Familiarity with social partners influences affiliative interactions but not spatial associations

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ABSTRACT

To successfully navigate complex social environments, animals must manage their relationships with familiar group members and strangers introduced via fission-fusion or demographic processes by deciding who, how often, and when to interact. However, it is not clear how animals balance the risks and benefits of interacting with familiar and stranger conspecifics. We studied whether familiarity among group members affect the patterning and timing of spatial associations and affiliative interactions in a captive group of 22 monk parakeets (*Myiopsitta monachus*) captured from four geographically distinct sites. We tested whether familiar and stranger dyads differed in the presence, strength, and timing of spatial and affiliative relationships. We found that general patterns of spatial proximity between birds were unaffected by capture site. In contrast, all affiliative interactions, like allopreening and beak touching, occurred significantly more often among familiar birds compared to stranger dyads. These affiliative interaction networks were also more densely connected, but relationships were not always stronger among familiar birds compared to strangers. Familiar and stranger birds did not differ in the timing of initiation of spatial proximity, while most affiliative interactions among strangers occurred significantly later in the experiment compared to familiar birds. In contrast, we found that the familiar and stranger spatial networks were equally well-connected, but associations were stronger among familiar birds. Our results show that monk parakeets discriminate between familiar and unfamiliar birds and suggest that birds use their previous experiences to make affiliative social decisions. By investigating the effect of familiarity on spatial and affiliative interactions we gain a better understanding of how individuals manage the costs and benefits of interacting with unfamiliar individuals.

KEYWORDS: *AFFILIATIVE RELATIONSHIPS, PROXIMITY, FAMILIAR, NOVEL RELATIONSHIPS, PARROT, SOCIAL NETWORK*

INTRODUCTION

Group-living provides many benefits, but social groups often change in size and composition as individuals disperse to a new group or area and seek to form relationships or pair bonds with novel individuals, or strangers (Shizuka & Johnson, 2020; Silk et al., 2014). These intrinsically dynamic social environments require that individuals manage the presence and strength of preexisting relationships with group members and potential relationships with strangers, but balancing associations between familiars and strangers presents a trade-off that can affect reproductive success, health, and longevity (Archie et al., 2014; Cameron et al., 2009; Yang et al., 2017). How animals navigate this dilemma is not well understood, and we have limited quantitative information on how strangers initiate and develop relationships with each other.

Individuals may maintain strong stable relationships, or pair bonds, with a few partners that persist across multiple years (Bales et al., 2021), and these relationships can provide substantial benefits including enhanced longevity and reproductive success in birds, fish, and mammals (Archie et al., 2014; Cameron et al., 2009; Nowicki et al., 2018). By maintaining relationships with social partners, pairs develop familiarity or trust through repeated positive experiences (Carter et al., 2020; Sánchez-Macouzet et al., 2014; van de Pol et al., 2006). For example, familiar pairs may become more efficient or coordinated in behaviors like resource acquisition and defense (Nowicki et al., 2018), pair displays (Prior et al., 2020), and parental care (Griggio & Hoi, 2011; Sánchez-Macouzet et al., 2014). Familiarity with social partners can create a more stable or predictable social environment which can buffer individuals from negative effects of novel social environments or social instability (Cimarelli et al., 2021; Schaffner & Smith, 2005; Young et al., 2014). While maintaining familiar relationships minimizes the time and energy costs associated with searching for suitable mates, investing substantial time and energy into one another can be costly or even lethal (Blumstein et al., 2018; Weber et al., 2013; Yang et al., 2017) and could prevent animals from forming relationships with potentially higher quality partners.

Alternatively, maintaining relationships may not be feasible in social groups that experience high rates of turnover (due to immigration/emigration/births/deaths), or animals may disperse from their natal group to seek reproductive partners. In such cases, establishing relationships with novel individuals could provide increased social opportunity for high quality partners and mates (Kohn et al., 2015), increased access to social information (Aplin et al., 2012; Garg et al., 2022), or facilitate social stability (Lewis, 2008). Forming novel relationships may also function as a social bet-hedging strategy to minimize negative effects associated with losing any one social partner (Carter et al., 2017) or to maintain social network position (Firth et al., 2017). However, initiating and developing novel relationships can involve some level of risk. When first interacting with strangers, individuals may have minimal or unreliable information about other's threat level in case of aggression (Chaine et al., 2018), propensity to affiliate, or reliability as a social partner (Carter et al., 2020). Interacting with familiar and novel individuals includes costs and benefits, and to successfully navigate complex social environments, animals must decide who to interact with, how often, and when to initiate interactions with strangers.

Understanding when and how animals decide to associate with familiars and strangers can lend insight into animal social decision-making processes and clarify the importance of social history on informing future affiliative decisions (Schusterman et al., 2000; Taborsky & Oliveira, 2012). To identify how effectively animals balance relationships with familiars and strangers, quantitative assessments of spatial associations and affiliative interactions are necessary. A multimodal approach can provide a more nuanced understanding of the relative importance of different association types. Without considering several association types, researchers risk an incomplete understanding of social preferences and may underestimate the effect of familiarity on social interactions. Parrots (family: Psittaciformes) are a compelling avenue for exploring this relationship because despite their suspected cognitive and social complexity (Hobson et al., 2014; Luescher, 2006), we lack quantitative data to test fundamental assumptions about their socioecology. This gap limits opportunities for effective conservations strategies aimed at many species of parrots whose populations are declining or considered vulnerable, endangered, or critically endangered (Uehling et al., 2019; Vergara-Tabares et al., 2020).

We assessed how monk parakeets (*Myiopsitta monachus*) spatially associate and affiliatively interact with familiar and stranger birds to better understand how birds may balance the risks and benefits of navigating a novel social environment. Monk parakeets are a highly social parrot native to South America (Bucher et al., 1991; South & Pruett-Jones, 2000) although they have established breeding colonies globally (South & Pruett-Jones, 2000; Uehling et al., 2019). Throughout their native and introduced range, monk parakeets typically live in resident colonies where 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 often form strong affiliative bonds with 1-2 group members regardless of sex (Eberhard, 1998; Hobson et al., 2014). Neighboring monk parakeet colonies often temporarily fuse to forage resulting in large foraging flocks that may consist of up to hundreds of individuals (Bucher et al., 1991; Hobson et al., 2014; South & Pruett-Jones, 2000). These patterns mean that parakeets may regularly encounter novel social environments and are therefore an apt system to explore the effect of familiarity on relationship formation. Additionally, 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., 2023a) indicating that social history is important for future social decision-making.

Given 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 the presence, strength, and initiation of spatial associations and affiliative investments would be shaped by familiar/stranger relationship status. We created a novel social group of feral monk parakeets by introducing subgroups captured from four geographically distinct sites into a large flight pen. During the experiment, we recorded several behavioral types (two spatial associations and five affiliative interactions) that occurred between individuals from the same capture site (familiar) and from different capture sites (strangers). We predicted that birds from the same site would preferentially spatially associate with one another, and that all behaviors would be more common and more frequent among familiar dyads than stranger dyads. Similarly, we expected that familiar dyads would initiate associations earlier compared to stranger dyads. If there are preferential associations and differences between the presence, strength, and differences in timing of relationship initiation, then this would provide support for our hypothesis and suggest that monk parakeets differentiate between familiar and stranger birds potentially due to the risks and benefits of associating and interacting. Alternatively, birds may readily form novel relationships. In this case, we would assume that familiarity might not be a factor when deciding to associate and the risks of associating and interacting are relatively equal. Ultimately, our results will lend insight into how monk parakeets navigate complex social environments.

METHODS

Ethics statement

We declare we have no competing interests. All animal-related research activities were approved by the University of Cincinnati (IACUC protocol#AM02-19-11-19-01) and the USDA NWRC (Quality Assurance #3203)**.** The United States Department of Agriculture, Wildlife Services, National Wildlife Research Center (USDA WS NWRC) captured birds from southeast Florida. During experiments, observers were blind to the experimental bird's sex and capture site.

Bird capture sites and experimental social group

We performed experiments at the USDA, Florida Field Station, in Gainesville, FL, USA. Our experiments were performed in February 2021 with feral-caught monk parakeets (n = 22; 8 females and 14 males) from four geographically distinct capture sites across southeast Florida (Site 1: n = 5, Site 2: n = 6, Site 3: n = 7, and Site 4: n = 4). The average distance between capture sites was 16.06 km (range: 3.28 - 30.85 km). We treated birds 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 unfamiliar to one another because the minimum distance between our capture sites exceeded twice the reported dispersal distance (2.4 km). Our setup provided the opportunity for a maximum of 179 possible novel relationships and 52 familiar relationships. Monk parakeets are sexually monomorphic, and we did not know the sex of the birds prior to the experiment. Birds were genetically sexed prior to the start of the experiment.

To preserve unfamiliarity between birds from different sites, we quarantined groups of 2-3 birds from the same capture site for two weeks prior to the experiment following their capture. Quarantining birds was necessary to prevent the spread of infectious disease and to ensure birds were fit for experimentation. These pairs or trios were quarantined in 2 x 2 m cages in a covered outdoor aviary in which birds could be in physical contact with their cage mate(s), and visual and auditory contact with same-site individuals. Birds captured from different sites were visually separated, but all birds in the aviary were in vocal contact with each other during the quarantine period.

For individual identification, birds were given a uniquely numbered metal leg band. Additionally, birds were randomly assigned a unique three-color combination. To aid in identification during the experiment, the color ID was applied with nontoxic permanent markers (Sharpie, Inc.®) (Hobson et al. 2014) across each bird’s head, cheeks, and chest. Color marks remained conspicuous throughout the experiment.

To begin the experiment, we simultaneously released all birds in a large 2,025 m² semi-natural outdoor flight pen on April 5, 2021. The flight pen contained artificial and natural perches used for enrichment and shade. We marked the area with a grid using string on the ground to assist observers in identifying the locations of the birds (see details below). We observed the birds for 22 days, ending on April 26,

2021. During this time birds were allowed to interact freely and remained undisturbed (aside from daily husbandry and two observers recording interactions from blinds within the flight pen). Birds had constant access to food (seed mix provision) and water which were replaced daily, and birds were able to forage on grass within the flight pen. We began collecting proximity and social interaction data as soon as all birds were released into the flight pen (see details below). Daily observations took place between 08:00 and 19:00 by a total of four observers from three different blinds. To maximize the amount of data recorded, all observers collected data simultaneously, and breaks between observers were taken in shifts such that at minimum three observers were present.

Spatial and social data collection

During observation hours, we recorded seven behaviors to analyze spatial associations and affiliative interactions (Table 1). We examined patterns across multiple behaviors to capture aspects of flocking and affiliative relationships and because the tradeoff between forming a novel relationship and maintaining exclusively familiar relationships might vary depending on the social context or behavior (i.e., shared space or social grooming) (Carter et al., 2020; J. Silk et al., 1999). All interaction observations were recorded in real time directly onto iPads 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. To collect proximity associations, observers scanned the entire flight pen every five minutes and recorded which grid cell each bird was in, creating a “snapshot” of each bird’s X and Y coordinates within the flight pen. During data analysis, we calculated Euclidean distances between all identified birds for each scan. Any birds within three meters or less of each other were scored as in proximity. We chose three meters because it was less than the median (n = 4) Euclidean distance observed across scans and was consistent with past spatial association distances (Hobson et al. 2014). We used nearest neighbor associations to identify birds in peaceful proximity. Nearest neighbor associations were collected in the absence of social interactions where observers scanned the flight pen and recorded the identity of the closest bird within one meter for each bird.

We quantified five affiliative contact interactions: (1) s*houlder-to-shoulder* interactions, (2) *allopreening*, (3) *beak touching*, (4) *allofeeding*, and (5) *copulation* events (see Table 1). Affiliative interactions were recorded as they occurred using an all-occurrence sampling method (Altmann, 1974). These behaviors best reflect affiliative relationships among same and opposite sex monk parakeets in the wild and in captivity and are consistent with previous research with this species (Bucher et al., 1991; Eberhard, 1998; Hobson et al., 2014).

Table 1: Description of the seven behaviors observed.

Behavior	Description
Proximity	Shared space: birds found within a 3m radius of one another; Indicates flock membership
Nearest neighbor	Identity of the bird perched closest to the observed individual, within a minimum distance of 1m; Indicates spatial preference within a flock
Shoulder-to-shoulder	Two birds sitting in physical contact side by side
Allopreen	Two birds preen (groom) each other’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

Prior to data analysis, we filtered our data to include only positively identified individuals where the behavior was one of our seven behaviors of interest (Table 1). Because we had multiple observers and because some behaviors were sampled at different frequencies, we also filtered our data to include a maximum of one observation per dyad per behavior per 5-minute observation interval.

Statistical analyses

We performed all data analyses in R version 4.2.2 (R Core Team 2021). We used igraph (Csárdi et al., 2024) for network analyses and created figures using ggplot2 (Wickham 2016) and igraph.

We used social network analysis to quantify patterns of assortativity and to test for differences in the distribution and intensity of associations. We used permutation-based reference models, a common tool to analyze non-independent data like social interactions, to test for differences between observed patterns compared to those expected if familiar/stranger status was randomized (Croft et al., 2011; Hobson et al., 2021). Reference models are generated over thousands of iterations in which key features of the data are permuted while other aspects of the network structure are maintained. In this way, potential correlations between observed structure of the association data and the feature of interest are broken. A test statistic which captures the relationship of interest is calculated for each iteration of the reference model resulting in a distribution of test statistics. Comparisons can then be made to determine whether there are meaningful differences between the observed values of the test statistic and the permuted values by quantifying the proportion of permuted values that are more extreme than the observed (Farine & Carter, 2022; Hobson et al., 2021). Our reference models maintained all aspects of the network structure including the identity of the dyad, the behavior used, and the number of birds from each site. For each iteration (n = 10,000), we permuted the site each bird was captured from therefore randomizing the type of relationship (i.e., familiar or stranger) between dyads. We calculated *P*-values by quantifying the proportion of permuted values that were more extreme than the observed value in a one-tailed comparison. The observed coefficients were considered significantly different than the permuted coefficients if the observed value was less than 5% of the permuted coefficients. A result of $P = 0$ would indicate that 100% of permuted values were less extreme than the observed value (either all higher or all lower, depending on whether the observed value fell above or below the reference distribution).

Testing for preferential associations between familiar and stranger dyads

To examine whether birds preferentially associate with familiar conspecifics, we first created weighted and undirected networks for each behavior. Weighted networks, which consider the frequency of interactions among nodes, or birds, are more robust to sampling noise when calculating assortativity compared to binary networks which represent only the presence of associations (Farine, 2014). We then calculated assortativity coefficients, r_a, using the function assortativity_nominal() (Csárdi et al., 2024). This function returns a value ranging from negative one to one to indicate the degree of homophily, or the tendency for birds to associate with others with similar traits (i.e., other birds from the same site). Values close to one indicate that birds from the same site tend to associate, and values close to negative one indicate that birds from the same site tend not to associate. We constructed a permutation-based reference model to test for statistical significance of observed assortativity for each behavior. We quantified assortativity coefficients with the same function described above to identify the level of assortativity. We then compared the observed asortativity coefficients to those produced by each iteration of the permuted networks. We predicted that birds would preferentially associate across all behaviors by site, so we expected that observed assortativity coefficients for each behavior would be greater than the randomized relationships in the reference distribution.

Quantifying differences in the presence and strength of relationships

We then tested how familiarity may affect the presence of associations by first creating separate networks for stranger and familiar birds and for each behavior and calculating *density* for each network. Network density indicates the proportion of the total possible connections (edges) that were observed, and values range from zero to one. High density or a value near one would indicate a highly connected network in which birds interact 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 associate with a few possible social partners. To compare connectivity between familiar and stranger associations networks, we subtracted the density of the stranger network from the density of the familiar network. Values range from negative one to one. A positive difference would indicate that density among familiar dyads is greater than density among strangers, and a negative difference would indicate that density among strangers is greater than among familiar birds. A greater difference would indicate a larger discrepancy between the connectedness or familiar and stranger networks. We predicted network density for all behaviors among familiar dyads to be greater than that of stranger dyads, and we expected that observed differences in network density to be greater than the values produced by the reference model. We used the same reference model as before to permute capture sites of birds while maintaining all other aspects of network structure, and the differences in network density as our test statistic to test for meaningful differences between the observed values and values produced by the reference model.

Similarly, we tested how familiarity may affect the frequency of associations by quantifying *strength* for each network. Strength describes how frequently dyads interact by summing the weights of the edges that connect them. In our case, values can vary depending on the frequency of associations and interactions, but higher values indicate more associations and stronger relationships, and lower values indicate less associations and weaker relationships. We used Cohen's d from Welch's T-test to compare association strength between familiar and stranger dyads. We used the function cohensD() from the lsr package (v.0.5.1 Navarro 2015). Network strength served as the dependent variable and the independent variable was a binary distinction between 'familiar' or 'stranger'. Given that the birds were in captive conditions, all individuals were equally likely to be observed, and we did not have any sampling biases for individuals, sexes, or sites. This approach allowed us to incorporate the necessary constraints within the reference model that might otherwise need to be addressed with other statistical tools (Franks et al., 2021; Hart et al., 2022). We predicted association strengths to be greater among familiar dyads compared to strangers, so we expected observed Cohen's d values to be negative. We also expected that values produced by the reference model to be greater than the observed. We determined if the observed values were significantly different from the permuted values using a one-tailed comparison.

Testing for differences in the timing of relationship initiation

To test how familiarity may account for differences in relationship initiation, we identified the day that each behavior was initiated, or the first day behaviors were observed, among dyads over the course of the experiment. Because the data were not normally distributed, we used a one-tailed Mann-Whitney U test to test for significant differences between the median initiation days between familiar and strangers for each behavior. To quantify the magnitude of differences between familiar and strangers, we calculated the rank-biserial correlation (r_{bc}), the effect size of a Mann-Whitney U test, with the function wilcox_effsize() from the rstatix package (Midroit et al., 2021; Kassambara 2023). Rank-biserial correlation values range from zero to one. Coefficient values near zero would indicate a small effect, and values near one would indicate a large effect. We predicted that familiar dyads would initiate all behaviors earlier compared to strangers, and we expected that the observed rank-biserial correlation coefficients would be greater than the coefficients produced by the reference model.

We used the same framework as the reference model described above. However, this reference model permutes the raw data used to construct the network rather than the summarized network data itself. This is to maintain the date and time that the associations were observed. We determined if the observed coefficients were significantly different from the permuted coefficients using a one-tailed comparison.

RESULTS

We observed the experimental group comprised of 179 possible strangers 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. We observed over 16,500 spatial associations and affiliative interactions among familiar dyads, and over 23,000 among strangers.

Testing for preferential associations between familiar and stranger dyads

Assortativity coefficients (r_a) from weighted undirected networks ranged from -0.05 to 0.76. Proximity networks were slightly disassortative and were not significantly assorted by familiarity (r_a = -0.05, P = 1.00). This result is likely because proximity coefficients produced by the reference model were nearly the same as the observed because proximity networks were fully connected among familiar dyads, and nearly entirely connected among strangers (see next section for details on network connectivity). Although the observed nearest neighbor associations were slightly disassortative, we found that these networks were significantly more assortative by site than expected by chance (Fig. 2a-b; r_a = -0.04, P = 0.03). We found all dyads positively assorted by site for all affiliative behaviors and these were statistically significant. Of the affiliative networks, shoulder-to-shoulder and allopreening interactions were the least assortative (Fig. 2a-b; r_a = 0.28, P = 0.00; and r_a = 0.24, P = 0.00, respectively) meaning that dyads often but not always perched with or allopreened familiar birds. Assortativity coefficients for beak touching, allofeeding, and copulation interactions were very high (Fig. 2a-b; r_a = 0.58, P = 0.00; r_a = 0.76, P = 0.00; r_a = 0.59, P = 0.00) suggesting birds typically used these behaviors with familiar birds.

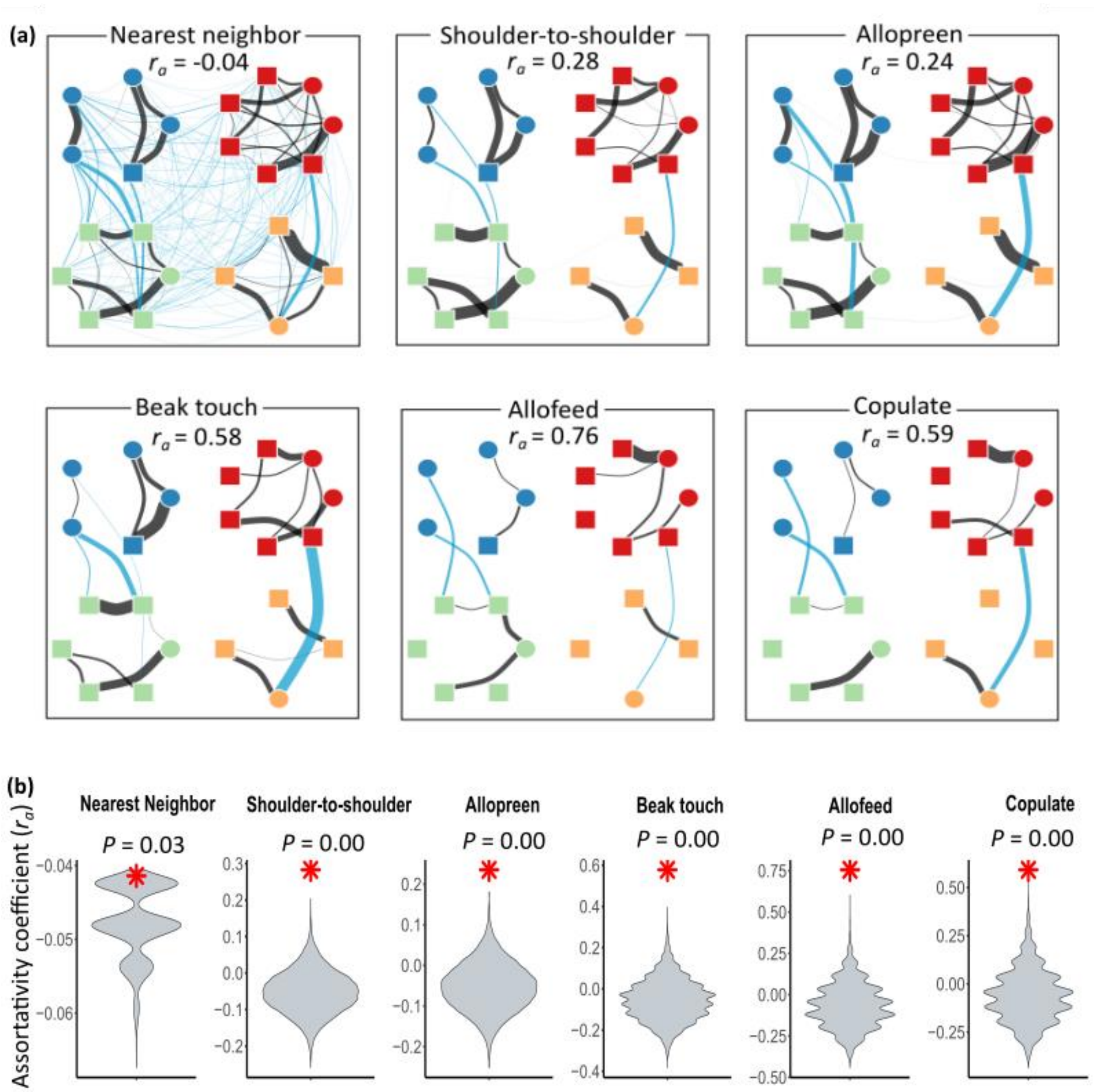

Figure 2: Networks of six behaviors showed differences between stranger and familiar relationships and several differences in assortativity across the entire study period. Panel a shows observed association networks for each behavior, where individuals are represented by colored nodes and are connected by an edge if one individual was ever observed behaving towards the other using one of the six behaviors. Node color represents capture site (blue = Site 1, green = Site 2, red = Site 3, and orange = Site 4). Node shape indicates sex (males = square and females = circle). Black edges represent associations between familiar birds, or birds from the same site. Blue edges represent associations between stranger birds, or birds from different sites. The width of the edge indicates association strength. The thicker the edge, the more pairs associated. Edge weights were scaled to the maximum edge weight per behavior. Panel b shows how observed values of assortativity for each behavior compared to values generated from random expectations. Observed values are indicated in red and significant values are indicated by an asterisk; randomized distributions are shaded in grey. See Figure 3 for network density measures.

Quantifying differences in the presence and strength of relationships

Observed differences in network density were equal to or greater than zero for all behaviors, indicating that familiar networks were equally, or more densely connected compared to stranger networks. We found no significant difference in network density between familiar and stranger proximity networks, as both networks were completely connected (difference = 0.0; $P = 1.00$). Nearest neighbor density between strangers and familiar birds also did not significantly differ (Figure 3a-b, difference = 0.02; $P = 0.35$). In contrast, the affiliative networks between familiar dyads were more densely connected than among stranger dyads and the magnitude of this difference was significant (Fig. 3a-b, shoulder-to-shoulder: difference = 0.41; $P = 0.00$; allopreening: difference = 0.34, $P < 0.001$; beak touching: difference = 0.33, $P = 0.00$; allofeeding: difference = 0.25, $P = 0.00$; and copulation: difference = 0.20, $P = 0.00$).

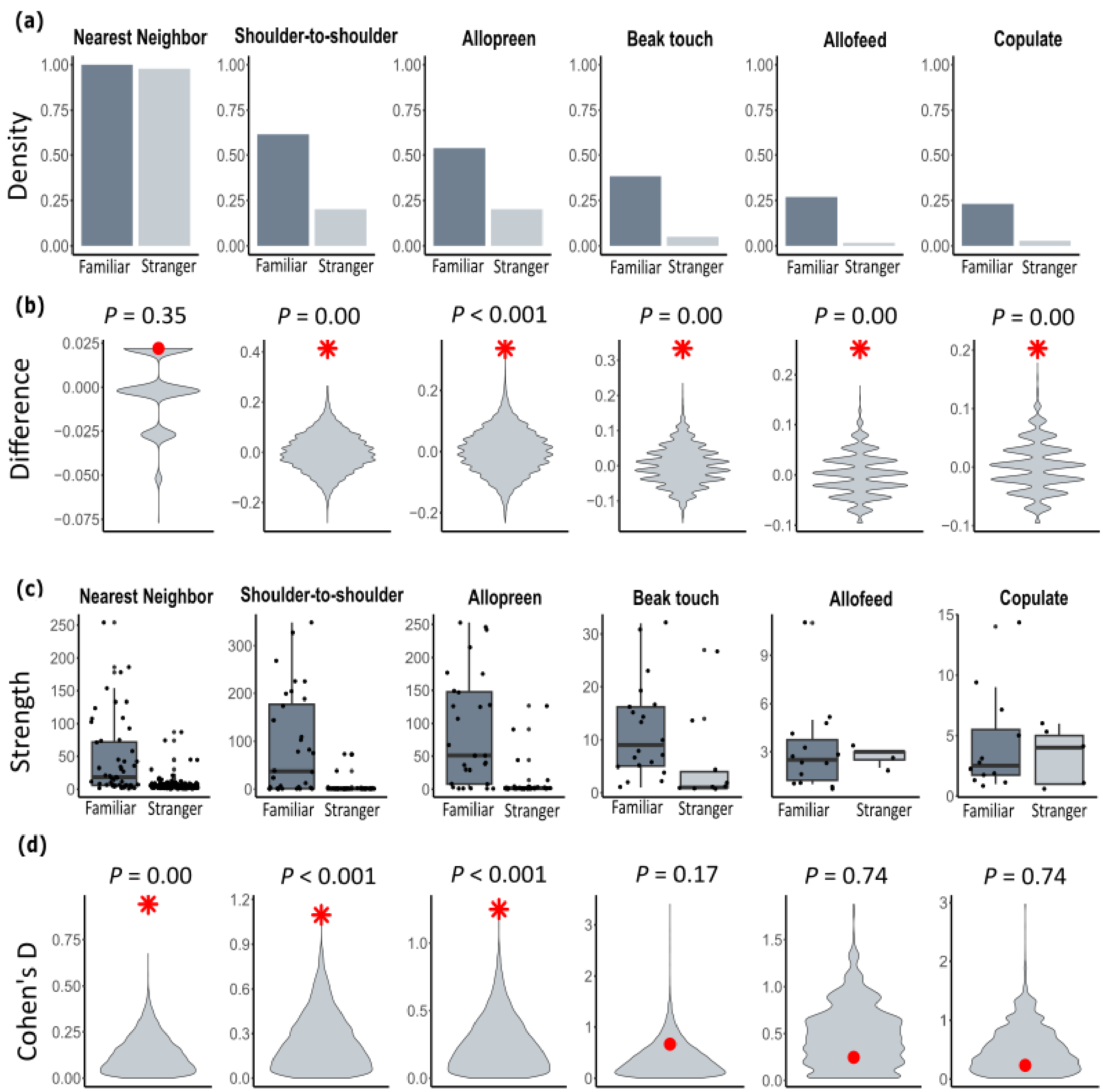

Figure 3: Together the plots show differences in the presence and strength of some but not all behaviors between familiar and stranger dyads. Panel a shows the observed density of familiar and stranger networks for each behavior, and panel b shows the observed difference in network density (indicated in red) compared to the distribution of differences produced by the reference model (shaded in grey). Panel c shows observed association strengths among familiar and stranger dyads for each behavior. Panel d shows how the observed Cohen’s d value, or effect sizes, (indicated in red and significant values are indicated by an asterisk) compared to the distribution in values produced by the reference model for each behavior (shaded in grey).

Cohen’s d effect sizes ranged from 0.24 to 1.25, and the observed association and interaction strength between familiar and stranger dyads are shown in figure 3c and 3d. Proximity and nearest neighbor associations were significantly stronger among familiar birds compared to strangers (Proximity: Cohen's d = 1.10, P = 0.00; and Figures 3c-d; Nearest neighbor: Cohen's d = 0.94, P = 0.00). Similarly, shoulder-to-shoulder and allopreening interactions were significantly stronger among familiar birds (Fig. 3c-d; Cohen's d = 1.10, $P < 0.001$; Cohen's d = 1.25, $P < 0.001$, respectively) indicating a large effect of familiarity on relationship strength. Beak touching, allofeeding, and copulation interactions were smaller indicating a smaller effect of familiarity on relationship strength but were not significant (Fig. 3c-d; Cohen's d = 0.67, P = 0.17; Cohen's d = 0.25, P = 0.74; and Cohen's d = 0.24, P = 0.74, respectively).

Testing for differences in the timing of relationship initiation

All proximity associations for both familiar and stranger dyads were initiated within the first two days of the experiment (Fig 4a), and we did not find a significant difference between days (r_{bc} = 0.34; P = 0.08). We observed more variability in the days nearest neighbor associations were initiated. The median initiation day occurred on day one (range = 1-15) among familiar dyads and day two among strangers (range = 1-17; Fig. 4a), and we found significant differences between days nearest neighbor associations were initiated (Fig. 4b; r_{bc} = 0.25; P = 0.00). Similarly, we found significant differences between initiation days for shoulder-to-shoulder and allopreening interactions (Fig. 5b; Shoulder-to-shoulder: r_{bc} = 0.42; P = 0.00; Allopreen: r_{bc} = 0.46; P = 0.00) which occurred four days earlier among familiar dyads compared to strangers for both behaviors (Fig. 4a). Beak touching, allofeeding, and copulation interactions were initiated much later in the experiment, and were initiated 4.5, 15.5, and 2.5 days (median) earlier among familiar dyads compared to strangers (Fig. 4a). We found significant differences between the days beak touching and allofeeding interactions were initiated (Fig. 4b; Beak touch: r_{bc} = 0.39; P = 0.03; Allofeed: r_{bc} = 0.52; P = 0.02). However, we did not find a significant difference between copulation interactions (Fig. 4b; r_{bc} = 0.34; P = 0.20).

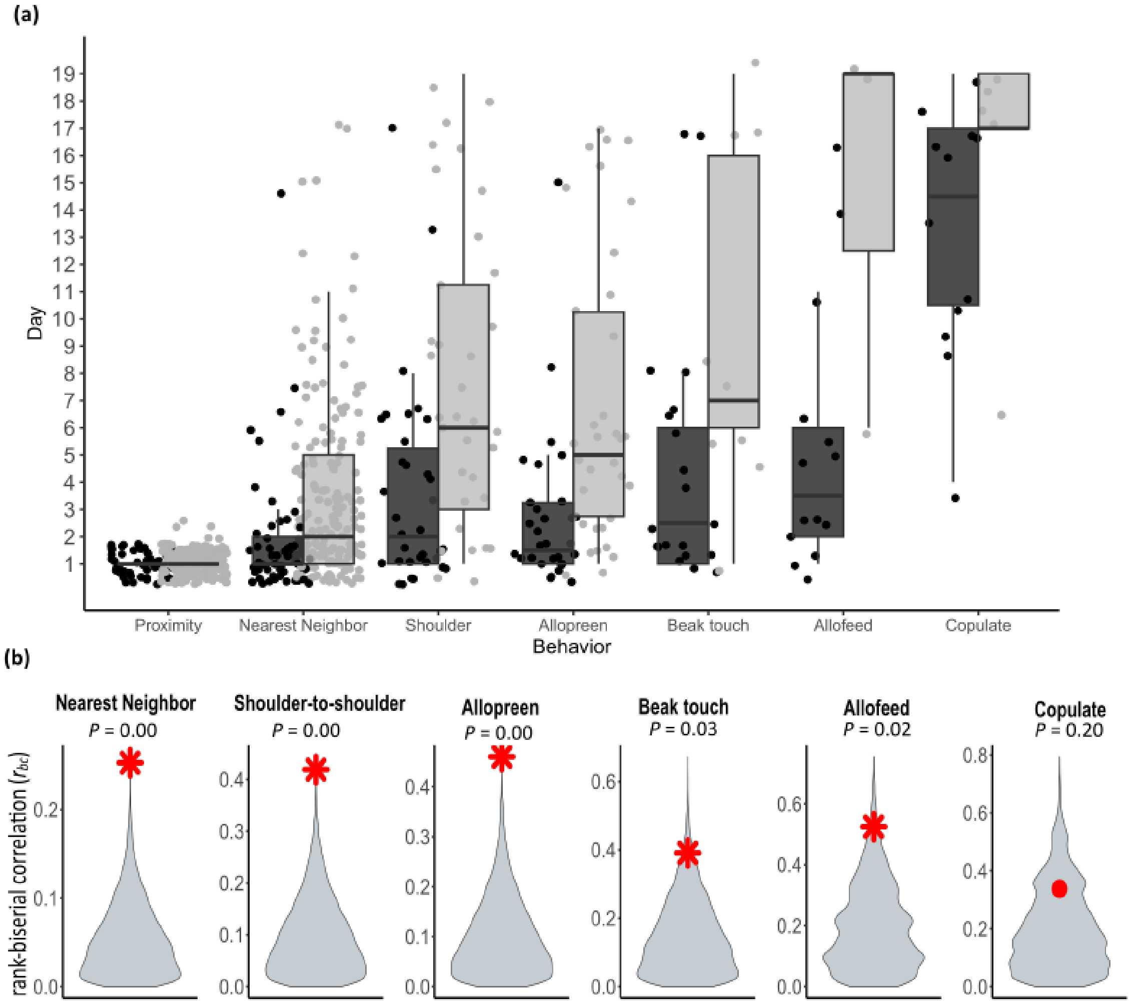

Figure 4: The days dyads were observed initiating behaviors were different between stranger and familiars. Panel a shows the days familiar and stranger dyads were observed initiating behaviors throughout the entire study. Panel b shows how observed rank biserial coefficients (indicated in red and significant results are indicated by an asterisk) for each behavior compared to coefficients generated from random expectations. Randomized distributions are shaded in grey.

DISCUSSION

Using a novel social group of monk parakeets, we examined whether familiar and stranger dyads differed in the presence, strength, and timing of spatial associations and affiliative interactions. We found that general patterns of spatial proximity between birds were unaffected by capture site, and familiar and stranger birds did not differ in the timing of initiation of spatial proximity. In contrast, all affiliative interactions, like allopreening and beak touching, occurred significantly more often among familiar birds compared to stranger dyads. These affiliative interaction networks were also more densely connected, but relationships were not always stronger among familiar birds compared to strangers. Most affiliative interactions among strangers occurred significantly later in the experiment compared to familiar birds. In contrast, we found that the familiar and stranger proximity networks were equally well-connected, but associations were stronger among familiar birds. Although our results for spatial associations and affiliative interactions differ, the observed patterns provide evidence that monk parakeets differentiated between familiar and unfamiliar birds in their affiliative interactions and indicate that known strangers could form affiliative relationships relatively quickly. 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.

Strangers readily formed flocks but stayed close to familiar birds

We found that birds were not in spatial proximity by site more than expected by chance. Nearest neighbor associations were significantly assortative by site. Proximity, but not nearest neighbor associations were initiated around the same time for familiar and stranger dyads. Spatial networks were equally well-connected among familiar and stranger dyads but were stronger among familiar dyads. Taken together, these results indicate that familiar and stranger birds readily formed flocks but maintained closer proximity to familiar birds. This result is 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., 2014; South & Pruett-Jones, 2000).

Although the spatial results were contrary to our prediction, we do not think that proximity relationships are necessarily indicative of familiarity between birds from different capture sites. We suspect that the potential benefits of sharing space outweigh the risks of associating with strangers. Maintaining spatial proximity is a relatively low-risk, low-investment way for conspecifics to increase vigilance and predator awareness or to increase foraging efficiency (Sorato et al., 2012; South & Pruett-Jones, 2000; van der Marel et al., 2019). Playback experiments in a captive group of monk parakeets indicate that sharing space may beneficial for predator avoidance (Estien et al., 2020). Additionally, by sharing space with strangers monk parakeets may assess individual identity through unique vocal signatures (Smeele et al., 2023; Smith-Vidaurre et al., 2020) or conspecific's fighting ability (Beltrão et al., 2023; Hobson & DeDeo, 2015; van der Marel et al., 2023b) while minimizing the risk of receiving aggression and maximizing the amount of time to flee or prepare for defense if rejected (Narizano & Carter, 2020; Silk et al., 1996). Social perturbation experiments in captive groups demonstrated that birds can infer the rank of others though observing fights among group mates and use previous experiences with group mates to inform future agonistic decisions (Hobson et al., 2014; Hobson & DeDeo, 2015; van der Marel et al., 2023). Additionally, proximity may offer the opportunity to asses conspecific's suitability as an affiliative partner (Carter et al., 2020).

Distances between capture sites were close enough for birds to travel (Dawson Pell et al., 2024), so it is possible birds from different capture sites could have encountered one another while foraging. However, birds would not need to travel far from their capture site to access food resources or nesting material because each capture site was located near a park or agricultural field and a body of water. Additionally, to access mutual foraging patches, birds would need to cross sites separated by urban-suburban areas and highways which may be difficult. Genetic evidence suggests that long-distance dispersal ranging from 10 – 100 km is possible in monk parakeets (Borray et al., 2023; Gonçalves da Silva et al., 2010). More research is needed to determine how typical this pattern is and to assess noise in samples. Although we cannot be certain that birds from different capture sites had not encountered each other, our results suggest that birds discriminate between same site and different site. Future research is needed to clarify how familiarity with social partners shapes affiliative social decisions.

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

Shoulder-to-shoulder and allopreening interactions were the only behaviors to match our predictions. Unlike the other affiliative contact behavior, shoulder-to-shoulder and allopreening interactions were more common among familiar birds, were stronger and were initiated earlier among familiar dyads. Like other affiliative contact behaviors, strangers may delay initiating shoulder-to-shoulder contact or allopreening because they are riskier and require some investment to the actor. Similarly, the presence and strength of these relationships initiated early in the experiment among familiar birds could provide additional support that affiliative relationships from birds from the same capture site maintained their relationships post-release, but we cannot be certain. Unlike beak touching, allofeeding, and copulation, perching shoulder-to-shoulder and allopreening group mates likely do not require as high of an investment but still require contact, so there is some risk involved. We hypothesize that these behaviors may be important "transitionary" behaviors as novel relationships develop. For example, female common vampire bats (*Desmodus rotundus*) test the waters with potential cooperative partners before escalating their relationship by sharing blood meals (Carter et al., 2020) and play among male Verreaux's sifaka (*Propithecus verreauxi*) is used to initiate social grooming relationships with unfamiliar males (Antonacci et al., 2010). However, further research on the order and timing behaviors are initiated among strangers is needed to clarify how behaviors are used to establish familiarity during relationship formation.

As predicted, we found that all affiliative interaction networks were assortative by site and were more densely connected among familiar birds compared to strangers. We found that shoulder-to-shoulder and allopreening, but not beak touching, allofeeding, or copulation interactions, were stronger among familiar birds. All affiliative behaviors, except for copulation, were initiated earlier among familiar birds compared to strangers. These results indicate that birds tended to affiliate with familiar partners but could form strong novel relationships relatively quickly. We suspect that affiliative interactions, like beak touching, allofeeding or copulating, are a relatively higher investment to dyads and are also riskier for dyads to initiate compared to sharing space. Allofeeding, for example, results in a direct nutritional cost to the actor and is therefore particularly costly if the allofeeding is not reciprocated (Carter et al., 2020; de Kort et al., 2006). These behaviors could be particularly risky for strangers to initiate and may be the reason this behavior occurred later among stranger than familiar dyads. Affiliative contact behaviors initiated relatively early in the experiment among familiar birds could indicate that previously established relationships prior to experimentation might have remained intact following release into the flight pen (Ripperger et al., 2019). However, we cannot be sure about the experimental birds' social relationships prior to our experiment. It is interesting that these high-risk, high-investment behaviors among strangers were often as strong as familiar dyads and that they were initiated around the same time. Similarities between the strength and timing of these behaviors could suggest that strangers can develop familiarity with affiliative partners relationships quickly as is the case in other species like zebra finches (*Taeniopygia castanotis*) (Svec et al., 2009) and guppies (*Poecilia reticulata*) (Griffiths & Magurran, 1997). A similar captive experiment with monk parakeets also found that monk parakeet affiliative relationships can develop quickly (even among same sex pairs); however, this study was conducted with long-term captive resident birds with unknown past social histories prior to their capture, and it was unclear if there were familiar/stranger relationships (Hobson et al., 2014). Alternatively, similarities between the strength and timing of affiliative interactions could indicate that birds may have needed time to adjust to their new environment and assess whether it was safe or suitable for raising offspring (Barclay, 1988). These two possibilities are not mutually exclusive.

In summary, we expected that birds would preferentially associate with familiar individuals across all behaviors. What we found was that birds spatially associated with both familiar and stranger birds, but affiliatively interacted preferentially with familiar birds. Our results provide support that birds from different capture sites were likely unfamiliar with each other. 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. While spatial mixing gives strangers the opportunity to socialize, not all chose to affiliate. However, some strangers developed affiliative relationships relatively quickly. The differences in patterns and timing of distinct association types between stranger and familiar birds suggest that familiarity with group members is likely important in affiliative social decision making, and that familiarity could be gained quickly. Our results indicate that the tradeoff of associating with large groups and the tradeoffs of associating with individuals varies and interacting with strangers may be risky in some social contexts, specifically those that require physical contact or an investment of time or energy. We do not think these results are an artifact of captive conditions (Webster & Rutz, 2020), but rather the result of decisions the birds were making about their locations relative to others and the ways they interacted. Future work should investigate how familiarity is gained during novel relationship formation and development.

Overall, our results are consistent with research across a diverse range of taxa which demonstrate preferential association with familiar conspecifics in different contexts (Gutmann et al., 2015; Keller & Reeve, 1998; Kohn et al., 2015; Prior et al., 2020; Ripperger et al., 2019; Tuliozi et al., 2018). Our experiment and analysis with monk parakeets provide an important reference point for understanding variation in parrot socioecology. Our results lend insight into how social behavior may influence effective conservation management practices including relocations, reintroductions, and the development of captive breeding programs that prioritize social welfare (Aydinonat et al., 2014; Berger-Tal et al., 2011; Greggor et al., 2016; Snijders et al., 2017). Without this knowledge, we cannot fully understand the social factors affecting species' vulnerability or resilience to environmental changes like human-induced climate change, urbanization, and deforestation.

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.

ACKNOWLEDGEMENTS

The research was supported in part by the US Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center. We thank the USDA staff, particularly Danyelle Sherman, Palmer Harrell, Eric Tillman, and John Humphrey for their help with animal care and support during experiments. We also would like to thank Xavier Francis and Cesar O. Estien for helping collect data during experiments, and Xavier Francis, Chelsea Carminito, and Sanjay Prasher for helpful feedback during data analysis. We acknowledge our fieldwork was conducted on the unceded land of the Seminole and Timucua people, and analyses and writing took place on the native homeland of the Delaware, Miami, and Shawnee tribes.

FUNDING

CLO and EAH were supported by NSF CAREER grant (#223909), and AM was funded a FONDECYT postdoctoral fellowship (#3220742).

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