The effect of familiarity on the temporal dynamics of spatial and affiliative associations in monk parakeets

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Abstract

To successfully navigate dynamic social environments, animals must manage their relationships by deciding who to interact with, how often, and when. Relationships may develop between familiar group members, but novel relationships can also form as strangers join groups. The process through which relationships form among strangers is not well-known for most species. We used a captive population of monk parakeets (*Myiopsitta monachus*) with known familiar and stranger relationships to test how novel relationships form among strangers. We established a novel social group by combining 22 parakeets captured from four geographically distinct locations. We quantified how familiar relationships differed from stranger relationships and whether we could detect convergence of the patterning and timing of spatial and affiliative associations across three contexts: general spatial proximity, nearest neighbor identity, and affiliative interactions. We found that familiar networks were consistently more well-connected during the experiment, but relationships did form between former stranger birds across all three behavioral contexts. Spatial proximity associations formed readily for both familiar and stranger birds, while nearest neighbor and affiliative interactions occurred more quickly among familiar dyads, indicating that the rate and patterning of how these relationships were formed differed. We found that the birds consistently preferred familiars across all behavioral contexts with no clear patterns of convergence between familiars and strangers, but the degree of preference depended on the social context. Overall, these findings suggest that parakeets recognize and differentiate between birds they might have encountered previously and that relationships with familiar and stranger conspecifics are not interchangeable. We discuss the differences in the effect of familiarity on spatial associations compared to affiliative contact and the extent to which these results suggest that monk parakeets balance the risks and benefits of associating with familiar and stranger birds.

Keywords: Affiliative relationships, proximity, familiar, novel relationships, parrot, social network

Introduction

A considerable amount of research across diverse animal species demonstrates an ability to recognize conspecifics (Tibbetts & Dale, 2007), and that the presence of familiar conspecifics plays a key role in shaping social interactions among social group members. Social animals tend to preferentially associate and affiliate with conspecifics they previously shared space (Shizuka et al., 2014), groomed (Carter et al., 2020), cooperated (Ripperger et al., 2019), or successfully reproduced with (Yanagitsuru et al., 2024). Preferentially associating with familiar social partners may provide individuals with a predictable social environment and increase social stability (Aragón et al., 2007; Senar et al., 1990). Maintaining stable relationships with social partners can enhance efficiency and coordination during resource acquisition and defense (Nowicki et al., 2018), pair displays during courtship (Prior et al., 2020a), and parental care (Griggio & Hoi, 2011; Sánchez-Macouzet et al., 2014). Relationships with familiar social partners can have important consequences for individual fitness (Archie et al., 2014), breeding success and offspring survival (Culina et al., 2020; Riehl & Strong, 2018).

However, social groups often change in size and composition. Unfamiliar individuals, or strangers, may encounter one another as neighboring groups may temporarily fuse with one another to forage (Silk et al., 2014) or as individuals permanently disperse to a new group or area and seek to form relationships or pair bonds with novel partners (Shizuka & Johnson, 2020). The presence of strangers can also shape social interactions. Establishing novel relationships can provide alternative benefits compared to familiar relationships such as increased social opportunity for high-quality partners and mates (Kohn et al., 2015) or access to social information (Aplin et al., 2012; Garg et al., 2022) or may function as a social bet-hedging strategy to minimize negative effects associated with losing a social partner (Carter et al., 2017).

Ultimately, successfully navigating dynamic social environments requires animals to decide whom to interact with, how, and when. When individuals encounter a novel social environment where both familiar and unfamiliar conspecifics may offer distinct social benefits, they face a trade-off (Cohen et al., 2007). Before engaging with strangers, individuals may take time to assess the risks inherent to associating and overcoming social uncertainty (Antonacci et al., 2010), evaluate potential social options, and gain familiarity (Carter et al., 2020; Griffiths & Magurran, 1997).

Although we expect that novel relationships sometimes form, it is often difficult to observe when and how strangers encounter one another for the first time and to quantify how these interactions evolve over time. As a result, our understanding of how unfamiliar individuals become familiar social partners remains limited for many social species (Carter et al., 2020; Cohen et al., 2007; Prior et al., 2020b; Ripperger et al., 2019). By comparing trends between the patterning and timing of social associations between relationship types (familiars and strangers) and assessing whether and how relationships with strangers develop to resemble those with known partners could provide important insight into how relationships develop and how and when familiarity is established with social partners. Understanding these dynamics can provide insight into the mechanisms that drive social bond formation and maintenance across different species.

We assessed how monk parakeets (*Myiopsitta monachus*) spatially associated and affiliatively interacted with familiars and strangers over time to test how new relationship differ from familiar relationships. Monk parakeets are a highly social parrot making them a suitable system for exploring the effect of familiarity on affiliative relationship formation. They are native to South America (Bucher et al., 1991; South & Pruett-Jones, 2000) and have established breeding colonies globally (Edelaar et al., 2015; South & Pruett-Jones, 2000; Uehling et al., 2019). Throughout their native and introduced range, monk parakeets typically live in resident colonies which often temporarily fuse with neighboring colonies to forage resulting in large flocks that may consist of up to hundreds of individuals (Bucher et al., 1991; Hobson et al., 2014; South & Pruett-Jones, 2000). Experimental social manipulations of monk parakeet social groups show that aggression among group members is likely structured by previous interactions rather than individual characteristics, like badges of status or relative size (Hobson & DeDeo, 2015; van der Marel et al., 2023) indicating that social history is important in social decision-making processes. Within social groups, pairs are the fundamental social unit (Avery et al., 2012; Bucher et al., 1991; Hobson et al., 2014), and in the wild and in captivity, parakeets form strong affiliative bonds with 1-2 group members regardless of sex (Eberhard, 1998; Hobson et al., 2014). Quantitative assessments of monk parakeet social structure in an experimentally formed captive social group showed that affiliative relationships can develop quickly and were relatively stable compared to flocking and agonistic relationships (Hobson et al., 2013). However, this study was conducted with birds with unknown past social histories prior to their capture, and it was unclear if there were familiar/stranger relationships or how these results may be affected by the presence of strangers. Despite the clear importance of affiliative relationships (Hobson et al., 2013, 2014, 2015) and social history in monk parakeet societies (Hobson & DeDeo, 2015; van der Marel et al., 2023), there has yet to be a study which explicitly accounts for familiar/stranger relationships in this species.

Because monk parakeets are likely to encounter novel individuals in the wild and the significance of past experiences on social interactions in an agonistic context, we hypothesized that familiarity would shape spatial associations and affiliative interactions. We refer to birds from the same capture site as *familiar* and birds from different capture sites as *strangers*; we focused on these initial stranger relationships to quantify novel relationship formation. We refer to any combination of two birds as a *dyad* and use the term *social partner* for any bird with which one bird associated or affiliative interacted (partner status does not indicate a breeding pair).

To quantify how relationships between stranger and familiar birds differed and how preference may change over time, we combined groups of parakeets captured at different locations into a single large social group. We then quantified how the presence and patterns of spatial associations and affiliative interactions changed over several weeks. We predicted that if familiarity had a strong effect on associations, birds would prefer to associate and interact with group members from the same capture location (familiars), and that this preference would lead to differences in the presence of associations between familiar and stranger birds across the experiment. We expected that dyads that were already familiar with each other would exhibit associations earlier compared to dyads that were initially strangers because previously connected birds would readily express those relationships in the flight pen, while strangers would need to initiate novel relationships which we expected to take more time to develop. We also predicted that as the birds associated with individuals who were initially strangers, the preference for familiar social partners over strangers would diminish over time. Once association patterns between familiars and strangers converged, we expected them to remain stable.

Methods

Ethics statement

All animal-related research activities were approved by the University of Cincinnati (IACUC protocol #AM02-19-11-19-01) and the United States Department of Agriculture, Wildlife Services, National Wildlife Research Center (USDA WS NWRC) (Quality Assurance #3203).

Bird capture sites and experimental social group

The experiment was performed at the USDA WS NWRC, Florida Field Station, in Gainesville, FL, USA. We used 22 feral monk parakeets captured by the USDA WS NWRC in February 2021.

Parakeets were captured from four geographically distinct capture sites in southeast Florida (Site 1: n = 5, Site 2: n = 6, Site 3: n = 7, and Site 4: n = 4) that were on average 16.06 km (range: 3.28 - 30.85 km) apart from one another. We treated birds captured from the same site as potentially familiar with each other because observational studies of populations within their native range reported high site fidelity and short dispersal distances (1.2 km) (Bucher et al., 1991; Dawson Pell et al., 2021; Martín & Bucher, 1993). We assumed that birds from different sites were likely strangers and unfamiliar to one another because the minimum distance between our capture sites was twice as far as the reported dispersal distance.

Following their capture, the USDA quarantined the birds for two weeks prior to the experiment. During quarantine, birds from the same capture site were housed together in small groups of 2-3 birds in 2 x 2 m cages in a covered outdoor aviary. Animal care was performed by the USDA staff following their standard care protocol. All birds from the same capture site were in visual contact with each other. To preserve unfamiliarity/stranger status, birds captured from different sites were visually separated. All birds in the aviary were in vocal contact with each other during the quarantine period. All birds were genetically sexed, but the sexes were not known until after the experiment (8 females and 14 males).

To allow for visual identification of individuals, we randomly assigned each bird a unique three-color combination which was applied with nontoxic permanent markers (Sharpie, Inc.®) (Buhrman-Deever et al., 2008; Hobson et al., 2013, 2014, 2015; Hobson & DeDeo, 2015; van der Marel et al., 2023) across each bird's head, cheeks, and chest several days before the experiment began. We refreshed color marks immediately before the birds were released into the flight pen, and the marks remained conspicuous throughout the experiment. Ink and dye-based color marks are useful alternatives to traditional methods like leg bands for species like parrots because these marks enhance visibility from various angles and long distances and are unable to be manipulated or removed by the birds (Buhrman-Deever et al., 2008; Ellis & Ellis, 1975; Kennard, 1961; Klump et al., 2021). Additionally, we chose this method for identification because a full view of the monk parakeets' tarsi is often obstructed by feathers and resighting bands can be time-consuming or impossible depending on the bird's position (Senar et al., 2012; Toft & Wright, 2015).

The experiment took place in a large 2,025 m^2 semi-natural outdoor flight pen which was marked with a grid (roughly 5 x 5 m) using string on the ground to assist observers in identifying the locations of the birds. The flight pen contained a bioactive substrate which promoted natural nutrient cycling and did not require cleaning. The pen also included planted grasses and several trees which the birds could use for foraging and perching, as well as six artificial perch structures and a large shelter used for enrichment and shade. Birds had constant access to food (seed mix provision) and large shallow water trays (for drinking and bathing) which were located at three stations which were 5-10 meters apart within the flight pen. Food and water were replaced daily. The flight pen was large enough and resources were distributed such that birds from different capture sites could have isolated in distinct areas in the flight pen each with access to their own perches, shade, food, and water without being considered in proximity. During the experiment, birds were exposed to natural light, weather conditions, and perception of natural potential predation pressure from activities of the resident animals outside the flight pen. Observers performed a visual welfare check on birds before daily observations began.

To begin the experiment, we simultaneously released 22 uniquely-marked birds into the flight pen on April 5, 2021. We observed the birds for 19 days, ending on April 26, 2021. Observers were blind to the birds' capture sites and sex. During the experiment, birds interacted freely and remained undisturbed (aside from daily husbandry and two observers recording interactions from blinds within the flight pen). Observers began collecting proximity and social interaction data as soon as all birds were released. Daily observations took place between 08:00 and 19:00 by a total of four observers from three different blinds and were typically split into morning and evening sessions to capture periods of the day where birds' activity was the highest. For all but one day during the experiment, all observers took a break mid-afternoon (mean = 1.73 hrs.; min. = 1.08; max. = 2.67); this coincided with periods where activity levels were low. Daily observations resumed following this break for the afternoon session. To maximize the amount of data recorded during sessions, all observers collected data simultaneously, and observers took breaks in shifts such that at minimum two observers were present. To ensure interobserver reliability, all observers were trained in consistent data collection prior to the experiment using a social group of monk parakeets who were not part of the study in the same flight pen as the experimental group.

Spatial and social data collection

We used both scan and all-occurrence sampling (Altmann, 1974) to record seven spatial associations and affiliative social interactions (Table 1). All observations were recorded in real time directly onto two iPads (one for scan data and one for all-occurrence data) using the Animal Observer application (Caillaud, 2016; Luescher, 2006; van der Marel et al., 2022).

We assessed spatial associations in two ways: (1) *spatial proximity* and (2) *nearest neighbor* associations (Table 1). Whether birds flock and maintain peaceful proximity associations is an active choice and are common indices to quantify social structure in birds (Morales Picard et al., 2020).

We used inter-individual spatial distances to indicate flock membership. To record bird locations, observers completed scan samples every five minutes by scanning the entire flight pen and recorded each birds' X and Y coordinates within the flight pen and their activity (i.e., vigilant, foraging perching, resting, preening, nest building), creating a "snapshot" of each bird's location and behavior. We used the location coordinates to find the distance between each dyad during each scan. We categorized dyad members as being associated during a scan if their inter-individual distance was less than 3m.

We used nearest neighbor associations to indicate fine-scale dyadic proximity preferences for birds in peaceful proximity. To collect nearest neighbor associations, observers recorded the identity of the bird perched closest to each bird within a maximum distance of one meter using an all-occurrence sampling method (Altmann, 1974). To ensure nearest neighbor associations were consistently sampled, nearest neighbor associations were recorded at least every five minutes (independently of the scan sampling procedure to collect spatial proximity data) in addition to opportunistically recording associations in the absence of social interactions. We quantified affiliative contact with five distinct interactions: (1) s*houlder-to-shoulder* interactions, (2) *allopreening*, (3) *beak touching*, (4) *allofeeding*, and (5) *copulation* events (Table 1). Affiliative interactions were recorded as they occurred using an all-occurrence sampling method (Altmann, 1974). We pooled these affiliative physical contact behaviors for analyses because these behaviors typically reflect strong affiliative relationships among same and opposite sex dyads of monk parakeets in the wild and in captivity (Bucher et al., 1991; Eberhard, 1998; Hobson et al., 2014).

Table 1: Description of the seven behaviors observed.

Behavior	**Description**
Spatial proximity	Shared space: birds found within 3m of one another; Indicates flock membership
Nearest neighbor	Identity of the bird perched closest to the observed individual, within a maximum distance of 1m; Indicates spatial preference within a flock

Shoulder-to-shoulder	Two birds sitting in physical contact side by side
Allopreen	A bird preens (groom) another bird’s feathers
Beak touch	Two birds simultaneously and rapidly touching culmens together; often occurs while posturing upwards with heads raised
Allofeed	Birds regurgitating (or simulating regurgitation) food into each other’s beaks
Copulation	Two birds touch cloacas

Quantifying proximity, nearest neighbor, and affiliative associations

We performed all data cleaning and analyses in R version 4.2.2 (R Core Team, 2021) and created figures using ggplot2 (Wickham, 2016).

To determine spatial proximity associations, we used data collected from scan sampling. During data cleaning, we filtered the data by including scans where more than 50% of birds were identified, then we further filtered scans to include scans where 80% or more of the birds’ behaviors were identified and their exact location was known. This procedure ensured that scans were representative of persistent spatial associations where individuals had the opportunity to interact with, observe or learn socially from each other. To quantify dyadic proximities from scan location data, we calculated Euclidean distances between all dyads in each scan. Dyads within three meters or less of each other were scored as in proximity. We chose three meters because it was less than the median (4m) distance observed across scans and was consistent with flocking distances reported in captive experiments with this species (Hobson et al., 2014). The flight pen’s large size (45mx45m) and resource distribution allowed birds to avoid each other if desired and the three-meter threshold ensured that we captured smaller-scale grouping patterns that were more likely to be the result of birds' active decisions about which group members to remain near.

We used our all-occurrence dataset to quantify nearest neighbor associations and affiliative interactions. We used a two-step process to filter the all-occurrence data. We included only records where the individual was positively identified, and the behavior recorded was one of our six behaviors of interest. To standardize the temporal scale at which different behaviors were sampled and remove any duplicated associations recorded during observations, we then filtered to include a maximum of one observation per dyad per behavior per five-minute observation interval.

To quantify daily patterns of preferential associations, we constructed separate weighted, undirected networks for proximity, nearest neighbor, and pooled affiliative interactions for each day of the experiment. Weighted networks account for the frequency of interactions among individuals, with edge weights reflecting how often nodes, or birds, are observed together. In each network, edges (i.e., relationships) represent the proportion of observed associations between dyads relative to the total possible associations. The method for determining the total possible associations varied depending on the type of association being measured. For associations based on spatial proximity, the total possible associations were determined by the total number of daily scans completed. For nearest neighbor and affiliative interactions, the total possible associations was determined by the number of five-minute observation intervals per day. While the definition of association probability remained consistent (observed associations relative to total possible), the denominator in this proportion was adapted to reflect the observational limitations to each specific type of association/data collection method.

Quantifying associations by sex

To determine the availability of same/different-sexed potential social partners, we quantified the proportion of possible dyads by sex per relationship type for each bird. We calculated this proportion by dividing the number of possible same- and different-sexed dyads per familiarity status by the total number of dyads per familiarity status for each bird. To assess group-level trends, we also summarized these proportions across individuals. Proportions range from zero to one. A proportion near .5 would indicate that a particular bird had equal availability of potential social partners of both same- and different-sex; proportions near one would indicate that potential social partnerships were possible exclusively with either same or different-sexed individuals.

To compare how each bird associated and interacted with same/different sexed dyads, we quantified each bird's observed proportion of dyads by sex across aggregated familiar and stranger affiliative interactions. We calculated this proportion by dividing the number of observed same- and different- sexed dyads per familiarity status by the total number of associates per familiarity status for each bird. To assess group-level trends, we also summarized these proportions across individuals. Like our analysis of the sexes of potential social partners, the proportion of observed affiliative interactions with proportions near .5 would indicate that a bird affiliated with an equal number of same and different-sexed social partners and values near one would indicate that affiliative interactions were observed exclusively with either same or different-sexed individuals.

Quantifying the presence of relationships by familiarity status

To compare the presence of familiar and stranger relationships within each behavioral context, we calculated network density, or the proportion of social connections in each network. We calculated density by dividing the total observed edges in stranger and familiar networks by the total number of possible edges by familiarity status. Density values range from zero to one, and a high density or a value near one would indicate a highly connected network in which birds interacted with many of the available social partners. A low density or a value near zero would indicate a sparsely connected network in which birds only associated with a few possible social partners.

To assess overall network connectivity, we first calculated familiar and stranger network density for each behavioral context across the entire experiment. We then assessed daily trends in connectivity, where we calculated daily familiar and stranger density for each context. We expected to find a greater overall network density among familiar birds compared to strangers, which would suggest familiar birds established more relationships compared to strangers. Additionally, we predicted that this difference would be evident in daily network densities, with familiars consistently showing denser networks each day.

Testing for differences in the timing of associations by familiarity status

To assess whether associations were observed earlier among familiars compared to strangers, we calculated the cumulative proportion of relationships observed during each hour of the experiment. To compare the time to first association between familiar and stranger dyads, we performed a Kaplan-Meier survival analysis, using the R packages "survival" (version 3.7-0) (Therneau et al., 2024) and "survminer" (version 0.4.9) (Kassambara et al., 2021). With this approach, we calculated the probability of observing a relationship for the first time for each hour of the experiment, and we used a non-parametric log-rank test to determine whether familiarity status had an effect on the observation hour relationships were first observed for each behavioral context. The null hypothesis was that the distribution of first association times would be identical for familiars and strangers, while the alternative hypothesis was that these distributions would differ. This analysis assumes non-informative censoring. The analysis also assumes there is no recruitment bias of experiencing an association, and that the timing of events are precise (Goel et al., 2010; Etikan et al., 2017).

Censoring occurred for dyads that had not been observed associating/interacting for the first time by the end of the experiment. We assume that this censoring was non-informative, and that these dyads had the same probability of experiencing association at any given time as those dyads who were observed associating within the experiment. We expected that familiar dyads would exhibit associations earlier compared to stranger dyads, as we assumed that previously connected birds would readily reestablish relationships in the flight pen, whereas strangers would require more time to initiate novel relationships.

Assessing assortment by familiarity status

To determine whether preferences for familiar individuals varied by behavior, we compared the pooled daily assortativity values calculated for each behavioral context using a one-way ANOVA, and given a significant effect, we used a Tukey Honest Significant Difference (HSD) post-hoc test to identify pairwise differences between behaviors.

To detect daily patterns in assortativity, we calculated assortativity (r_a) using the assortment.discrete() function from the assortnet package (Farine, 2023) using weighted networks for proximity, nearest neighbor, and affiliation. Weighted networks are well-suited for calculating assortativity because they are more robust to sampling noise compared to binary networks which represent only the presence of associations (Farine, 2014). Assortativity ranges from negative one to one: values near one would indicate that birds captured at the same site preferentially associated with each other and preferred familiars while assortativity near negative one would indicate birds captured at different sites preferentially associated with each other and preferred strangers (assortativity near zero would indicate no differentiation of preference based on stranger or familiar status). We expected that parakeets would preferentially assort with familiar birds, resulting in positive spatial and affiliative assortativity values.

We tested whether observed daily associations for each behavioral context differed from random expectations using a permutation-based reference model. Permutation approaches are often used to test for patterns within non-independent data like social interactions (Croft et al., 2011; Farine, 2017; Hobson et al., 2021). Reference models are generated often over thousands of iterations by permuting key features of the data while maintaining other aspects of the network structure. In this way, potential correlations between the observed structure of the association data and the feature of interest can be broken. A summary measure which captures the relationship of interest is calculated for each iteration of the reference model resulting in a distribution of expected values under the null hypothesis. To determine statistical significance, we quantified the proportion of expected values from this distribution that are at least as extreme as the observed (Farine & Carter, 2022; Hobson et al., 2021). Using a one-tailed comparison, we considered a result statistically significant if the observed value was more extreme than 95% of the reference values. We report this as a P-value, representing the proportion of reference model values that exceed the observed value. A P-value of 0 indicates that none of the reference model values were more extreme than the observed data.

We used this reference model approach to randomize each bird's capture site in each network. The resulting assortativities produced by each iteration were those expected if the birds interacted exactly as observed, but without regard for each other's capture sites or familiar/stranger status. The model maintained all aspects of the daily network structure including the identity of the dyad, and the type and frequency of behavior used. We used 1,000 permutated datasets to build our expected reference distribution if the capture site did not affect association patterns. If assortativity was positively affected by familiarity status, we expected our observed assortativities would be significantly higher than assortativities from randomized data, with less than 5% of randomized values being as high as our observed ($P<.05$) indicating that birds preferred familiar social partners.

Detecting the convergence and stability of preferences between familiars and strangers

To detect changes in preferences between familiars and strangers in spatial and affiliative associations, we assessed whether assortativity values converged to random expectations over time. We expected that birds would initially prefer to associate with familiar social partners and these metrics would be significantly different from random expectations but that as birds got to know each other, their assortativity preferences would decrease and be indistinguishable from random association patterns. These patterns would indicate a convergence in patterns of associations between familiars and strangers.

Additionally, we expected that once assortativity preferences converged, they would remain converged. To further assess patterns of stability, we fit a linear regression to model the effect of time on network assortativity values for each behavioral context. We used the slope to determine whether assortativities increased, decreased, or remained constant over time to indicate stability. A positive slope would indicate that assortativity tended to increase over experimental days, while a negative slope would indicate that assortativity tended to decrease. A slope close to zero would suggest stability over time, or a lack of association between assortativity and study day. We expected that assortativity would be stable and slopes would be near zero once the stranger effect disappeared.

Results

We observed the experimental group comprised of 52 possible familiar and 179 possible stranger dyads for a total of 132.30 observation hours across 19 observation days. Each day we observed an average of 6.96 (± 1.54 SD) hours. After data cleaning, our dataset included 28,431 spatial associations collected from 359 scans, 3,514 nearest neighbor associations, and 6,310 affiliative interactions (3,117 shoulder contact interactions, 2,785 allopreening interactions, 289 beak touching interactions, 52 allofeeding interactions, and 67 copulations).

Quantifying associations by sex

When we quantified the proportion of possible social partners by sex among familiars and strangers for each bird, we found that birds were generally not constrained in how they could form affiliative relationships with others by sex by familiarity status. Only three birds were constrained to only one category of potential social partners; within familiar relationships, these three birds had only different-sexed potential social partners. When we compared social partner availability within familiar birds and strangers, we found similar mean proportions of different- and same-sexed potential partners (Figure 1a; mean ± sd [range]; familiar same sex: 0.67 ± 0.19 familiar different sex: 0.42 ± 0.29 (0.20-1.00); stranger same sex: 0.50 ± 0.15 (0.24-0.76); stranger different sex: 0.50 ± 0.15 (0.24-0.76). These results indicate that each individual generally had a mix of available same/different sexed potential social partners among both familiar and stranger birds.

When we compared how birds were observed affiliating with others based on the sex of the social partner we found that birds were affiliative with both same and different sex partners and that the mean proportions were similar to the availability of social partners (Figure 1b; familiar same sex: 0.63 ± 0.17 (0.33-1.00); familiar different sex: 0.56 ± 0.27 (0.33-1.00); stranger same sex: 0.45 ± 0.22 (0.10-1.00); stranger different sex: 0.60 ± 0.20 (0.25-1.00)). Together, these results suggest that sex did not play a strong role in shaping familiar/stranger relationships in this group.

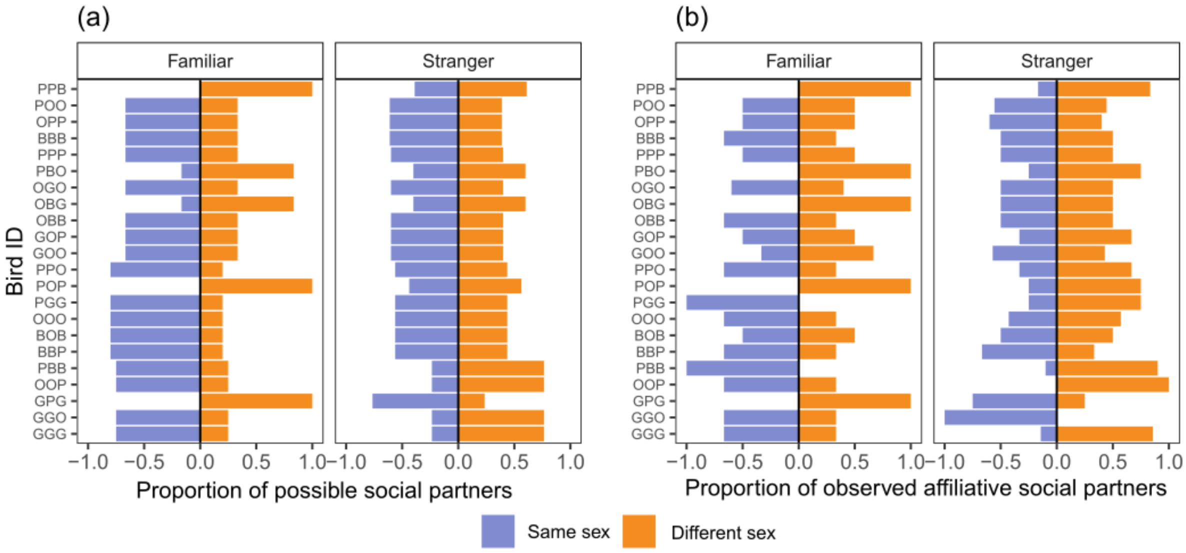

Figure 1: Summary of the (a) proportion of potential same sex and different sex social partners in the study population and (b) the proportion of observed affiliations with same sex and different sex social partners. Bar color shows same sex (purple) or different sex (orange) proportions for each bird, taking into account each bird’s sex and the sex of its potential social partners, split by familiar/stranger status.

Quantifying the presence of relationships by familiarity status

When we quantified network density among familiars and strangers across aggregated spatial proximity, nearest neighbor associations, and affiliative interaction networks, we found that familiar and stranger proximity networks were equally well-connected (Figure 2a; familiar density = 1.00, stranger density = 1.00), and nearest neighbor networks were nearly equally well-connected (Figure 2a; familiar density = 1.00, stranger density = .98). Affiliation networks were more well-connected among familiar birds compared to strangers (Figure 2a; familiar density = 0.69, stranger density = 0.32).

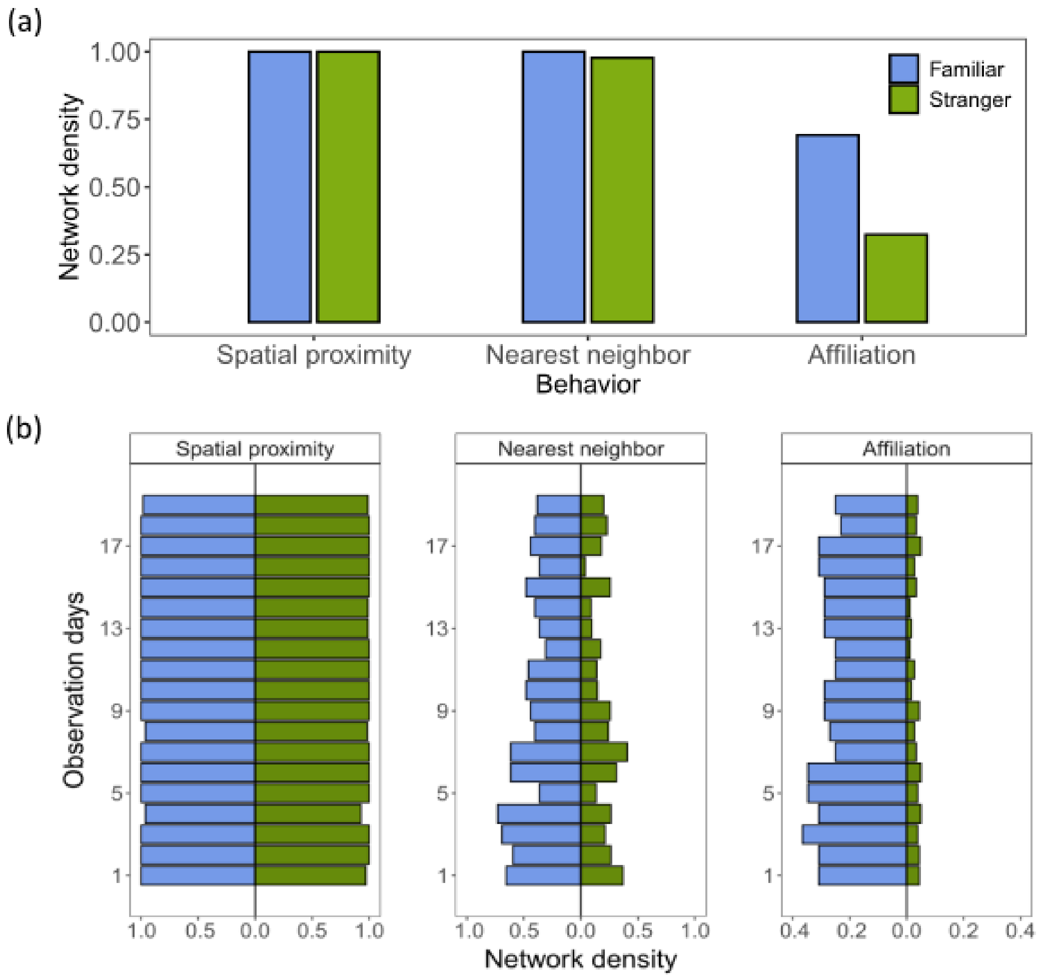

Figure 2: Spatial relationships were as common among familiar (blue) as stranger birds (green), and affiliative contact interactions were more common among familiars. These patterns were reflected in (a) overall networks aggregated across the experiment and (b) daily network trends.

When we compared daily network densities between familiars and strangers for each behavioral context, we found that spatial proximity networks were consistently equally well-connected among familiars and strangers while nearest neighbor and affiliation networks were more well-connected among familiar birds compared to strangers (Figure 2b; Supplementary table 1). These results suggest that familiar networks were consistently more well-connected during the experiment, but at least some stranger birds formed relationships across all three behavioral contexts.

Differences in the timing of behavior initiation

When we compared the cumulative proportion of familiar and stranger dyads observed for the first time for each behavioral context, we found no difference in median proportions for spatial proximity associations, a moderate difference for nearest neighbor associations, and the highest difference for affiliative interactions (Figure 3). Median observation times for spatial proximity associations between familiar and strangers were similar while median times for affiliative interactions for familiars were earlier compared to strangers (Figure 3). The median cumulative proportion of familiar and stranger dyads in spatial proximity were observed in hour 3 of the experiment (familiar: range = 1-5; stranger: 1 -11; Figure 3a). The median cumulative proportion of nearest neighbors were observed in hour 3 and strangers in hour 12 (familiar: 1-120; stranger: 1-146; Figure 3b). The median cumulative proportion of affiliative interactions were observed in hour 15 and in hour 42 between familiars and strangers, respectively (familiar: 1-141; stranger: 1-166; Figure 3c). These results suggest that familiars and strangers readily formed spatial proximity associations and that familiars readily formed nearest neighbor associations and affiliative interactions but that strangers took time to develop nearest neighbor associations and affiliative interactions.

However, when we compared the distribution of first association times (observation hours) between relationship types with a Kaplan-Meier survival analysis, we found significant differences in the time to first proximity association ($x^2 = 7.5$, df = 1, p = .006; Supplemental Figure 2a), nearest neighbor ($x^2 = 20.5$, df = 1, p < .001; Supp. Figure 2b), and affiliation ($x^2 = 38$, df = 1, p < .001; Supp. Figure 2c) indicating that familiar birds exhibited these behaviors in relationships more quickly across behavioral contexts compared to strangers.

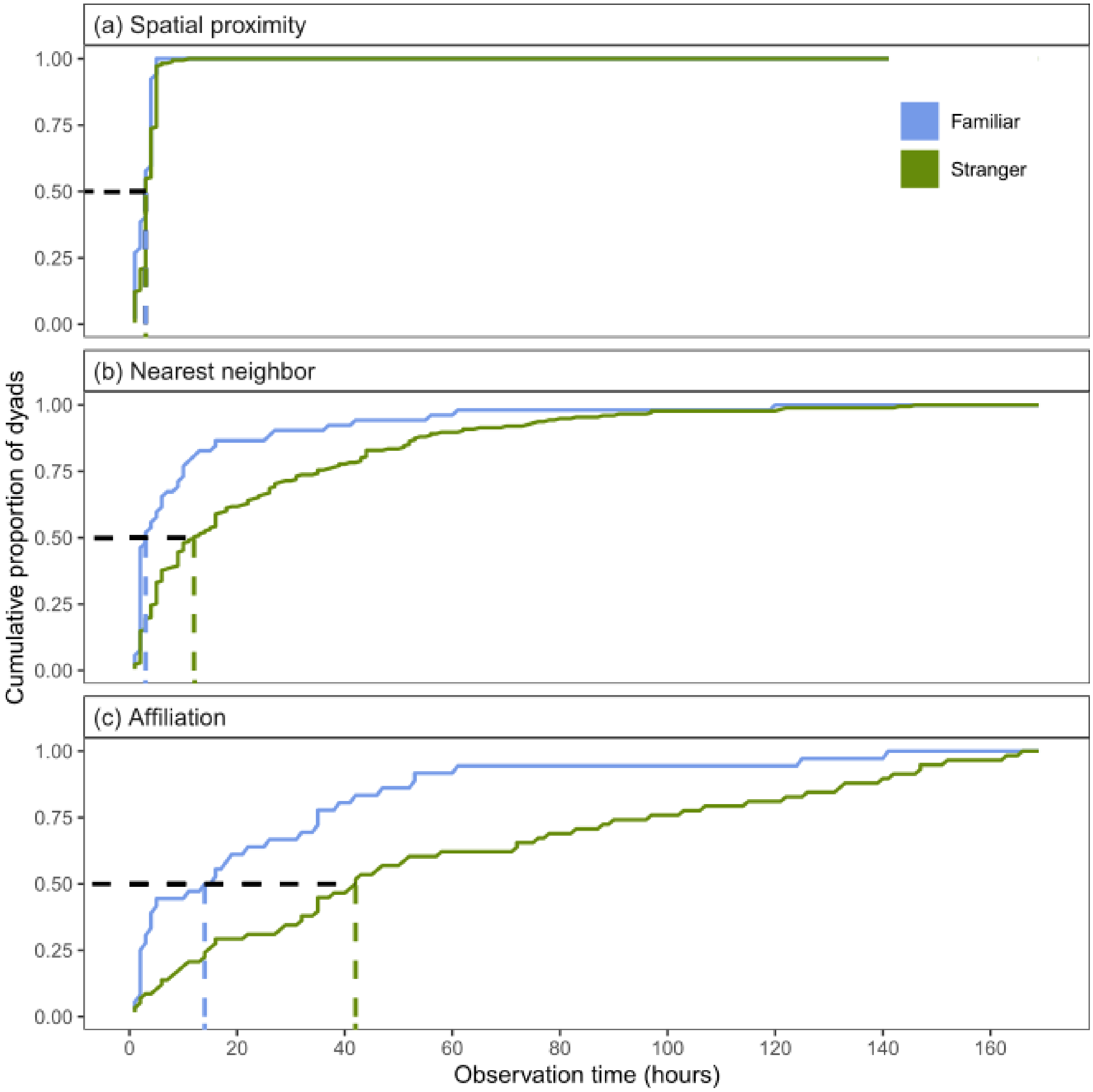

Figure 3: Cumulative proportion of relationships observed between familiar (blue) and stranger (green) dyads observed associating/interacting for the first time shows no differences between median observation times (back dashed line) of (a) spatial proximity associations and a moderate difference between (b) nearest neighbor associations, and the highest difference between (c) affiliative interactions.

Assortment by familiarity status

When we compared observed daily assortativity values for proximity, nearest neighbor, and affiliation, we found significant differences in assortativity across the three contexts (mean: proximity = 0.03; nearest neighbor = 0.59; affiliation = 0.88; F (2, 54) = 423.5, $p < .001$). A Tukey HSD post hoc test confirmed that all pairwise comparisons between behaviors were significantly different indicating distinct levels of assortativity for each behavior ($p < .001$; Supplemental Table 3). Assortativity was lowest for proximity associations, moderate for nearest neighbor associations, and highest for affiliative interactions (Figure 4). These results show that the birds assorted preferentially with familiar birds across all contexts but that the strength of this preference was much stronger for nearest neighbor and affiliative associations compared to spatial proximity. The birds had the least preference for familiar birds for proximity associations and were often in proximity with strangers.

When we compared the pooled daily observed assortativity values to those produced by the reference model, we found that associations across all three contexts were significantly more assortative than expected if the familiarity status was randomized (Figure 4). However, when we compared the proportion of reference values that were as extreme as the minimum observed assortativity, we found that the extent to which these behaviors differed from random differed across contexts. Proximity assortativites were slightly higher (Figure 4a; P = .004), and nearest neighbor assortativities were moderately higher than expected assortativities when familiarity status was randomized (Figure 4b; P = .001). Affiliative assortativities differed completely from random expectations (Figure 4c; P = .00). This result suggests that the extent of the preference for familiars varied by behavior.

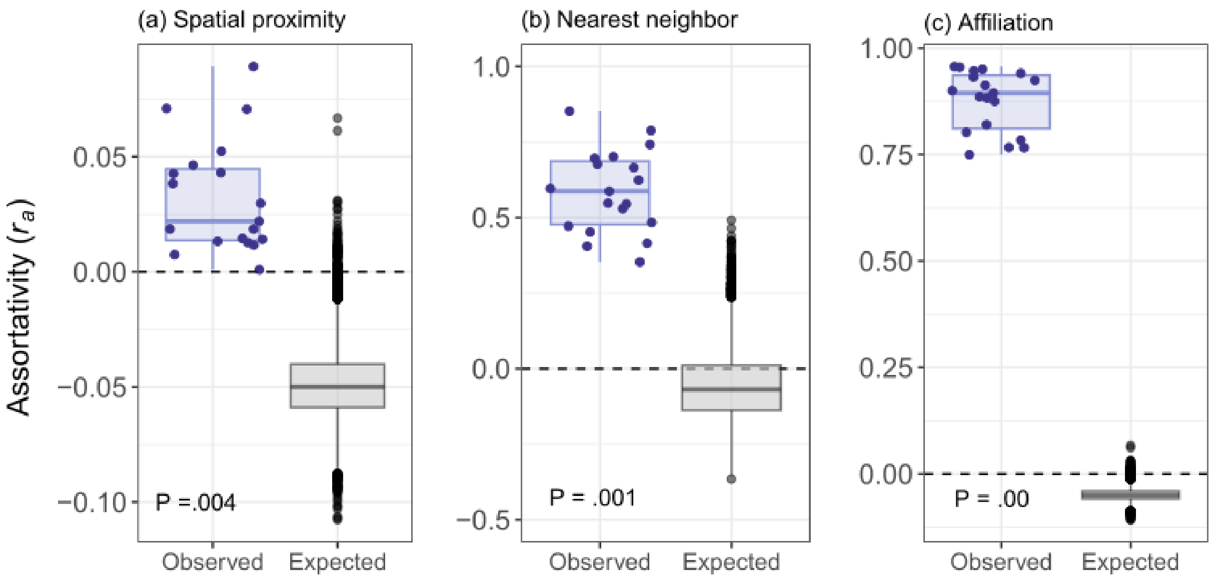

Figure 4: Daily observed assortativity values (purple) compared to the reference model's random expectations (gray) for (a) proximity, (b) nearest neighbor, and (c) affiliative behaviors. Positive assortativity values indicate preferences for familiars, values near zero indicate neutral preferences, negative assortativity values indicate preference for strangers.

When we compared values of assortativity to those produced by the reference model for each day, we found that all observed assortativity values were higher than all assortativities calculated from the randomized data (*P* = .00 for all days and behavioral contexts, see Supp. Table 4). These results indicate that the birds maintained preferences for familiar birds throughout the experiment.

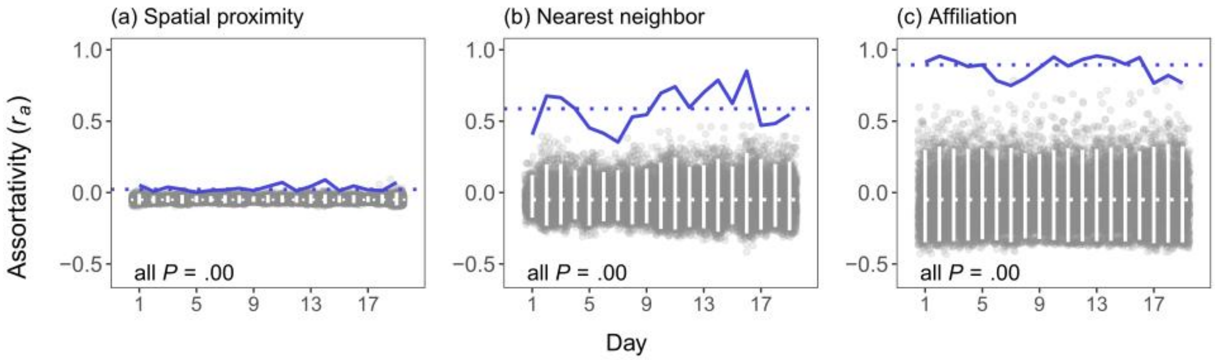

Figure 5: Comparisons of the daily observed (a) spatial proximity, (b) nearest neighbor, and (c) affiliation assortativity values (purple line) to daily random expectations (gray distribution) show that the birds maintained preferences for familiars throughout the experiment, and these patterns remained constant over time. The horizontal dotted lines represent the median observed assortativity in purple and the median reference assortativity values in white. Vertical white lines indicate the daily 95% confidence intervals of the reference distribution.

Detecting the convergence and stability of patterns between familiars and strangers

Contrary to our predictions, none of the assortativity values in any of the three behavioral contexts consistently decreased over time or converged to random expectations (Figure 5; Supplemental Table 4). These results suggest that the birds maintained their preferences for familiars and the patterning of these associations were distinct from associations with strangers across all contexts. When we fit the observed assortativity values to linear models, we found that spatial proximity and nearest neighbor slope coefficients were positive and near zero (Proximity: $\beta = 0.001$, $R^2 = 0.07$, F (1,17) = 1.36, p= .26; nearest neighbor: $\beta = 0.006$, $R^2 = 0.07$, F (1,17) =1.28, p= .27), and affiliative slope coefficients were negative and near zero ($\beta = -0.003$, $R^2 = 0.05$, F(1,17)= 0.83, p = .38). These results indicate that the degree of preference for familiar partners remained constant over time.

Discussion

Using a novel social group of captive feral monk parakeets, we examined temporal changes in preferences for familiars and stranger social partners by comparing the presence and timing of relationship formation and assessing the convergence and stability of assortativity across spatial and affiliative contexts. We found that familiar networks were consistently more well-connected during the experiment, but relationships did form between some strangers across all three behavioral contexts. Overall, our results suggest that parakeets recognize and differentiate between birds they might have encountered previously and that relationships with familiar and stranger conspecifics are not interchangeable. However, we also found that novel relationships could form between former strangers within a relatively short time period. We discuss the differences of the effect of familiarity on spatial associations compared to affiliative contact and the extent to which these results suggest that monk parakeets balance the risks and benefits of associating with familiar and stranger birds.

Strangers readily formed flocks but stayed close to familiar birds

We found that proximity networks were equally well-connected among familiars and strangers and were established within the first several hours of the experiment. This rapid mixing with strangers was contrary to our prediction that birds from different capture sites would initially spatially avoid strangers. We detected significant differences in when we observed the first association between familiars and strangers, indicating that the rate and patterning of how these relationships were formed differed. We also found that birds showed preferential spatial associations with familiar birds, but this preference was not as strong as affiliative associations. We suggest that the statistical differences detected between when relationships were first observed and patterns of assortativity may be due to the high-resolution of data obtained and allowed us to detect fine-scale patterns which could have increased the likelihood of detecting differences between familiars and strangers. These results may not necessarily reflect strong biological significance. For example, rather than observing subgroups of familiar birds spatially isolating from one another, we found that all spatial proximity associations were observed within the first two days of the experiment. Taken together, these results indicate that birds readily formed mixed flocks, but birds maintained closer proximity to familiar birds.

Our results are consistent with observations of wild and captive monk parakeet social groups which indicate that forming foraging flocks is central to their socioecology (Bucher et al., 1991; Hobson et al., 2013, 2014; South & Pruett-Jones, 2000). Throughout their native and non-native range, monk parakeets can flock in groups of hundreds of individuals although much smaller groups of 5-10 birds are more common particularly during the breeding season (Bucher et al., 1991; South & Pruett-Jones, 2000). A similar study on the formation of monk parakeet social structure in captivity found that spatial proximity associations were the most common among birds and that nearest neighbor associations stabilized more quickly compared to other association contexts (Hobson et al., 2013). This assessment of spatial proximity only reported on flock size, composition, cohesion, and did not explicitly examine how relationship status may affect their formation or maintenance. Our results provide a novel perspective on monk parakeet flock composition and formation.

Establishing spatial associations with strangers could provide important benefits which outweigh the risks of associating. Maintaining spatial proximity requires little investment of time or energy, and individuals may benefit from increased foraging efficiency or increased vigilance and predator awareness (Sorato et al., 2012; van der Marel et al., 2019). Assessments of monk parakeet flocks in their non-native range found that individuals initiated fewer scans for predators and spent less time scanning as flock size increased (South & Pruett-Jones, 2000) suggesting that the risk of predation may play a significant role on the formation of spatial relationships in this species. Maintaining proximity may also allow individuals the opportunity to safely gain important social information about foraging techniques (Kulahci et al., 2016; Schnoell & Fichtel, 2012; J. B. Silk et al., 1996) or assess conspecific's suitability as an affiliative or cooperative partner (Carter et al., 2020) which can be important for optimizing social decisions. These benefits could explain why mixed flocks were established early in the experiment.

Birds tended to affiliate with familiar partners but could form novel relationships quickly

We found that birds consistently had the highest preferences for affiliating with familiar partners, but that affiliative relationships could develop quickly among unfamiliar birds. These results suggest that birds were selective about whom they form affiliative relationships with and that familiarity could play an important role in shaping these relationships. We did not find a strong preference for different-sexed social partners indicating these preferred relationships might not always reflect reproductive pairs. Preferred affiliative relationships are widely considered to be an important aspect of parrot socioecology (Luescher, 2006; Seibert, 2006). Although these relationships are often assumed to be exclusive to long-lasting reproductive partners, these relationships may be more flexible than assumed for some parrot species. For example, juvenile spectacled parrotlets (*Forpus conspicillatus*) form multiple non-exclusive allopreening relationships with group mates (Garnetzke-Stollmann & Franck, 1991) and cockatiels (*Nymphicus hollandicus*) engage in allopreening relationships with same- and opposite sex partners (Seibert & Crowell-Davis, 2001). Similarly, our results suggest that monk parakeet affiliative relationships are an important aspect of their socioecology and birds may develop preferred affiliative relationships with partners regardless of sex potentially to avoid being a singleton.

We found that strangers often initiated affiliative behaviors much later in the experiment and after sharing proximity. In group-living species, the importance of social contact, often social grooming, is widely recognized for its importance in establishing trust and reducing stress and social uncertainty among group members. For example, resident male Verreaux's sifakas (*Propithecus verreauxi*) initiate play before establishing social grooming relationships with non-resident unfamiliar males (Antonacci et al., 2010). Similarly, female common vampire bats (*Desmodus rotundus*) first initiate low-cost grooming relationships with potential cooperative partners before escalating to sharing blood meals (Carter et al., 2020). Our findings offer preliminary evidence for a similar progression, where proximity escalates to affiliative contact as relationships develop. Further research should clarify the mechanisms by which familiarity is developed among strangers during affiliative relationship formation.

The formation and stabilization of a novel social group

We detected a consistent effect of familiarity on the presence, timing, and patterning of associations, but the extent of the effect depended on the association context. We did not find convergence of associations or interactions between strangers and familiars. It is unclear whether we would be able to detect convergence if the experiment were to continue or how long it would take for this pattern to emerge. Although our results are consistent with characterizations of social structure formation and stabilization in monk parakeets across spatial and affiliative behaviors (Hobson et al., 2013), without details of the familiar birds’ social histories prior to their capture, it is unclear how the nature (e.g., affiliative/agonistic) of their relationship may have affected these results.

Potential limitations

For this study, we have assumed that birds captured at different capture sites were likely strangers and had not previously interacted. However, distances between capture sites were potentially close enough for birds to travel to meaning birds from different capture sites could in theory have encountered one another following a dispersal event or while foraging. Observational studies in monk parakeets native range reported short dispersal distances (median = 1.2 km) (Martín & Bucher, 1993) suggesting that monk parakeets have high site fidelity. However, genetic evidence suggests that long-distance dispersal ranging from 10 – 100 km is possible in monk parakeets (Borray et al., 2023; Dawson Pell et al., 2021; Gonçalves da Silva et al., 2010), although more research is needed to determine how typical this pattern is. Additionally, despite the potential for dispersal, birds would not need to travel far from their capture site to access food resources or nesting material because each capture site is located near a park or agricultural field and a body of water, and to access mutual foraging patches, birds would need to cross urban-suburban areas and highways. However, without tracking social histories of the parakeets in the wild, we cannot be certain that birds from different capture sites had not encountered each other. Although we could not confirm birds from different capture sites were definitively strangers, our results provide support that birds from different capture sites were likely unfamiliar with each other. If birds from different sites had prior familiarity with one another, the distinct patterns of social discrimination we observed would likely have been less pronounced, as such familiarity would have blurred the differences in their associations and interactions.

Another potential limitation of the study is the captive setting, which can affect behaviors in some species and contexts (Webster & Rutz, 2020). Because we used recently trapped feral birds, the possibilities that long-term captivity affected the behavior of the birds was minimized. It is also unlikely that the social results we report here were solely an artifact of captive conditions. This is because the flight pen was large enough that subgroups of birds from capture sites could have formed and isolated from each other without being in proximity to others or interacting with others. Instead, our results were more likely the result of decisions the birds were making about their locations relative to others and the ways they interacted. Additionally, our results are consistent with reports of monk parakeet social behaviors in wild settings throughout their native and nonnative ranges (Bucher et al., 1991; Eberhard, 1998; South & Pruett-Jones, 2000).

Conclusions

We found that birds spatially associated with both familiar and stranger birds, but affiliatively interacted preferentially with familiar birds, although the stability of these patterns varied. While our results differed from our predictions, where we expected that birds would initially prefer familiar individuals across all behaviors, and that these preferences would diminish over time as strangers associated and gained familiarity, we also showed that even though birds interacted differently with strangers, affiliative relationships between birds who were initially strangers could and did form within our study period. Our results contribute to a broader understanding of monk parakeet social structure by providing additional insight into how the behavioral context and presence of strangers may affect social structure formation and stabilization. Understanding how monk parakeets develop and stabilize relationships is especially relevant given their status as one of the most abundant and widely distributed non-native parrot species (Uehling et al., 2019). Continued capture practices to facilitate the pet trade, accidental and intentional releases into non-native areas (Russello et al., 2008), and eradication efforts, like nest removal and individual capture (Avery et al., 2002), are likely to disrupt monk parakeet social dynamics and may cause social groups to collapse and novel social groups to form (Hobson et al., 2013). These results provide an important reference point for understanding the importance of social dynamics in other non-native parrot species like Indian ringneck (*Psittacula krameri*) and nanday parakeets (*Aratinga nenday*).

Overall, our results are generally consistent with research across a diverse range of taxa which demonstrate preferential associations with familiar conspecifics in different contexts (Gutmann et al., 2015; Keller & Reeve, 1998; Kohn et al., 2015; Prior et al., 2020a; Ripperger, Carter, Duda, Koelpin, Cassens, Rüdiger, et al., 2019; Tuliozi et al., 2018) but highlight the importance of considering several behaviors and across different temporal scales for complete understanding of the effect of familiarity. Without considering multiple behavioral contexts, researchers risk an incomplete understanding of social preferences and may underestimate the effect of familiarity on social decision-making processes. Aggregating behavioral data, while useful for identifying general trends, obscures temporal trends which could indicate a more complex or informative picture of the underlying dynamics.

Author contributions

CLO and EAH conceptualized the idea for the manuscript. CLO and AM performed the experiment and collected data. CLO analyzed the data and drafted the manuscript. EAH oversaw data collection and provided advice on data analyses. AM and EAH provided feedback on drafts of the manuscript. All authors edited and approved its final version.

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Competing interests

We declare we have no competing interests.

Data Availability

The datasets and plots generated and/or analyzed during the current study are available at 10.5281/zenodo.15609409

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