ANIMAL SOCIAL NETWORKS

Research Article

A citizen science approach reveals long-term social network structure in an urban parrot, *Cacatua galerita*

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Abstract

1. Parrots are often referenced in discussions of social and cognitive complexity, yet relatively little is known of their social organization in the wild. In particular, the presence of long-lasting social ties has been highlighted as a hallmark of social complexity; however, the presence of such ties can be masked in fission–fusion systems like that exhibited by most parrot species. Social network analysis has the potential to elucidate such multi-level dynamics.

2. While most parrot species are tropical canopy dwellers, a subset has successfully colonized urban habitats, where they are often the focus of much public interest. Our study takes advantage of this to use citizen science to collect observations of wing-tagged sulphur-crested cockatoos in central Sydney and record their social associations over multiple years.

3. Using a specifically designed mobile phone application '*Wingtags*', we collected over >27,000 citizen science reports of wing-tagged cockatoos, and built social networks from spatial-temporal co-occurrences in observations for 130 tagged birds. To validate this novel methodology, we GPS-tagged a subset of wing-tagged birds and compared networks built from both data collection methods. We then examined correlates of social network structure before exploring the temporal dynamics of network structure and social associations.

4. Social networks constructed from GPS data and citizen science data were highly correlated, suggesting that this novel methodology is robust. Network structure exhibited little seasonal variability and was largely driven by roost site choice; however, individuals also showed a surprising degree of mixing between roosts in their foraging associations. Finally, within this larger fission–fusion system, individuals tended to maintain specific social ties for long periods of time. There

was an effect of age on these temporal dynamics, with aging individuals increasing both social stability and longevity of associations.

5. Our findings highlight the utility of citizen science to measure social networks in urban species, and add to the evidence that long-lasting social associations can persist in fission–fusion social systems such as those observed in wild sulphur-crested cockatoos.

1 | INTRODUCTION

The social structure of animal populations can fundamentally impact individual fitness, influencing survival and reproduction through such diverse means as access to resources and information (Aplin & Morand-Ferron, 2017; Giraldeau & Beauchamp, 1999) (Aplin, Farine, Morand-Ferron, & Sheldon, 2012), and risk of disease (Christley et al., 2005). While they are often more difficult to study, social relationships in long-lived animals may both be long-lasting and have a heightened importance (Silk et al., 2009). Recent advances in dynamic social networks have provided techniques to examine social behaviour of individuals over time and across contexts (Farine, 2018; Pinter-Wollman et al., 2014), giving an opportunity to explore social relationships in long-lived animals, and to quantify the effects of such dynamics on social structure.

To date, long-lasting social relationships have been mostly identified and studied in species that live in stable kin groups. For example, in baboons, a series of studies have demonstrated that females form long-term stable bonds, usually with kin (Silk, Alberts, Altmann, Cheney, & Seyfarth, 2012). These bonds enhance females' ability to cope with stress (Wittig et al., 2008), reproductive success, and the survival of offspring (Silk, Alberts, & Altmann, 2003; Silk et al., 2009). Yet, recent evidence has also begun to show that in some species, long-term relationships are not limited to kin, or even to stable groups (Frere et al., 2010; Kerth, Perony, & Schweitzer, 2011; Loretto et al., 2017). When such relationships are maintained despite larger fission–fusion dynamics, it has been further proposed that these emergent multi-level social dynamics might be an indicator of social and cognitive complexity (Bugnyar, 2013; Kerth et al., 2011).

Parrots (Psittacidae) are famously long-lived (Wirthlin et al., 2018), and have been repeatedly highlighted in discussions of the evolution of cognition and social complexity (Emery, 2006; Gutiérrez-Ibáñez, Iwaniuk, & Wylie, 2018; Hobson, 2014; Olkowicz et al., 2016; Pepperberg, 2002). Yet there is surprisingly scarce evidence for these claims of social complexity. The logistical constraints of tagging and following parrots, most of which are tropical canopy dwellers, have meant that there is little research on the patterning of social interactions in wild populations. Studies of sociality in wild parrots have instead largely relied on two indirect lines of evidence; population genetics and bio-acoustics (Wright & Dahlin, 2017).

This body of work has demonstrated that many parrots exhibit fission–fusion dynamics within relatively stable communal roost sites (Berg & Angel, 2006; Lindenmayer, Pope, Cunningham, Donnelly, & Nix, 1996; Salinas-Melgoza & Wright, 2012) that can be distinguished by vocal dialects (Wright & Dahlin, 2017), even with some low level of movement (Wright, Dahlin, & Salinas-Melgoza, 2008).

While the study of many parrot species presents a non-trivial challenge, a subset of species are successful persisters in, or colonizers of, urban environments (Hobson, 2014; Sol, Lapiedra, & González-Lagos, 2013). In such environments, free from direct persecution and provisioned by people, populations can become relatively habituated. In this study, we capitalize upon this by using citizen science to study social networks in a population of sulphur-crested cockatoos *Cacatua galerita* in the city centre of Sydney, Australia. We collated >27,000 reports over 6 years by users of the '*Wingtags*' mobile phone app. and use these to identify spatio-temporal co-occurrences by tagged birds. The use of citizen science to study social behaviour is largely untested, and we therefore first explore the veracity of this data collection method by (a) quantifying the error rate in reports and (b) comparing patterns of social associations in a subset of birds that were both GPS-tagged and wing-tagged. Second, we describe social networks and assess potential drivers of network structure. Finally, we explore temporal dynamics by (a) examining how association rates change or persist over time and (b) exploring the effect of age on social stability.

2 | MATERIALS AND METHODS

2.1 | Study system

The study was conducted on urban sulphur-crested cockatoos, a widespread species of large (800 g to 1 kg), granivorous parrot. Sulphur-crested cockatoos are both long-lived and slow breeding, with birds not reaching sexual maturity until >7 years old and potentially living for multiple decades (Young, Hobson, Lackey, & Wright, 2012). Little is known about the life history or social system of this species, but breeding pairs are thought to defend nest hollows, potentially year-round. These breeding pairs do not appear to be territorial, and multiple pairs can occasionally be seen breeding

in a single tree and/or clustered in a stand of hollow-bearing trees. Suitable hollows are a highly limiting resource, and most of the population consists of non-breeders who sleep at communal roost sites that can be maintained over many years (Lindenmayer et al., 1996). Birds leave these communal roosts in smaller foraging flocks, membership of which is thought to follow fission–fusion dynamics.

Sulphur-crested cockatoos are native to the Sydney region; however, numbers have increased steadily in the urban area over the last three decades (Davis, Taylor, & Major, 2011). In particular, birds appear to benefit from exotic trees planted in streets and gardens (e.g. fruit trees). Sulphur-crested cockatoos in the central urban area become readily habituated to humans, and are also often the target for bird feeding activities. The core study site was the Royal Botanic Gardens in central Sydney; a 64-ha area of mixed lawns, exotic and native vegetation that includes significant stands of hollow-bearing native trees used by cockatoos for breeding (33.8642°S, 151.2166°E) as well as a non-breeding roost. This core area supports a variable local population of 100–300 individuals (Davis, Major, Taylor, & Martin, 2017), and birds tagged in the botanic gardens were subsequently re-sighted within the gardens, in the nearby central Sydney business district, and in the surrounding suburbs. The large majority of tagged birds remained within a 10-km radius of this site (Davis et al., 2017).

2.2 | Tagging and field observations

Over a 2-year period from September 2011 to 2013, 96 sulphur-crested cockatoos were captured at the Royal Botanic Gardens Sydney and fitted with unique metal leg rings from the Australian Bird and Bat Banding Scheme and wing-tags numbering from 1 to 96; see Davis et al. (2017) for details on capture and tagging procedures: Figure 1a,b. Four birds were additionally caught in early 2014 (97–99, 101), and 35 (102–136) between September and December 2016. Once caught, birds were sexed using blood samples, and aged as juveniles (<7 years) or adults (>7 years) by eye colour. Re-sighting probability of tagged individuals was very high; a recent study estimated that from 2013 to 2016, wing-tag retention rate (at least one tag) was 95%, and the mortality rate was <2% per year (Davis et al., 2017).

In September–December 2016, nine wing-tagged birds were re-caught and fitted with high-resolution solar-powered 10 g GPS tags (e-Obs Digital Telemetry): Figure 1c. Five GPS tags were deployed at catching locations close to the Royal Botanic Gardens and four in Clifton Gardens Reserve, a nature reserve at approximately 4-km distance where wing-tagged birds were also observed breeding and roosting. Tags weighed <1.5% of body weight and were attached using a standard backpack harness design. The GPS recorded up to 1 s locational fixes with high battery power and 12-min locational fixes under low power, recording between 05:00 and 19:00 daily. One bird removed its tag after 4 days; however, all other tags were retained, giving data on eight birds over a 12-month period: Figure 1d and Figure S1.

Most observations of wing-tagged birds were collected through a citizen science approach. A smart-device application 'Wingtags' was launched in 2012, where members of the public could report birds as they observed them (e.g. see iOS Appstore:
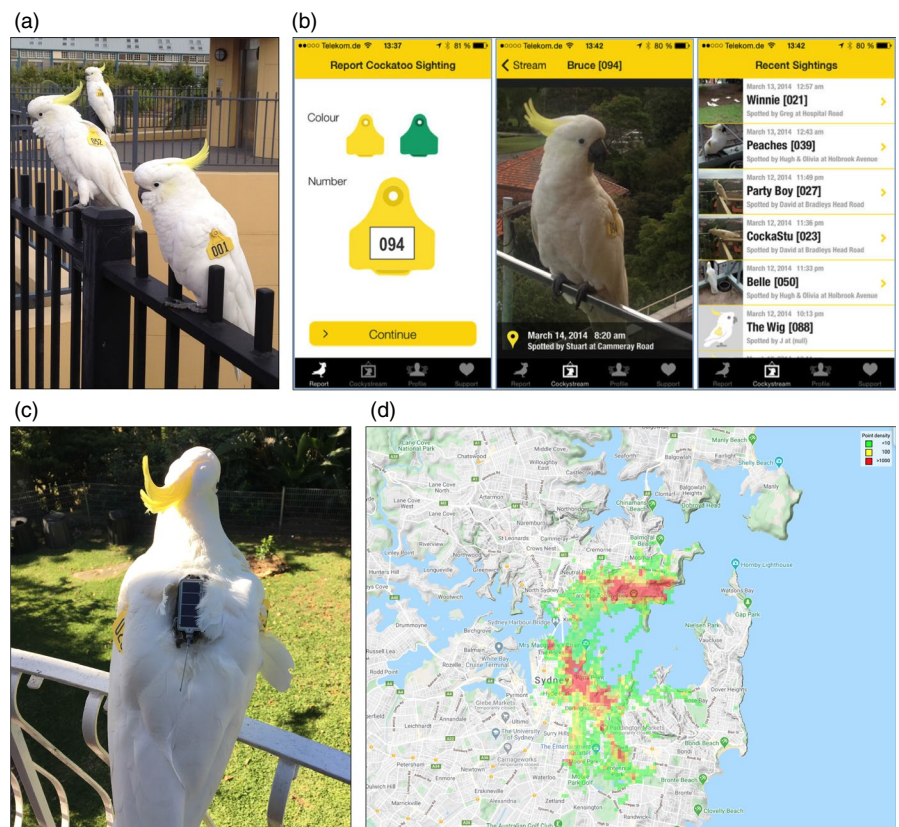

FIGURE 1 (a) Example of a flock of sulphur-crested cockatoos showing numbered wing-tags. Photographed on an apartment building adjacent to the Royal Botanic Gardens, Sydney. (b) Wingtags app, with screenshots of progressive screens that encourage citizen scientists to enter the wing-tag number and photograph of an observed bird. Reports are rewarded with information on the bird and other recent sightings. (c) Photograph showing 10-g GPS transmitter on sulphur-crested cockatoo 028. (d) Map showing point density of GPS locational fixes for eight GPS-tagged birds

Wingtags). The *Wingtags* app. allows people to upload a photograph of the tagged birds(s) they are observing along with the wing-tag number, and the app simultaneously collects a GPS location and time stamp: Figure 1b. Participants are rewarded with information on the observed bird and on other recent sightings of birds. Citizen science reporting of wing-tagged sulphur-crested cockatoos continues to be very popular, with >27,000 reports and >900 participants to date.

In order to determine the error rate in this citizen science reporting, a subset of 8,340 photographs of cockatoos was collected from the *Wingtags* app reports (2012–2016). Photographs were scored by volunteers as part of the Australian Museum '*DIGIVOL*' scheme (https://australianmuseum.net.au/digivol), where online volunteers were asked to record the wing-tag numbers present in each photograph along with other relevant information. The results were then compared with the wing-tag number in the matching *Wingtags* app report.

2.3 | Measuring social associations

Social associations between individuals were calculated from these citizen science reports whereby membership of the same group for two individuals was assigned if they were reported within 30 min and 100 m of each other. In practice, citizen-scientists often reported multiple birds in a flock, so reports were often clustered in time and location (e.g. Figure 1a). We then used group membership data to create social networks, whereby a gambit of the group approach was used to calculate association strengths using the simple ratio index (Farine & Whitehead, 2015). Here, social associations were scaled between 0 (never observed in the same group) and 1 (always observed in the same group): Cairns and Schwager (1987). A social network was created for each year from 2013 to 2018, with 1 year representing 12 months between the start of spring and the end of the following winter. This led to 5 1-year-long social networks: 1 September to 31 August 2013–2014 ($n = 85$), 2014–2015 ($n = 93$), 2015–2016 ($n = 93$), 2016–2017 ($n = 86$) and 2017–2018 ($n = 106$). To test whether the resulting networks were non-random (unlikely to have arisen by chance), we performed permutations on the data stream for each dataset, controlling for number of observations and group size, and restricting swaps to within months. The observed patterns of associations were considered to be non-random if they fell outside the 95% distribution range of the permuted networks (Farine & Whitehead, 2015). All analyses were conducted in R (R Core Team, 2012), in the ASNIPE package (Farine, 2013).

A citizen science data collection method might have inherent biases. To test for this possibility, we used the subset of GPS-tagged birds to compare the social network built from citizen science reports from September 2016 to September 2017 to one built from GPS-tag fixes for the same time period. In the case of the GPS dataset, the data were subsetted to only include one locational fix per 12 min for each individual. Social associations in both

cases were calculated using exactly the same method, where birds were considered in the same social group if detected within 30 min and within 100 m. To test for the degree of similarity between the two association matrices we then performed a Mantel test in the R package VEGAN.

2.4 | Correlates of network structure

In order to understand the potential drivers of the observed social structure, we tested the relationship between three individual-level variables (sex, age and roost-site choice) and three network measures: unweighted degree centrality, weighted degree centrality (strength) and network assortativity (Croft, James, & Krause, 2008). These respectively measure (a) the number of individuals that the focal individual has been observed associating with, (b) the sum of an individual's edge weights, representing the 'strength' of their associations and (c) the mixing patterns exhibited by individuals. As age changes over time, this analysis was conducted on networks in two discrete time periods where we had most confidence in our assignment of age class—the first and last years of data collection. For the first year of social network data collection, all age was taken as that assessed at tagging. However, as sulphur-crested cockatoos are not sexually mature until 7 years old, individuals tagged as juveniles in 2012 could feasibly be juveniles or adults in 2017–2018. For the last year of social network data collection, birds tagged as juveniles in 2012 were therefore listed as unknown age unless they had been observed breeding or been re-caught and aged as adults in the interim.

Sulphur-crested cockatoos sleep in communal roosts (Lindenmayer et al., 1996), here usually located in a small number of city parks (e.g. at Rushcutters Bay Park: 33.8753°S, 151.2315°E). These roosts often overlap with semi-colonial breeding sites, also clustered in parklands (e.g. at the Botanic Gardens: 33.8642°S, 151.2166°E). While such roost sites can be maintained over long periods of time (Lindenmayer et al., 1996), the choice of the roost sites by individuals could potentially change over time. To test for this, we first identified each individual's roost site choice by assigning it to the nearest known roost site to the majority of its citizen science reports. This was undertaken for all individuals in 3-month periods over the total 5 years of observation. For all GPS-tagged birds, this assignment was confirmed in those time periods; for other birds the assignment was also occasionally confirmed by opportunistic observations. Roost site choice was highly consistent five short time periods, with individuals using an average of only 2.5 roost sites (range: 1–5) over 5 years of observation. For the analysis of network structure, we therefore assigned each individual to a single roost site location for each time period using the above method.

Linear models were used to compare weighted or unweighted degree centrality to either age or sex in each time period (2013–2014, 2017–2018), with roost site choice added as a fixed effect. Both degree centrality measures were log-transformed in the model to normalize their distributions. Network assortativity was

calculated in the ASSORTNET package (Farine, 2014) using weighted edges. A separate analysis was run for each individual-level variable (sex, age, roost site) in each time period, and standard errors were calculated by using the default jack-knife function in the ASSORTNET package.

2.5 | Change over time

We assessed whether there were seasonal differences in network structure by comparing each summer (September–February) or winter (March–August) to the following summer or winter. Because the numbers of individuals contained in networks can influence centrality measures, we subsetted each pair of matrices such that they contained the same set of individuals (mean $n = 67$ [60–86]; Farine & Whitehead, 2015). Three network measures were then calculated for each network; weighted and unweighted degree centrality (see above), and transitivity. Transitivity is a measure of how closed trios tend to be, and captures the level of clustering in the network (Farine & Whitehead, 2015). Seasonal effects on these measures were examined in linear mixed models with weighted degree, unweighted degree or clustering coefficient as the response variable, and season, sampling effort (number of records), year and identity of the match pair as fixed effects, and with individual identity as a random effect. As above, the response variable was log transformed to normalize the distribution.

Second, we examined the social stability of individuals across years using a method adapted from Hobson, Avery, and Wright (2013) and Stanley, Mettke-Hofmann, Hager, and Shultz (2018), that gives an idea of the change in each individual's association strengths over consecutive networks. As above, matched pairs of matrices in consecutive years were subsetted to the same set of individuals (mean $n = 74$ [65–82]). Each matrix was then subtracted from the previous one, and the absolute change in the edge weights for each individual were summed. Therefore, an individual would get a value of 0 if there was no observed change in its social connections to its associates, and a higher value if its associates changed and/or the strength of its connections to those associates changed. This was computed for each year of observation for each individual (maximum 5 years) and compared in a linear mixed model where the response variable was the social stability index, the explanatory variable was the year of observation, and individual ID was included as a random effect. The effect of age on this pattern was additionally examined by including an interaction between year of observation and age at tagging (juvenile/adult).

Finally, the stability of specific social associations over time was measured using lagged association rates, here defined as the probability of two individuals being observed re-associating in successive 3-month periods from 3 to 63 months after a previous association (Whitehead, 2008). To test whether this re-association rate was significantly more than expected under random-mixing, 10,000 permutations of the data stream were conducted, and the 95% distribution range compared to the observed values. Lagged association rates and permutations were conducted in the ASNIPE package (Farine, 2013).

3 | RESULTS

Over a 5-year period from September 2013 to September 2018, 19,082 citizen science reports were made of 130 wing-tagged sulphur-crested cockatoos, with an average of 147 records per bird, and an average of 40 reports per bird per year (25–60). Birds were reported over an area of approximately 150 km^2, with the majority of individuals roosting at four locations—the Royal Botanic Gardens, Sydney (33.8642°S, 151.2166°E), Rushcutters Bay Park (33.8753°S, 151.2315°E), Centennial Parklands (33.9011°S, 151.2304°E) and Chowder Head Bushland (33.8422°S, 151.2534°E). While individuals were relatively site faithful, movement between roost sites did occur, with individuals using an average of 2.5 (1–5) habitual roost sites over the 5 years.

All eight birds that were GPS-tagged between September 2016 and September 2017 recorded locational fixes throughout that period. However, as data logging depended on solar battery power, not all birds recorded a GPS fix in every 15-min time step, resulting in an average of 5,448 (3,374–8,057) locational fixes per individual. The GPS data indicated that the birds were using three major roost sites during the 12-month period of active data collection—Royal Botanic Gardens, Sydney, Rushcutters Bay Park and Chowder Head Bushland. Only one bird was observed using more than one roost site, 'AC' wing-tag 006, using both the Royal Botanic Gardens and Chowder Head Bushland (on <5 occasions); Figure S1.

3.1 | Validating the citizen science approach

Our re-assessment of tag numbers in a sample of photos that accompanied citizen reports resulted in an estimate that 1.9% of reports were unreliable. This was likely to be a conservative estimate, as it does not account for any additional error introduced through the *DIGIVOL* validation process. It therefore suggests that the vast majority of citizen-scientists were accurately recording the identity of the birds they reported. We then assessed possible inherent biases in citizen science reporting by comparing networks built from either GPS data or citizen science data for a subset of eight birds that were both wing-tagged and GPS-tagged. While the citizen science network was sparser than the GPS network, the matrices were very highly correlated: Mantel test $R = 0.95$, $p < 0.001$ (significance based on 10,000 permutations): Figure 2.

3.2 | What explains network structure?

Permutation tests confirmed that all yearly and seasonal networks demonstrated significantly non-random structure ($p < 0.001$ for all networks). While no substantial difference between the seasons in social structure was observed, for example, birds exhibited communal roosting behaviour and social foraging in all seasons, winter networks exhibited a significantly higher weighted degree than summer networks (LMM: $t_{1642} = 6.3$, $p < 0.001$), and a higher clustering coefficient (LMM: $t_{1642} = 2.8$, $p < 0.005$). There was no difference between the seasons
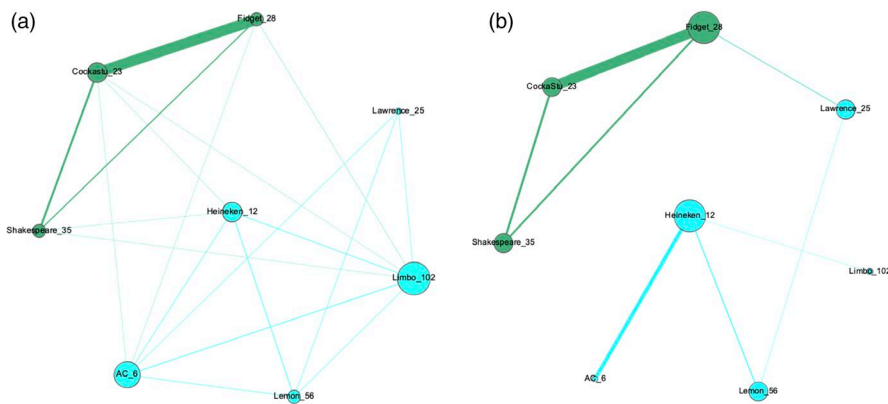
FIGURE 2 Social networks for the same set of eight birds built from GPS data (a) and citizen science data (b) over a 12-month period. Node size indicates increasing association strength (also shown in edge weights), while colour represents community membership as assigned by the *spinglass* community detection algorithm in the R package IGRAPH
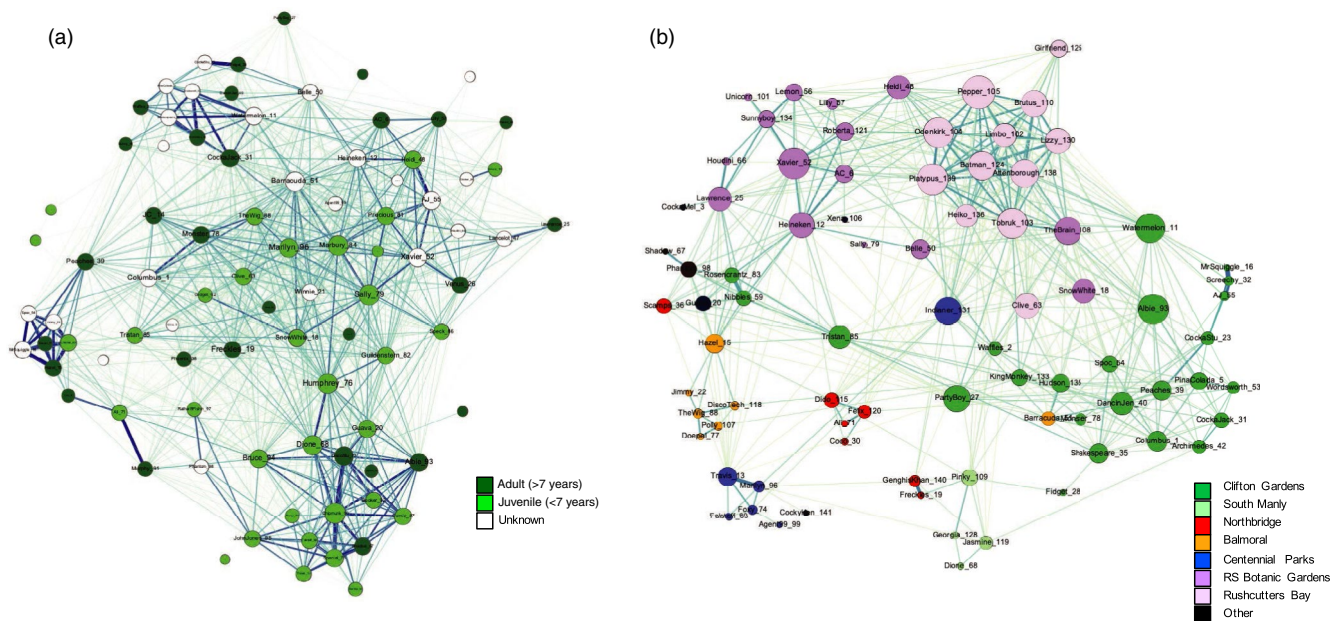

FIGURE 3 (a) Social network of sulphur-crested cockatoos for a 12-month period from September 2013 to September 2014, where increasing node size indicates increasing association strength (also shown in edge weights), while colour represents age class. In addition to roost site assortment (not shown), there is significant assortment by age, and juveniles tend to have a higher weighted degree centrality. (b) Social network of sulphur-crested cockatoos for a 12-month period from September 2017 to 2018; increasing node size indicates increasing association strength (also shown in edge weights), while colour represents roost-site membership for each individual. Individuals are significantly assorted by roost-site choice, and by age (not shown)

in unweighted degree (LMM: $t_{1642} = 0.11$, $p = 0.92$). This suggests that individuals were maintaining similar numbers of social associations throughout the year, but were spending proportionally more of their time engaged in social behaviour in the winter (non-breeding) season, tending to forage in more tightly knit groups with a higher density of ties.

In both the years that we examined network structure, individuals were positively assorted by roost site, suggesting a strong spatial component to the patterning of social associations: 2013—$r_{85} = 0.40$, $SE = 0.02$; 2017—$r_{85} = 0.74$, $SE = 0.02$ (Figure 3a). There was no effect of sex in either year on unweighted centrality (2013—LM: $t_{49} = -1.05$, $p = 0.30$; 2017—LM: $t_{57} = 1.52$, $p = 0.13$) or weighted centrality (2013—LM: $t_{49} = -1.40$, $p = 0.17$; 2017—LM: $t_{57} = 1.23$, $p = 0.22$), and no evidence for assortment by sex in either year (2013—$r_{56} = -0.02$, $SE = 0.04$; 2017—$r_{63} = -0.0005$, $SE = 0.05$). There was a significant effect of age, with both networks showing positive assortment by age class, although

this effect was weaker than roost-site choice: 2013—$r_{64} = 0.15$, $SE = 0.04$; 2017—$r_{73} = 0.17$, $SE = 0.05$ (Figure 3b). Finally, while there was no effect of age class on the number of connections (2013—LM: $t_{58} = 1.53$, $p = 0.13$; 2017—LM: $t_{66} = 2.11$, $p = 0.04$), juveniles tended to have stronger social associations than adults in both years (2013—LM: $t_{58} = 1.53$, $p = 0.13$; 2017—LM: $t_{66} = 2.15$, $p = 0.035$). We did not make a specific effort to identify breeding pairs and so pair bonds in the network were not analysed formally; however, known breeding pairs appeared to have a relatively high, but not atypical association strength (Figure S2).

3.3 | How stable are association preferences?

Individuals increased their social stability over successive years of observation, measured by a reduction in the absolute change in their

edge weights—LMM: $t_{254} = -3.05$, $p = 0.003$. There was an interaction between the slope of this change and age class, with birds tagged as juveniles showing a higher intercept and slower reduction in social instability—LMM: $t_{254} = -2.81$, $p = 0.005$. For adults, the line of best-fit suggested a plateauing of this effect by the third
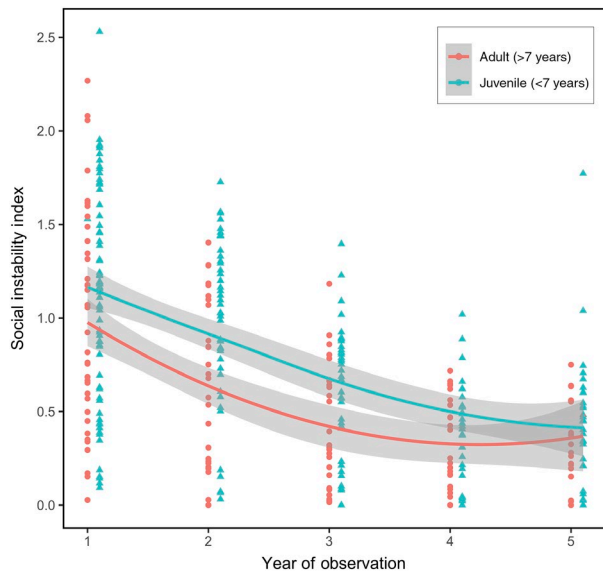
year of observation, with stable associations maintained thereafter (Figure 4).

Individuals had a high probability of re-associating after an initial association event (LAR = 0.49), and remained above the 95% range of permutations for the first 15 months (LAR = 0.33); association rates could not be distinguished from that expected under random mixing from 18 to 63 months (Figure 5a). The probability of re-association between juveniles was initially higher than for adults ($R_J = 0.52$, $R_A = 0.44$), but adults had a slightly longer stability in their associations (adults above 95% range of permutations for 15 months, juveniles above 95% range of permutations for 12 months): Figure 5b.

4 | DISCUSSION

Our study uses a combination of biologging from GPS-tags and observations from citizen-scientists to capture a unique insight into the social lives of a wild population of urban sulphur-crested cockatoos. First, we collated a multi-year dataset on social associations in 130 wing-tagged birds in central Sydney, Australia, using citizen science reports gathered via a mobile phone app (Davis et al., 2017). We validated this approach by comparing it to social proximity measured directly from GPS tags; networks generated from either method were highly correlated, suggesting that the citizen science dataset was capturing true association patterns. Second, we investigated correlates of social structure. Overall, and as expected, the main predictor of social assortment was a roost-site choice; however, networks were still connected, with individuals both moving between roost sites and associating with individuals from different roosts.
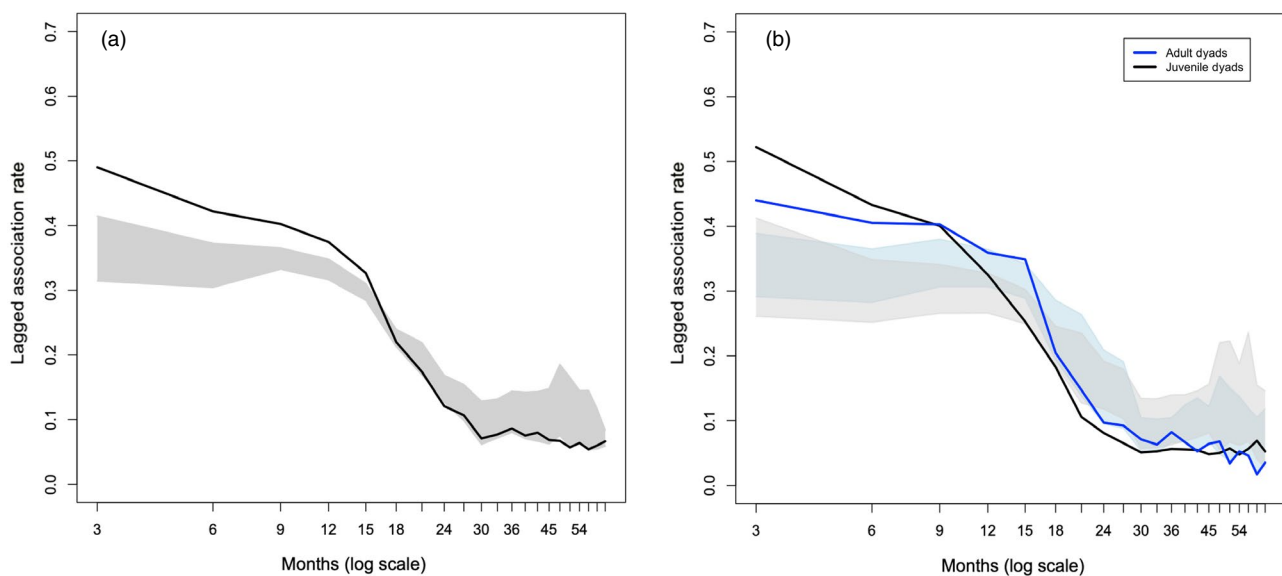

FIGURE 4 The relationship between year of observation (1–5) and the social instability of birds' associations, as measured by the absolute change in their edge weights over each pair of years. Shaded polygons represent 95% confidence interval of model fit. Circle/orange points and line show birds initially tagged as adults (>7 years), triangle/green points and line shows birds initially tagged as juveniles (<7 years)

FIGURE 5 Lagged association rates, showing the probability that a given dyad is observed re-associating in sequential 3-month time periods over the entire time of observation. Shaded area shows the 95% range of the lagged association rates calculated from 10,000 permutations of the dataset. Only birds that were observed in the final year of observation are included, as they are therefore alive and have retained tags throughout the entire period. (a) Lagged association rates for all individuals $N = 97$. (b) Lagged association rates for associations within adults and within juveniles. Blue line and polygon show dyads of birds initially tagged as adults (>7 years), black line and polygon shows dyads of birds initially tagged as juveniles (<7 years)

Seasonality also influenced the strength and cliquishness, but not number of these bonds. Finally, we found a high level of temporal stability in individuals' social relationships, with individuals further increasing in their social stability with age.

The importance of communal roost sites to social organization reflects the findings from field studies on other parrot species. A series of studies on amazon parrots, for example, has demonstrated that they exhibit roost-specific contact calls stable over 10–20 years (Wright, 1996; Wright & Dorin, 2001; Wright, Rodriguez, & Fleischer, 2005; Wright & Wilkinson, 2001). Similarly, in ringneck parrots *Barnardius zonarius*, contact calls differ between urban roost sites, and are hypothesized to enable groups to re-unify after independent foraging (Baker, 2000). However, a lack of individually marked birds has limited any investigation of fine-scale social structure within and between roosts. For instance, while previous studies have tended to assume that roost membership is stable (e.g. also in this species: Lindenmayer et al., 1996), our study observed that individuals also occasionally switched roosts, and often associated with individuals from different roosts when foraging. It would be interesting to identify whether roost-specific dialects still occur in this system, as if so, it would suggest a high degree of both flexibility and social conformity in vocalizations (Wright & Dahlin, 2017).

Our study additionally supports an influence of age on individual differences in the patterning and stability of associations, with younger individuals exhibiting stronger social bonds and weak positive assortment by age class, but with greater temporal instability than adults. It should be noted that individuals could only be aged as ±7 years; this pattern is likely to be clearer if the exact age was known for all individuals at each time step. While few previous studies in parrots have examined age structure in social organization, there is evidence for such effects in corvids, with non-breeding juvenile ravens *Corvus corax* communally roosting and engaging in fission–fusion foraging while adults (>3 years) remain territorial year-round (Braun & Bugnyar, 2012; Loretto et al., 2017). In this population of sulphur-crested cockatoos, in contrast, breeding adults do not appear to be territorial beyond the nest-hollow, and there are no age differences in the total number of social associations. Yet sulphur-crested cockatoos in this population defend their nest-hollow year-round and successful chick-rearing takes several months; it may be that these activities reduce their social foraging time, leading to the observed differences. More generally, age assortment has been observed in a wide range of species, from guppies (Croft et al., 2008), parids (Farine et al., 2015), to sea-lions (Wolf, Mawdsley, Trillmich, & James, 2007), and our study adds to the evidence that such demographic structure may be a common emergent property of animal social networks (Farine, 2014).

Sulphur-crested cockatoos have been considered a classic fission–fusion system, with birds departing roost sites in the morning in temporally-unstable foraging parties that re-join the roosting group at night (Wright, Stone, & Brown, 2003). Our results additionally suggest that individuals may be maintaining preferential relationships within this system, with individuals tending to exhibit highly stable social relationships with a few specific other individuals for up to 18 months. These findings reflect that of other long-lived species such as primates and cetaceans (Baird & Whitehead, 2012; Mitani, 2009; Silk et al., 2012; Stanley et al., 2018); however, such effects have usually been observed between kin (Mitani, 2009; Silk et al., 2012), or in stable groups (semi-feral horses: Stanley et al., 2018). Yet, three recent studies suggest that long-term relationships can also be maintained in fission–fusion systems more similar to that observed in this study (Carter, Brand, Carter, Shorrocks, & Goldizen, 2013; Kerth et al., 2011; Loretto et al., 2017). In particular, in one study on networks of Bechstein's bats where individuals were observed at roost sites over 5 years, older bats maintained stable associations with non-kin within larger fission–fusion dynamics, leading to multi-level social structure (Baigger et al., 2013; Kerth et al., 2011). Over shorter time-scales, this has also been proposed to occur in ravens (Braun & Bugnyar, 2012; Braun, Walsdorff, Fraser, & Bugnyar, 2012; Loretto et al., 2017), and in both these systems, the authors suggested that such social dynamics might be a hall-mark of social complexity or social cognition (Bugnyar, 2013).

Parrots are often referred to as similarly socially complex (Emery, 2006; Gutiérrez-Ibáñez et al., 2018; Hobson, 2014; Olkowicz et al., 2016; Pepperberg, 2002). Yet, there is actually relatively little research outside of captivity on the patterning of social interactions. In the most comprehensive set of studies to date, Hobson et al. (2013, 2014) and Hobson and DeDeo (2015) recorded social interactions in two groups of captive monk parakeets *Myiopsitta monarchus* and identified fission–fusion dynamics, but with stable male–female pairs forming a fundamental underlying social unit. While we did not make a specific effort to identify breeding pairs in our dataset, this does not appear to be reflected in our results, with the few known breeding pairs exhibiting high, but not distinctive bond strength. It seems likely that this is due to two reasons. First, and similar to other large parrot species, nest-hollows are a highly limited resource (Heinsohn, Murphy, & Legge, 2003; Legge, Heinsohn, & Garnett, 2004; Olah, Vigo, Heinsohn, & Brightsmith, 2014) and the large majority of sulphur-crested cockatoos are non-breeders without an clearly observable bonded mate. Indeed in our urban population, nest-hollows are particularly limited (Davis, Major, & Taylor, 2013, 2014). Second, breeding pairs exhibit year-round nest-guarding behaviour, where one individual of the pair remains to defend the nest hollow (Heinsohn & Legge, 2003). Given this, we may not necessarily expect foraging social networks to show a strong pair signal, with most overlap occurring at the nest site.

The stable social bonds outside of the pair-unit observed in our study rather perhaps most closely echo those observed in corvids, for example in ravens, where small subunits of 'affiliated partners' occur within large flocks, and potentially provide foraging benefits (Bugnyar, 2013). Sulphur-crested cockatoos share many superficial similarities with ravens, including similar relative brain sizes, unusual longevity, and a generalist foraging niche. Our results also suggest that they may share social characteristics also, with stable social associations within larger fission-fusion communal roosts. A fruitful research avenue may include more targeted comparative work between these two systems.

While many species of parrot are in rapid decline, others have successfully colonized human-modified habitats (Major & Parsons, 2010; Olah et al., 2016), where they can be relatively easy to observe, easily habituated to humans and are the focus of much interest from the local public. Our study takes advantage of this urban adaptability to use a citizen science approach to collect data from sulphur-crested cockatoos inhabiting an Australian city, providing multiple lines of evidence that such a data collection approach can provide useable and useful method to track parrots over broad spatial and temporal scales. In doing so, we provide a new insight into the social lives of an understudied taxa, contribute to the ongoing debate about the link between social systems and cognition, and highlight how long-term datasets can reveal underlying socio-temporal dynamics in such long-lived species.

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AUTHORS' CONTRIBUTIONS

L.M.A. conceived research question, conducted analysis and contributed to data collection; J.M.M., A.D. and R.E.M. designed the broader research project, including the *Wingtags* app and collected data; all authors wrote the paper.

DATA AVAILABILITY STATEMENT

The data supporting this manuscript are available at Edmond, the open access repository of the Max Planck Society https://doi.org/10.17617/3.41.

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SUPPORTING INFORMATION

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

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