, and high-intensity aggressions. We examined these potential correlations at two levels - within roost groups and between roosts.

4. Our result showed that while roosting groups were clearly defined, they showed little genetic differentiation. Between roost movement was high, with juveniles, especially females, repeatedly moving between roosting sites. Both within and across these roosting communities, individuals preferentially associated with kin. Supporting this, individuals were also more likely to allopreen kin. However, against our expectation, individuals preferred to direct aggression towards kin within roosts, but avoided aggressing kin of different roosts.

5. Our study demonstrates that sulphur-crested cockatoos prefer to associate with kin, both within and between roosting groups, and exhibit behavioural and context-dependent social interaction rules towards kin. Our results help reveal the drivers of social association in this species, while adding to the evidence for social complexity in parrots.

Keywords: *Cacatua galerita*, kinship networks, parrots, population genetics, social networks, urban ecology

Introduction

Living in groups can provide a range of benefits to all individual members (Brown and Brown, 1987). These benefits can be enhanced by preferentially associating with specific others (J. Krause et al., 2002). Associations with individuals sharing characteristics such as age (Aplin et al., 2021), sex (reviewed by Ruckstuhl, 2007), body size (Pitcher et al., 1986; Croft et al., 2005), or rank (Smith et al., 2007) can reduce conflict (Dadda et al., 2005) and predation risk (Sorato et al., 2012), and improve foraging efficiency (J. Krause et al., 2002). In particular, associations with kin have been shown to provide fitness benefits that range from higher reproductive success (Silk et al., 2009) and inclusive fitness (Hamilton, 1964; Grafen, 1984; Levin and Grafen, 2019, though see Birch, 2017) to reduced stress levels (Gerlach et al., 2007) and increased longevity (Silk et al., 2010). Conversely, associating with kin can be disadvantageous if such associations increase the risk of inbreeding, or lead to competition between relatives (Evans et al., 2021). However, these costs can be partly mitigated via context-dependent social decision-making, for example avoiding kin during the breeding season while preferring them at other times (Evans et al., 2021). Yet while the costs and benefits of associating with kin have been extensively explored, the underlying processes leading to such patterns warrants further research.

Association with kin might reflect active choice, but alternatively might arise from passive mechanisms such as limited dispersal (Klauke et al., 2016) or an inheritance of social position (Ilany et al., 2021. There are two likely avenues to help disentangle these alternative drivers for social associations. The first is to examine this question in social systems exhibiting fission-fusion social dynamics, where larger groups or communities frequently split into subgroups of variable composition. In systems with such fluid group membership, sex, age and breeding status have all been shown to affect associations, with individuals sharing these characteristics being more associated than expected by chance (Chiyo et al., 2011; Zeus et al., 2018; Aplin et al., 2021). When considering kinship however, the pattern is both more mixed and context-dependent. In species where individuals forms coalitions, preferred associates tend to be more related than expected by chance (e.g. dolphins, Krützen et al., 2003; Parsons et al., 2003; monk parakeets, Dawson Pell et al., 2021). While a more general tendency to associate with kin has also been reported (e.g., Elephants, *Loxodonta africana*: Chiyo et al., 2011; Geese,

Branta leucopsis: Kurvers et al., 2013; Giraffes, *Giraffa camelopardalis*: Carter et al., 2013), other species show no such preference; for example, roosting patterns in big brown bats (*Myotis bechsteinii*, Metheny et al., 2008) are not affected by kinship. Perhaps most intriguingly, a recent comparative study investigating kinship, social networks, and roost-switching behaviour in nine species of micro-bats (Wilkinson et al., 2019), found that the preference to associate with kin was stronger in species with more roost-switching. This suggests a possible non-linear relationship between social structure and kinship, where the benefits of associating with kin may not only be elevated in highly structured societies (e.g., cooperative breeding systems), but also be higher in social contexts where very few individuals are known to one another.

A second potential avenue is to examine variation in interaction decisions while controlling for their social opportunity. Here the assumption is that if individuals can recognise kin and are preferentially associating with them, they should also be more likely to direct affiliative behaviours towards relatives (e.g. grooming and food sharing), and be less likely to engage in aggressive interactions (reviewed by Hepper, 1986; Waldman, 1988). Supporting this, a meta-analysis of grooming in primates found a general positive correlation with kinship, although it also supported a larger role for direct reciprocity (Schino and Aureli, 2010). While the literature on social interactions is extensive, most studies have examined these questions in groups with high relatedness (e.g. in cooperative breeders, Madden et al., 2012) and there are relatively few examples of studies that combine these two approaches to examine the influence of kinship on social decision-making in more open, fission-fusion species.

Here, we examine the influence of kinship on social associations and interactions in sulphur-crested (SC-) cockatoos, *Cacatua galerita*. Similar to many parrot species (Hardy, 1965; Power, 1966; Styche, 2000), SC-cockatoos live in large-scale fission-fusion societies, where stable night-roost aggregations of up to several hundred individuals (Lindenmayer et al., 1996) break-up during the day into smaller flocks that forage in a collective home range around the roost site. These foraging flocks have a fluid membership and are of variable size depending on activity, environment, and season (Noske et al., 1982; Aplin et al., 2021). There is little evidence of any kin structuring within roosts in SC-cockatoos or other parrot species (Wright and Wilkinson, 2001, but see Blanco et al., 2021). In addition to these within roost dynamics, between-roost movements are common in SC-cockatoos (Aplin et al., 2021), although their predictors are largely unknown. These within- and between-roost social dynamics

confer a large choice of potential interaction partners, and previous work in this species has shown that SC-cockatoos form non-random social associations, with stable, long-term bonds beyond the pair (Aplin et al., 2021). However, little is known about the factors underlying these association preferences, or the predictors of social interactions such as allopreening or aggression.

Studies on parrots are often hindered by the non-trivial challenge of capturing and marking wild individuals (Beissinger and Bucher, 1992), and the difficulty of following individuals across large home-ranges (Bradbury, 2003). SC-cockatoos are urban persisters and in such environments, populations are relatively habituated (Davis et al., 2017; Kirksey et al., 2018), and appear to exhibit smaller home-range sizes (Aplin et al., 2021), giving a rare opportunity to conduct detailed behavioural observations. First, we habituated and marked 561 SC-cockatoos across three neighbouring roosting communities, collecting social information and genetic material for 205 individuals across three sites. Second, we performed an analysis of genetic relatedness on a larger dataset of 393 individuals, and built kinship networks for these sites. We then examined the correlation between kinship and sociality in multi- network analysis (Finn et al., 2019; Finn, 2021) that compared kinship networks with spatial proximity and three interaction networks - allopreening (an affiliative behaviour), and low- and high-intensity aggressive interactions. Finally, we examined behaviour at two scales: within and between roosting communities. This analytical approach removes the potential effect of spatial overlap and philopatry on any correlation between kinship and social associations, while allowing us to ask whether SC-cockatoos show behavioural or context-dependent social interaction rules towards kin that would infer both individual recognition and a degree of social complexity (Wilkinson et al., 2019).

Methods

Study system

Sulphur-crested cockatoos are large (700-1200g), slow breeding, long-lived parrots. They are common across a large native range in Australia and Papua New Guinea, and populations appear to be increasing, including in human-modified areas (Davis et al., 2017). For the purpose of this study, we focused on three neighbouring roost sites in northern Sydney (Figure 1a). In the Sydney population, the majority of individuals are non-breeding, forming stable communal roosts of tens to hundreds of

individuals, usually in parkland with remnant old growth trees, similar to previous descriptions at other sites (Lindenmayer et al., 1996). Tree hollows for nesting are a limited resource, and breeding pairs (approximately 20-40% of individuals, defend nearby nest hollows year-round, but often roost with the rest of the group when not actively breeding (*personal observation*). Most individuals are relatively site faithful, with a previous study on this population finding that birds used an average of two roost sites over a period of five years (Aplin et al., 2021). Within these roosts, SC-cockatoos exhibit fission-fusion dynamics, feeding on a variety of resources in the surrounding area in variably sized foraging flocks. In urban areas, these resources include human derived and provisioned food (Kirksey et al., 2018; Klump et al., 2021), making birds relatively easy to habituate.

Habituation, marking and morphometric data collection

Birds were habituated to human observers at suburban parks close to three focal roosts (Balmoral Beach "BA", Clifton Gardens "CG", and Northbridge Golf Club "NB"), and at the nearest two neighbouring roosts (Sydney Botanic Gardens "BG" and Ivanhoe Park "MA"; Figure 1a.) Over 2-3 weeks, individuals were attracted to the ground at the same time each day with small amounts of sunflower seed, a commercially available food commonly eaten by SC-cockatoos in urban and agricultural areas (Noske et al., 1982). The observer would remain as close as possible to the foraging flock until the birds began to forage on the ground around the observer and birds could be lightly touched on the back without eliciting an adverse response. Once birds were habituated, they were temporarily and non-invasively marked using non-toxic fabric dye (Marabu Fashion Spray, MARABU GMBH), with each individual receiving a unique mark of one to three colours placed on the middle of the back (Figure 1b). This method resulted in 536 uniquely marked individuals. In addition, 17 birds present in our study area had already been caught, ringed and wing-tagged as part of a previous study (Figure 1c, Davis et al., 2017, Aplin et al., 2021), and 8 birds were uniquely recognisable due to morphological variation (e.g., healed injuries). This resulted in 561 recognisable individuals, which we estimate to be >90% of the local population.

All individuals were sexed and aged by eye colour (brown = juvenile <7 years; red = adult female; black = adult male). Finally, feather samples were opportunistically collected without capture by

plucking feathers from the back of habituated individuals. Once collected, feather samples (n = 1-10 feathers per individual) were stored in paper envelopes until ready for processing. The feather tip (1-2mm; n = 351) was separated for genetic analysis (see below). This produced successful data for 244 samples; these were used to confirm morphometric sexing for adults, to assign sex for juveniles, and for relatedness analyses.

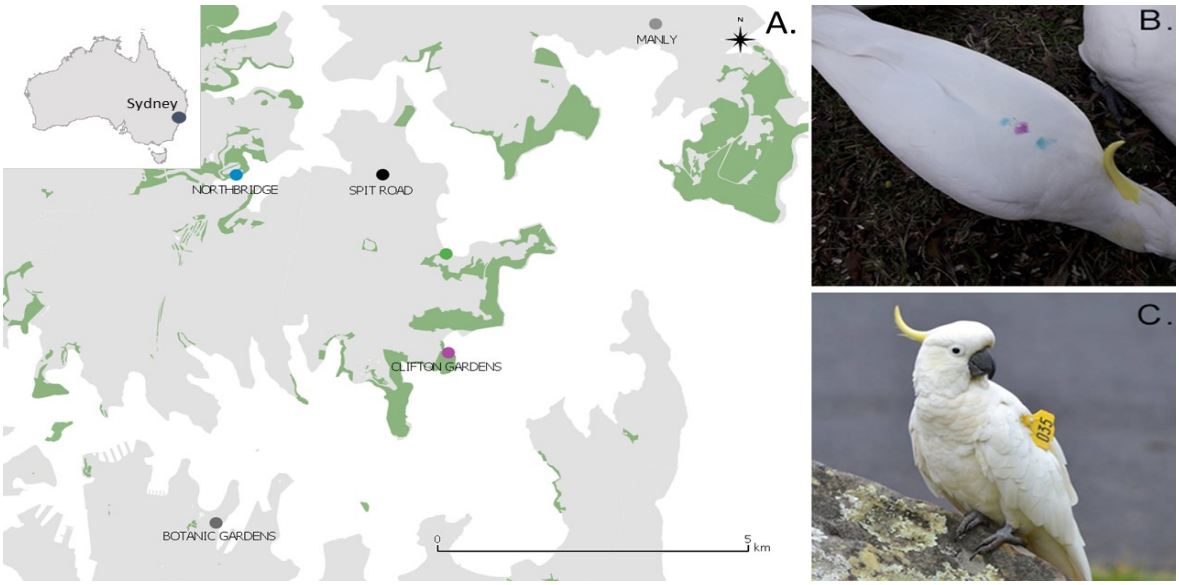

Figure 1: A) Map of Sulphur-crested cockatoo sampling locations where social data and feather samples were collected. Coloured circles represent focal roosts (green: BA, pink: CG, blue: NB); dark (MA) and light grey (BG) circles are nearest neighbouring roosts. The black circle represents the additional site for group scans, were birds from the three focal roosts mixed on a regular basis while being fed by locals. The map was constructed in QGIS (QGIS Development Team, 2009), using OpenStreetMap (OpenStreetMap contributors, 2017). B) Example of marking with temporary dye, "Teal-Pink-Teal", the marks remain visible for approximately 3 months, C) Example of a wing-tagged individual 035, named "Shakespeare".

Measuring social associations and interactions

We collected intensive social data at the three focal roosts in northern Sydney (Figure 1a) for ten days in July (July 8 - July 20) and ten days in September (September 19 - October 2) 2019. As for

marking, individuals were attracted to the ground using small quantities of sunflower seeds scattered over a large area to encourage ground foraging (e.g. of grass roots and shoots). Once the individuals were foraging on natural food sources, group scans (Altmann, 1974) were conducted every 10 minutes, over 3 hours (July 2019) or 2.5 hours (September 2019 - time at each group adjusted to fit within daylight) each day. Presence scans were additionally conducted at a fourth location where individuals from all three roost sites mixed when fed by local residents, helping to capture interactions between individuals of different roost-sites. The final dataset consisted of 819 scans.

In addition to social association data, affiliative and aggressive interactions were recorded *ad libitum* between scans (Altmann, 1974). The number for each type of interaction is presented in Table S1. Finally, we censused roost co-membership on three separate occasions (July 17th-21st, September 15th-20th, September 30th-October 3rd 2019). The observer stood under the roost trees pre-dawn, and attracted individuals down to the ground with sunflower seed as soon as the birds began to become active, recording all marked individuals present. We assigned birds to a particular roost if they had been observed sleeping at one roost site at least twice (n=153 individuals for whom roost-memberships could be classified).

Social network analyses

First, to create social networks for foraging associations, we created a group by individual matrix, where individuals were assigned to the same group if observed in the same presence scan. Given that estimates for rarely observed individuals may be inaccurate (Farine and Whitehead, 2015), we thresholded our data following the example of Aplin et al. (2013). In our case, removing individuals with fewer than 22 observations meant there was no significant relationship between number of observations and the binary degree. We then used the simple ratio index (SRI; Whitehead, 2008) to create an undirected network for each time period (July & September 2019) where edges between individuals were scaled between 0 (never observed in the same group) and 1 (always observed together). The association matrices for each period were highly correlated (Mantel test, n=72, r=0.63, $p<0.001$). Therefore, association data for both study periods were pooled together for further analysis, resulting in a social network of 254 individuals. We tested for evidence of non-random preferred associations

by examining whether the coefficient of variation (CV) of the observed SRI were significantly higher than permuted values. Permutations were conducted in the R package *asnipe* (**asnipe**), permuting individuals in close spatio-temporal proximity, keeping rows and columns constant.

Second, to create aggressive networks, we first *post hoc* split behavioural sequences of aggressive interactions into two distinct types of behaviours that clearly differed in risk: low intensity (no body contact) and high intensity (body contact & chases). One might expect different underlying drivers to these interactions, especially in interactions with kin, as only high intensity interactions involve a risk of injury. For each type of aggression, we calculated an undirected interaction matrix that additionally controlled for social opportunities to interact. For the low intensity aggressions, edge weights were obtained by calculating for each dyad the number of low-intensity interactions divided by the total number of scans in which individuals were associated. For the high intensity aggressions, we calculated the proportion of high intensity aggressions among all agonistic interactions between a given dyad, therefore controlling for the overall tendancy of two individuals to engage in aggressive interactions.

Finally, to create affiliative networks, allopreening events were recorded *ad libitum* over the entire observation period. Within an allopreening event, preenings were mostly reciprocated. They also occurred in trees, making it challenging to record the initiator of the event. We therefore constructed undirected networks where edge weights were obtained by calculating for each dyad the number of preening interactions divided by the sum of all preening events for both individuals. All social analyses were done using RStudio (version 1.4.1103; R version 4.0.4 (2021-02-15), R Core Team, 2021).

Genetic Analysis

DNA analyses

DNA was processed by Diversity Arrays Technology (DArT), using their proprietary restriction-enzyme-based genome complexity reduction platform called DArTseq™ (Kilian et al., 2012; Cruz et al., 2013). Four combinations of restriction enzymes were tested and the PstI-SphI combination was selected. After digestion, DNA was processed following Kilian et al. Kilian et al., 2012, using two different adaptors corresponding to two different restriction enzyme overhangs. Both adaptors

contained an Illumina flow cell attachment sequence, and the PstI-compatible adapter also contained a sequencing primer sequence and a barcode region. A PCR was performed on the resultant libraries as follows: initial denaturation at 94°C for 1 min, then 30 cycles of 94°C for 20 sec, 58°C for 30 sec and 72°C for 45 sec, and a final extension step at 72°C for 7 min. After PCR, equimolar amounts of the libraries underwent a c-Bot (Illumina) bridge PCR followed by single end sequencing for 77 cycles on an Illumina Hiseq2500. Additional details on this platform can be found in Kilian et al. Kilian et al., 2012 and Cruz et al. Cruz et al., 2013.

The resultant sequence data were processed using the proprietary DArT Pty Ltd analytical pipelines. Poor quality sequences were removed, and stringent selection criteria was applied to the barcode region to de-multiplex the sequence reads (minimum barcode Phred score was set at 30, while the minimum whole-read Phred score was set at 10). Sequences were then truncated to 69 bp and clustered with a Hamming distance threshold of 3. Low quality bases from singleton tags were corrected based on collapsed tags. These sequences were used for SNP calling using the proprietary DArTsoft14 pipeline based on DArT PL's C++ algorithm. True orthologous SNP variants were discriminated from paralogous sequences by assessing various parameters, including sequence depth, allele count and call rate. We calculated SNP error rates before and after filtering - i.e. the number of SNP mismatches between replicate pairs over the total number of SNPs that were not missing in both replicates. Analysis was based on the 13 replicate samples (Table S2) using R functions from Mastretta-Yanes et al., 2015.

SNP filtering

The DArTseq SNPs were filtered based on data quality, missing data and linkage using the R package dartR 1.0.5 (Gruber et al., 2018). The initial dataset comprised 58,740 SNPs. Loci that were genotyped in >80% of individuals were removed (i.e. call rate). DArT runs 30% of the samples in replicate in independent libraries and sequencing runs. Loci were removed that were not 100% reproducible, based on the consistency of the locus measured across these technical replicates. SNPs with a read depth <10 and a minor allele frequency <0.01 were removed. Putatively sex-linked markers based on SNPs that were mostly homozygous in males and mostly heterozygous in females, and/or SNPs that aligned with the Z-chromosome of the Finch genome were removed. Only one

SNP was retained per DArTseq marker to remove potentially-linked SNPs. After implementing these filters, the dataset comprised 12,447 SNPs.

Initially, we did not filter for Hardy Weinberg Equilibrium (HWE) as the dataset likely contains numerous family groups, violating the HWE assumption of random mating. However, as a conservative approach, we subsequently re-analysed a dataset with HWE filtering implemented to check for consistency. We performed the HWE test using the R package pegas 0.13 (Paradis, 2010), implementing 1000 Monte Carlo replicates. Loci with a p-value <0.05 based on the exact p-test were removed (removing a further 3507 SNPs).

Finally, before further downstream analysis, one of each of the replicate samples (with the least amount of missing data) were removed from the dataset. We then excluded one potential hybrid individual and one individual with $>60\%$ missing data; all other individuals had $<15\%$ missing data. This resulted in 393 individuals for the relatedness analysis, of which 205 belonged to the 5 roosts considered in our study.

Relatedness analysis

We compared eight relatedness estimators to determine which one was the most appropriate for the SC-cockatoo SNP dataset (Wang, 2011). This included seven estimators implemented in the COANCESTRY software package (Wang, 2011), and a maximum likelihood kinship coefficient, calculated using the R package SNPRelate 1.14 (Zheng et al., 2012). To assess the suitability of these relatedness estimators, we simulated 100 parent-offspring pairs, 100 full-sibling pairs, 100 half-sibling pairs, 100 cousin pairs and 100 unrelated pairs and assessed the correlation between the relatedness estimates and true relatedness values. These simulations were performed in COANCESTRY using the empirical SNP allele frequencies and missing data. We compared the estimates using base R functions and the R package related 1.0 (Pew et al., 2015). After selecting the most reliable relatedness estimator based on the simulation data, we performed a relatedness analysis on the empirical dataset. The reliability of the estimator was verified by assessing how well it approximated two known parent-offspring relationships included in the dataset.

Statistical analysis of kinship and social networks

To examine whether there was any genetic differentiation between roosts, we used mantel tests in the R package *vegan* (Oksanen et al., 2013), to correlate relatedness matrices with a spatial matrix of roost membership. This was performed using roost co-membership assigned for individuals at the three focal roosts by roost counts. As for the three focal roosts, marking location corresponded to roost-membership for 125 of 153 birds (Pearson's Chi-squared test, X^2=178.67, df=4, p<0.001), this analysis was expanded to all five roost sites by using marking location as a proxy for roost-membership.

To test whether associations, aggressive interactions and/or affiliative interactions were influenced by relatedness, we used multiple regression quadratic assignment procedures (MRQAP) via the *asnipe* package (Farine, 2013). In all MRQAP analysis, we used a continuous relatedness matrix. However, because we considered it unlikely for individuals to recognize second- or third-degree relatives, we also re-ran the same analysis on a binary matrix, specifying whether or not a given dyad were first degree relatives, i.e. that their relatedness was above or equal to 0.36 (Figure S1). These regressions were simplified with binary relatedness measures as the only predictor for between-roost analysis. Results are presented in the Supplementary Material (Tables S3, S4,S5, S6).

First, we tested whether social association strength was influenced by relatedness across the entire population, controlling for similarity in age, sex, and for roost co-membership. To disentangle whether patterns were driven by within-roost association preferences or by between-roost associations, we repeated the analysis: i) sub-setting all edges to within-roost only and restricting randomisations to within the same roost, and ii) sub-setting all edges to those occurring between individuals of different roosts. Second, we asked whether aggressive interactions were influenced by relatedness. In the first stage of this analysis, we explored the influence of pairwise relatedness, sex and age similarity, as well as roost co-membership on the proportion of low or high intensity aggressions within a given dyad. For both analyses, social association strength was not included as a co-variate because it was incorporated into the aggressive measure itself. To test whether patterns were driven by within-roost interactions, we repeated the analysis: i) sub-setting all edges to within-roost only and restricting randomisations to within the same roost, and ii) sub-setting all edges to those occurring between

individuals of different roosts. Lastly, we asked whether allopreening interactions were influenced by pairwise relatedness, sex dissimilarity or roost co-membership. As observations of allopreening events were relatively rare (Table S1), we did not threshold the networks for this specific analysis.

Results

Social organisation

In northern Sydney, 561 birds were individually marked or recognisable. Genetic material was successfully obtained from 164 birds across the three focal roost sites (Figure 3; BA: n=68; CG: n=55; NB: n=41), comprising 63 females and 72 males, of which 83 were adults, 45 juveniles and 37 birds of unknown age (Figure 2). Genetic material was collected from 41 birds at two additional roost sites (BG: n=17; MA: n=24), comprising 12 females and 23 males; 18 adults, 17 juveniles, and 6 birds of unknown age. The error rate for the full dataset was relatively low (median = 0.018; excepting one problematic replicate sample), and decreased after SNP filtering (median = 0.010) (Table S2).Of the eight relatedness estimators compared, the SNPRelate maximum likelihood kinship coefficient was most appropriate for this SNP dataset based on simulated dyads (Figure S1). This estimator had the highest correlation with the expected relatedness values (cor = 0.999; p0.001).

Overall, there was a weak tendency for individuals to be more related within than between roosting sites, but this was only present when considering all 5 roosts (focal roosts: Mantel Test, n=164, r=-0.003, p=0.60; all roosts: Mantel Test, n=205, r=0.011, p=0.049). This was not solely due to delayed dispersal in juveniles: within each roost site, the number of adult-adult close-kin dyads was higher than expected within each population under random mixing, and higher than expected under random mixing (t-test, t=2.28, df= 82, p=0.025). In addition, juveniles tended to be observed at more roosting sites than adults (Figure S2A; females estimate ± 95% confidence interval: ES= 0.553 [0.063-1.04], p=0.02, males: ES=0.739 [0.256-1.222], p<0.001; p-values calculated using Tukey adjustments for multiple testing). Juvenile females, but not juvenile males, tended to be less faithful to a specific site than adults of the respective sex (Figure S2B; females: ES=-0.107 [-0.216-0.002], p=0.06, males: ES=-0.058 [-0.151-0.035], p=0.37, p-values calculated using Tukey adjustments for multiple testing).

Analysis of the association patterns revealed strong evidence for non-random associations (Me-

dian CV random = 1.26, CV obs=1.25, P=0.003), suggesting that individuals had preferred and non-preferred associates. While the social association network was clearly clustered by roosting community (Figure 2A), individuals also exhibited extensive foraging associations with individuals from different roost groups (Figure 2B).

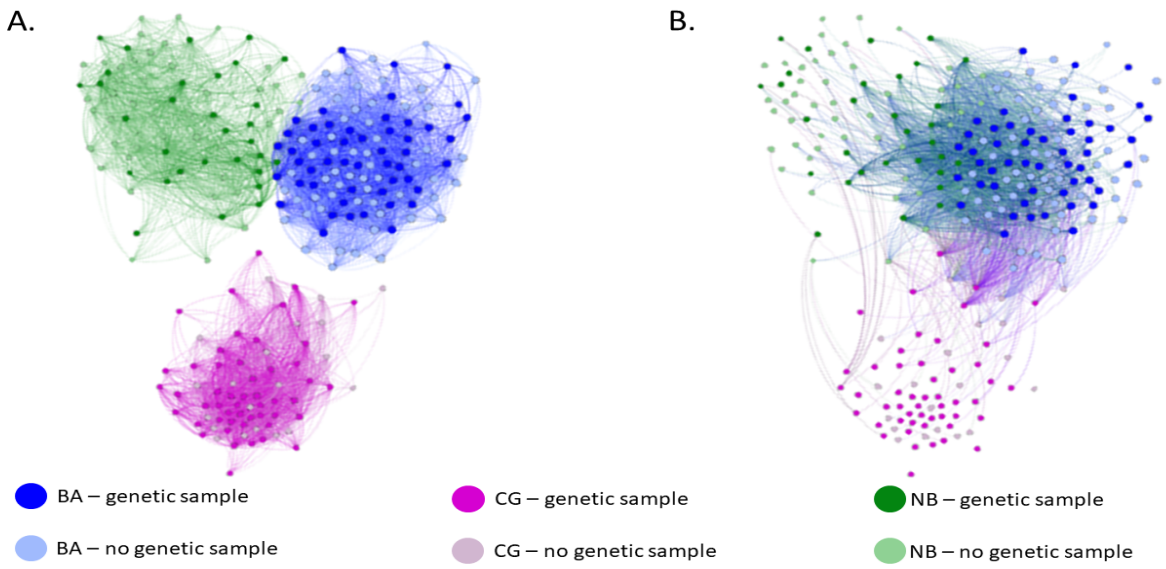

Figure 2: Association network of Sulphur-crested cockatoos across three roosting locations with A) representing associations between individuals of the same roost, and B) representing only associations between individuals of different roosts. Networks are thresholded to only include individuals with at least 22 observations. Nodes are coloured by roost (blue: BA, pink: CG, green: NB), and the shade of each colour illustrates whether a genetic sample has been collected (dark shades) or not (lighter shades). Edges between nodes represent association strength, and are thresholded to above 0.15 for visual clarity.

Relatedness and social networks

When the entire sub-population was considered, kinship significantly predicted social associations (Figure 2A & B, ES=0.097, p<0.001). As expected, roost co-membership and age similarity also predicted association strength (Figure 2, roost co-membership: ES=0.097, p<0.001, age: ES=0.006, p=0.012), but sex was not important (sex: ES=0.002, p=0.18). The results were similar when consid-

ering only within-roost edges (kinship: ES=0.11, p=0.005; sex: ES=0.006, p=0.24; age: ES=0.018, p<0.001), Figure 2A, Figure 3A). When sub-setting the dataset to edges between individuals of different roost locations (Figure 2B), the effect of kinship on association strength was still present (ES=0.086, p=0.001), with no effect of sex or age (sex: ES=-0.001, p=0.58; age: ES=0.0003, p=0.87). Finally, results were similar for all kin relationships and for close-kin dyads (Table S3).

Relatedness and aggressive interactions

Even after accounting for social opportunity, aggression occurred more frequently between individuals belonging to the same roost than with individuals visiting from different roosts (roost co-membership: ES=0.17, p<0.001). Kinship was also positively correlated with low intensity aggression (ES=0.41, p=0.020, Figure 3B), and there was a trend for age similarity to predict aggressions (ES=0.020, p=0.09), but no effect of sex (ES=0.01, p=0.23). When considering only within-roost edges, the results were similar (kinship: ES=0.78, p=0.03; age: ES=0.063, p=0.08; sex: ES=0.038, p=0.31), as were results when only considering close-kin dyads (Table S4). Between-roost aggressions, however, were not influenced by kinship, age or sex (kinship: ES=-0.025, P=0.41; age: ES=0.002, p=0.72; sex: ES=0.004, p=0.41), though there was a tendency to avoid directing low-intensity aggressions towards close-kin of different roost-membership (ES=-0.010, p=0.08, Table S4).

Similar to low intensity interactions, high intensity aggressive interactions occurred more frequently between individuals belonging to the same roost, rather than between residents and individuals visiting from different roosts (roost co-membership: ES=0.01, p<0.001). Kinship (ES=0.055, p=0.03) also predicted high intensity aggression (Figure 3C), but there was no clear effect of age or sex similarity (age: ES=0.003, P=0.17; sex: ES=0.003, P=0.09). Again, when considering only within-roost edges, high intensity aggressions were more frequent between related individuals (ES=0.011, P=0.01). Interestingly, when considering only between-roost edges, we again found a non-significant trend in the opposite direction, with individuals tending to avoid directing high intensity aggressions towards kin (ES=-0.02, p=0.10).

Relatedness and preening interactions

Observations of preening events were scarce, with 26 preening interactions involving 41 individuals (Table S1). Yet even so, individuals were observed engaging in preening events with multiple partners. These allopreening interactions were more likely to be observed between stronger social associates (ES=0.191, p<0.001, Figure 3), related individuals (ES=0.275; p=0.008), individuals of different roost-memberships (ES=-0.015, p=0.02), and tended to be more frequent between members of the opposite sex (ES=0.012, p=0.08).

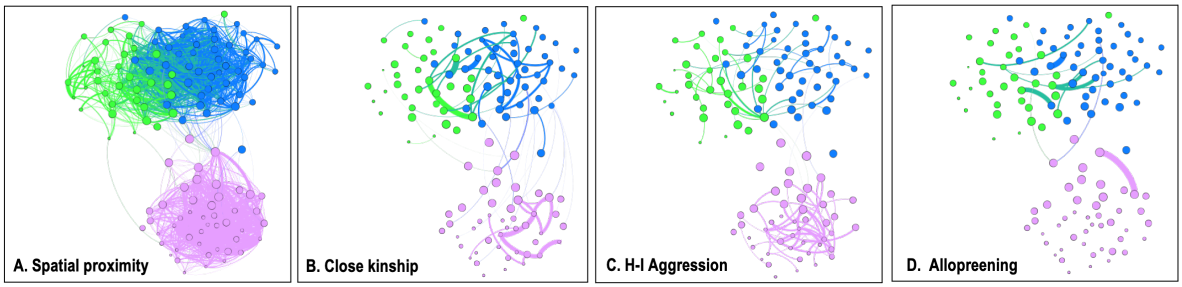

Figure 3: Social networks across three roosting communities. A) Spatial association network of cockatoos where edge width represents association strength. Edges are thresholded to above 0.15 for visual clarity. B) Association network subset to show edges between individuals with close kinship. C) Association network subset to show edges between individuals that engaged in high intensity aggressions. D) Association network subset to show edges between individuals that exchanged allopreening. In all networks, node size represents average association strength, nodes are coloured by roost (blue: BA, pink: CG, green: NB), and networks are thresholded to only include individuals with at least 22 observations.

Discussion

By combining relatedness data with extensive observations of social networks and interactions at multiple levels, our study gained an unprecedented insight into the social lives of a wild parrot species. First, we collected genetic material and built kinship networks for five neighbouring roosting communities in a 25km^2 urban and suburban area of Sydney. Our results showed a very weak genetic

differentiation between these roost sites, suggesting extensive gene flow. This was supported by our repeated observations of between-roost movements, especially for juvenile females. Second, we used multi-layered network analysis to show that despite a low-degree of kin structuring between roosts, and well-mixed social networks within roosts, individuals preferentially associated with close kin. Supporting this, individuals were also more likely to allopreen kin, an important affiliative behaviour in parrots (Morales Picard et al., 2020). However, against our expectations, aggressive interactions were also more likely to occur between kin within roost sites. Yet, intriguingly, this was either absent from between-roost interactions, or there was a non-significant trend for individuals to avoid directing aggressions towards kin.

A previous study in this system has shown that individuals maintain long-term preferred social associations (Aplin et al., 2021). Our work extends those findings to reveal one driver of these association choices, with kinship predicting social associations within roost sites, suggesting an active preference to associate with kin. Perhaps even more interestingly, we found that kinship was also correlated with association strength between individuals of different roost groups. This suggests that individuals continued to recognise and prefer kin even after dispersal. One benefit of such kin-based between-roost associations may be facilitated emigration into, or interactions with, groups containing closely related individuals (Van Hoof, 2000). For example, in cooperatively breeding brown jays (*Cyanocorax morio*), males tend to disperse into groups where male relatives are already established (Williams and Rabenold, 2005). In the case of the brown jay, the formation of alliances between related males may facilitate the entrance into the new social group. A similar behaviour was also described for invasive monk parakeets, where male siblings exhibited parallel dispersal, then often cooperated when building a new nest and breed (Dawson Pell et al., 2021). Cooperative breeding or the formation of coalitions has not been observed in SC-cockatoos, yet the observed preening interactions both between kin and individuals of different roosts is an intriguing indicator of the potential importance of maintaining relationships across groups.

In birds, preening is often described as having an essential role in maintaining pair bonds, such as mate bonding and partner retention across breeding seasons (Gill, 2012), or parental cooperation (Kenny et al., 2017). While our study does indeed identify allopreening between members of different sexes, it was not restricted to putative mates. Rather, individuals were observed engaging in preening

events with multiple partners, and these interactions were predicted both by kinship and by social associations. Allopreening is generally understudied in wild parrots (but see McCulloch, 1981; Diamond and Bond, 1999; Taylor, 2002). In captivity, allopreening patterns of nine parrot species were predicted by the time a dyad spent in close proximity (Morales Picard et al., 2020). Furthermore, a preference to preen related, rather than unrelated individuals, has been described in juvenile birds (e.g. corvids: Fraser and Bugnyar, 2010; e.g. captive parrots: Garnetzke-Stollmann and Franck, 1991), where it is hypothesised to help build bonds with important social partners. The number of preening events in our dataset was low, and conclusions need to be drawn with care. Yet our results suggest that SC-cockatoos may gain some direct or indirect benefits from building and maintaining strong social bonds with kin, even after dispersal. Future work should seek to quantify what benefit these between-roost kin relationships give to individuals.

Somewhat surprisingly, we found that SC-cockatoos preferred to aggress individuals within rather than outside their roost. A preference to aggress familiars could potentially reflect strategies for improving dominance (Hobson et al., 2014; Hobson et al., 2021), especially since 93% of all observed aggressive interactions involved only displacements that bear no direct risks of injuries for the individuals involved. If so, we would not necessarily expect interactions with kin to be avoided – especially given that all juveniles in our dataset were already independent of adults (2 to 7 years of age). Yet even after social associations were controlled for, individuals still preferred to aggress kin that shared roost co-membership. One potential explanation for this might come from the aggressive eviction hypothesis (Marsh, 1988, Wahlström, 1994), which states that increased aggression can act to drive emigration. For example, in western bluebirds (*Sialia mexicana*), dispersal, and dispersal distance, is influenced by aggressions from kin (Aguillon and Duckworth, 2015). Although this hypothesis was formulated for natal emigration, it seems reasonable to expect increased intra-group aggression to also drive secondary dispersals, and even short-term movements between social groups. This would be consistent with our observation that this preference to aggress kin is either lost, or perhaps reversed, when individuals interact with those of different roost-membership.

Overall, the multi-level social system of SC-cockatoos allowed us to disentangle association preferences from spatial overlap, with well-mixed social networks within clearly-defined roosting groups coupled with regular associations with individuals of different roosts. Our finding that individuals

prefer to associate and allopreen with kin both within and between roosting groups therefore suggests that: 1) individuals are able to recognise kin, including siblings, and actively prefer them, and 2) that this recognition is retained over a considerable time, including after dispersal. In passerine birds, cross-fostering experiments have demonstrated that kin recognition is often learned in the nest (Sharp et al., 2005). Yet the typical clutch size for SC-cockatoos is one or two chicks per year, and juveniles appear to be largely independent at 1 year of age, suggesting that kin recognition must also occur across broods. In zebra finches between-brood recognition is achieved through olfactory cues (E. T. Krause et al., 2012). However, given the evidence for extensive vocal learning in parrots (Wright and Dahlin, 2018), and the existence of parent-facilitated vocal signatures in parrotlets (*Forpus passerinus*, Berg et al., 2012; Berg et al., 2013), it seems likely that kin recognition in SC-cockatoos involves vocal learning. Finally, our work shows that interactions with related individuals are context-dependent, suggesting the existence of differentiated relationships. The full extent of social complexity in this species is only beginning to be revealed, and remains to be further investigated in the future.

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Conflict of Interest

The authors declare that no competing interests exist.

Authorship contributions

J.P., L.M.A., J.M.M. conceived the ideas and designed the study; J.P., L.M.A., B.C.K. and J.M.M. collected social and morphometric data and collected feather samples. K.M.E collated and analysed genetic data, and J.P. and L.M.A. performed analysis on sociality and kinship. All authors contributed to writing the manuscript and gave final approval for publication.

Data Availability Statement

Upon acceptance, the data supporting this manuscript will be made available at Edmond, the open access repository of the Max Planck Society, and the DOI provided in the manuscript.

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Supplementary Materials

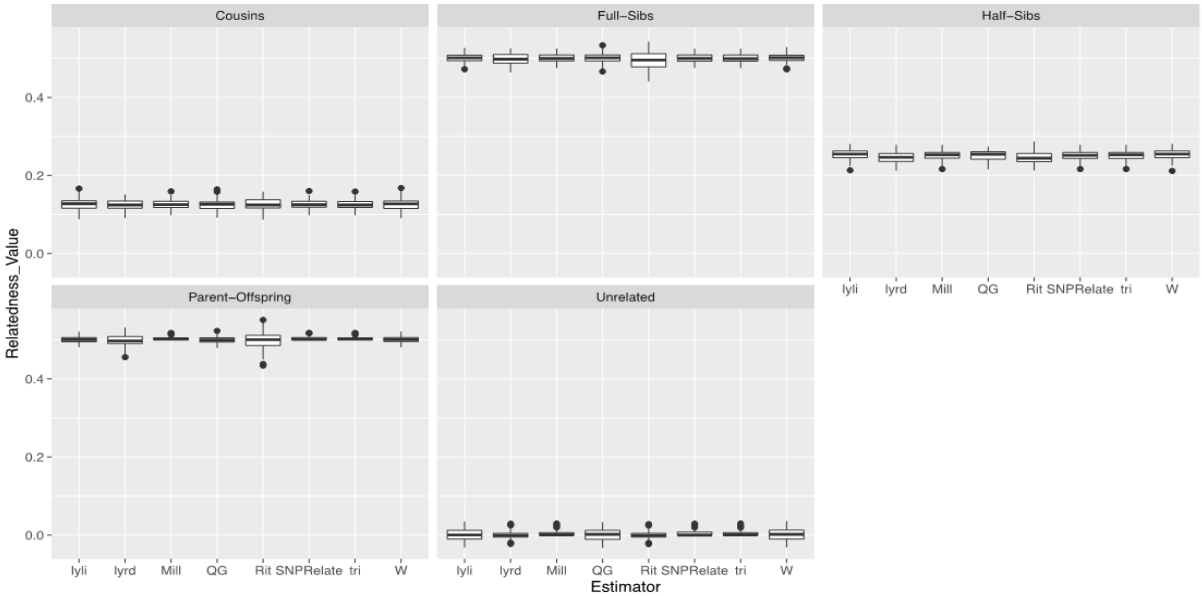

Figure S1: Distribution of relatedness values for eight relatedness estimators based on simulated data of five relationship types. lyli = Li et al. estimator; lyrd = Lynch and Ritland estimator; Mill = dyadic likelihood estimator; QG = Queller and Goodnight estimator; Rit = Ritland estimator; SNPRelate = SNPRelate maximum likelihood kinship coefficient; tri = Triodic likelihood estimator; W = Wang estimator.

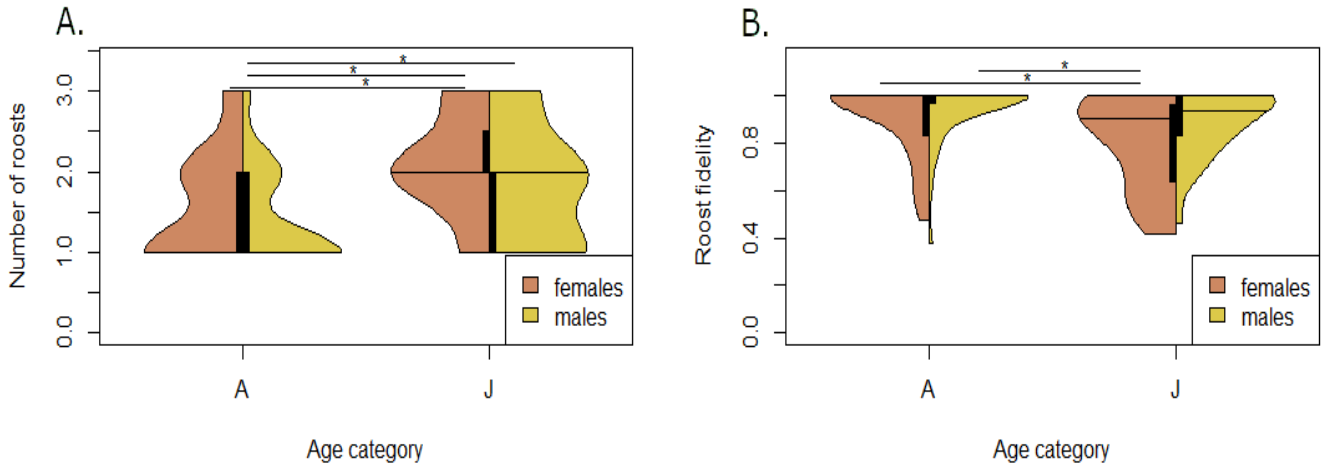

Figure S2: Between roost movements of SC- cockatoos according to their age-sex category. A: adults, J: juveniles. A) Number of roosts used by individuals of each age sex group (maximum 3 roosts). B) roost preference for each age-sex group. Preference is defined as the proportion of observations for a focal individual at its assigned roost by roost count, over to the total number of observations of this individual.

Table S1: Summary of the social data The number of observations (namely number of scans for the associations, number of interactions for preening and aggression) and number of individuals (with sex and age: J=juvenile, A=adults, U=unknown age) involved for each behaviour analysed in this study. Only individuals with at least 22 sightings are included.

Level of Analysis	Behaviour	n females (J/A/U)	n males (J/A/U)	n obs
Population	Association	73 (20/35/2)	72 (25/37/10)	864
Population	Preening	16 (6/7/3)	25 (7/10/8)	26
Roost	Aggression (low intensity)	56 (18/28/10)	74 (21/38/15)	1,457
Roost	Aggression (high intensity)	56 (18/28/10)	74 (21/38/15)	91

Table S2: Allele error rate calculated as the total number of alleles that mismatch between the replicate pair divided by the total number loci that were not missing in both samples. NB: some replicates have the same names, while others have different names, and triplicates include three pairwise comparisons. The high error rate in two of the S111 pairwise comparisons suggests a mislabelling issue for one sample, or a failed assay.

Replicate name	Allele error rate for full dataset (58,740 SNP)	Allele error rate for filtered dataset (12,447 SNPs)
S111 triplicate 1	0.200	0.282
S111 triplicate 2	0.023	0.010
S111 triplicate 3	0.200	0.289
S42/S160 replicate	0.018	0.011
S149 replicate	0.012	0.007
$\text{tag}_0 25a/S281 replicate$	0.012	0.003
$\text{tag}_1 07 replicate$	0.009	0.002
$\text{tag}_1 07/S254 replicate 1$	0.032	0.032
$\text{tag}_1 07/S254 replicate 2$	0.033	0.031
S379 replicate	0.017	0.008
$\text{tag}_0 35/S345 replicate$	0.011	0.002
S295 replicate	0.023	0.010
S302/S344 replicate	0.017	0.003

Table S3: Within and between roost associations predicted by close-kinship, sex and age.

type	coefficients	estimate	pvalue
overall	intercept	0.028	<0.001
	kin (binary)	0.052	<0.001
	sex	0.003	0.10
	age	0.006	0.01
	roost	0.097	0.01
between roosts	intercept	0.031	<0.001
	kin (binary)	0.022	0.04
	sex	/	/
	age	/	/
within roots	intercept	0.118	0.001
	kin (binary)	0.037	0.04
	sex	/	/
	age	/	/

Table S4: Low-intensity aggressions at roost level, predicted by close-kinship, roost-membership, age and sex.

type	coefficients	estimate	pvalue
overall	intercept	-0.008	0.42
	kin (binary)	0.095	0.09
	sex	0.016	0.15
	age	0.020	0.091
	roost	0.16	0.001
within roost	intercept	0.13	<0.001
	kin (binary)	0.10	0.08
	sex	/	/
	age	/	/

Table S5: High-intensity aggressions at roost level, predicted by close-kinship measures, roost-membership, age and sex.

type	coefficients	estimate	pvalue
overall	intercept	-0.0002	0.97
	kin (binary)	0.040	0.04
	sex	0.004	0.06
	age	0.003	0.17
	roost	0.011	0.001
between-roost	intercept	0.003	0.001
	kin (binary)	-0.003	0.063
	sex	/	/
	age	/	/
within-roost	intercept	/	/
	kin (binary)	/	/
	sex	/	/
	age	/	/

Table S6: Preening interactions predicted by close-kinship, associations, roost-membership, age and sex.

coefficients	estimate	pvalue
intercept	0.001	0.87
kin (binary)	0.10	0.05
association	0.19	<0.001
roost	-0.016	0.017
sex	/	/
age	/	/