

The effect of social context and social scale on the perception of relationships in monk parakeets

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Abstract Social relationships formed within a network of interacting group members can have a profound impact on an individual's behavior and fitness. However, we have little understanding of how individuals perceive their relationships and how this perception relates to our external measures of interactions. We investigated the perception of affiliative and agonistic relationships at both the dyadic and emergent social levels in two captive groups of monk parakeets (*Myiopsitta monachus*, $n = 21$ and 19) using social network analysis and playback experiments. At the dyadic social scale, individuals directed less aggression towards their strong affiliative partners and more aggression towards non-partner neighbors. At the emergent social scale, there was no association between relationships in different social contexts and an individual's dominance rank did not correlate with its popularity rank. Playback response patterns were mainly driven by relationships in affiliative social contexts at the dyadic scale. In both groups, individual responses to playback experiments were significantly affected by strong affiliative relationships at the dyadic social scale, albeit in different directions in the two groups. Response patterns were also affected by affiliative relationships at the emergent social scale, but only in one of the two groups. Within affiliative relationships, those at the dyadic social scale were perceived by individuals in both groups, but those at the emergent social scale only affected responses in one group. These results provide preliminary evidence that relationships in affiliative social contexts may be perceived as more important than agonistic relationships in captive monk parakeet groups. Our approach could be used in a wide range of social species and comparative analyses could provide important insight into how individuals perceive relationships across social contexts and social scales [*Current Zoology* 61 (1): 55–69, 2015].

Keywords Affiliative, Agonistic, Dominance, Eigenvector centrality, Emergent social property, *Myiopsitta monachus*, Parrot, Popularity, Rank, Social network analysis

The presence, type, and strength of an individual's social relationships can have profound effects on its behavior and fitness. Social relationships can form and operate within different social contexts and on different social scales. Relationships in different social contexts can form as some individuals interact in an affiliative context, such as grooming each other or sharing food, while others interact in an agonistic context, such as fighting with each other. Relationships within affiliative and agonistic social contexts can also form and operate on different social scales. Dyadic social relationships are those built from direct pairwise interactions or associations between two specific individuals (Hinde, 1976a; Hinde, 1976b), such as the affiliative relationships between females seen in many primate species (Seyfarth, 1977; Silk et al., 2003; Silk et al., 2009). Emergent social properties are also derived from interactions among

individuals, but develop at a more global level through all the direct and indirect interactions among individuals in the entire group, such as when many pairwise aggression events contribute to the formation of a group-level dominance hierarchy within which each individual holds a dominance rank (Sawyer, 2005; Bradbury and Vehrencamp, 2014). This rank becomes an emergent social attribute of the individual, and even individuals that did not interact can be referred to in terms of difference in rank.

The social context and social scale in which relationships form and operate can affect the types of benefits an individual gains from its social network. For example, stable affiliative relationships improve infant survival in female baboons (*Papio cynocephalus*, Silk et al., 2009), and associations with group members increase access to essential resources in herds of Grevy's

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zebra (*Equus grevyi*, Sundaresan et al., 2007). Female baboons and zebras each form social relationships within their groups based on direct interactions at a dyadic scale and it is through the strength of these affiliative dyadic relationships that participants benefit. In many primate groups, winning agonistic interactions and gaining dominance in a group allows males to monopolize mating opportunities and increase their long-term reproductive success (Kutsukake and Nunn, 2006). In this case, male aggression at the dyadic scale contributes to dominance status, which emerges from the entirety of the interaction history within the whole group. Males are able to monopolize access to mating opportunities through the emergent social property of dominance. In social birds such as manakins (*Chiroxiphia linearis* and *Pipra flicauda*), affiliative relationships among males that are formed at the dyadic social scale contribute to each individual's centrality in its social network at the emergent scale, and males that achieve higher centrality have higher success (McDonald, 2007; Ryder et al., 2008).

Despite these recent insights into the benefits of relationships in different social contexts and social scales, we have a limited understanding of how individuals perceive their relationships (Barrett and Henzi, 2002). Evaluating relationship perception critically depends on the underlying information used to quantify the dyadic and emergent social relationships. Network analysis is a tool that allows quantification and comparison of relationships across social contexts, such as affiliative and agonistic relationships, and across social scales, from dyadic relationships to emergent social properties (de Silva et al., 2011; Brush et al., 2013; Hobson et al., 2013; Pinter-Wollman et al., 2014; Bradbury and Vehrencamp, 2014). A researcher equipped with sophisticated analytical tools can use observed interactions to quantify the presence and strength of relationships among individuals across different social contexts or social scales. However, if the quantification of the relationship is not well correlated with the animal's perception of the presence or importance of its ties, dyadic network metrics and emergent social properties may fail to accurately predict individual behavior, social investment patterns, and the role that relationships play in fitness outcomes.

Audio playback is one potential method for evaluating how individuals perceive ties. In playback experiments, test subjects are presented with acoustic communication signals from other individuals and then aspects of the response, such as the response speed or

strength, are quantified. These responses can then be examined for associations with different types of relationships, allowing researchers to infer how an individual perceives the relative importance of different types of relationships with particular individuals. Playback experiments are widely used in animal behavior studies to determine whether individuals can discriminate among categories of calls. For example, playbacks have helped establish that animals preferentially respond to categories of individuals, and are able to discriminate between kin and non-kin, same-dialect and foreign dialect, associates and strangers, and mates and non-mates (Wanker et al., 1998; Wright and Dorin, 2001; Buhrman-Deever et al., 2008; Berg et al., 2011). Playback experiments have also established that emergent social relationships, such as dominance rank, are recognized by individuals in several primate species (Silk, 1999; Bergman et al., 2003; Kitchen et al., 2005; Schino et al., 2006). However, to our knowledge, playbacks have not been used to determine whether there are differences in the response patterns across both affiliative and agonistic social contexts and dyadic and emergent social scales or to evaluate how individuals perceive the relative importance of different types of social relationships.

We used a combination of network analysis, network visualization, and playback experiments to assess the perception of social relationships in the monk parakeet *Myiopsitta monachus* across social contexts and social scales. The monk parakeet nests colonially, often in communal structures, flocks undergo frequent fissions and fusions, and groups exhibit complex social structure (Eberhard, 1998; Spreyer and Bucher, 1998; Hobson et al., 2013; Hobson et al., 2014). Previous work has demonstrated that monk parakeets form and maintain social relationships at the dyadic scale, across both affiliative and agonistic social contexts (Hobson et al., 2013), and that individuals attain a dominance rank at the emergent social scale (Hobson et al., 2014). Here, we expand on our previous research to understand how individuals differentially respond to dyadic and emergent relationships across affiliative and agonistic social contexts.

For this study, we define the 'social context' of relationships as affiliative (based on peaceful proximity) and agonistic (based on aggressive events). We describe each individual's most preferred affiliative associate(s) as 'partners' rather than 'mates' because some of the strongest associations occurred outside of a breeding or pairbond context (i.e. between two males that were affiliative but did not exhibit courtship behaviors to one

another) and a few individuals had strong partnerships with more than one individual (Group 2 contained two triads that strongly interrelated, (Hobson et al., 2014)). We describe weaker associations as ‘non-partner’ relationships. We define the ‘social scale’ of relationships as dyadic (pairwise relationships between two individuals) and emergent (social attributes that summarize each individual’s societal position within the group). We define rank as an individual emergent attribute that reflects that individual’s direct and indirect interactions within the group in agonistic and affiliative contexts, with dominance rank based on patterns of aggression and popularity rank based on patterns of peaceful proximity.

The goals of this study were to (1) understand the association between affiliative and agonistic social relationships at both dyadic and emergent social scales, (2) develop a network visualization method that integrates across dyadic and emergent social scales to facilitate comparison between social contexts, (3) test whether responses to playback stimulus calls could be predicted by social context or social scale of the relationships, and (4) use playback response patterns to infer how individuals perceived different types of social relationships.

1 Materials and Methods

1.1 Study site & population

This study was conducted with a population of captive monk parakeets housed at the Florida Field Station of the USDA National Wildlife Research Center in Gainesville, Florida, from June through August, 2008. Individuals were given unique facial marks using permanent nontoxic pens (Sharpie, Inc.®) to facilitate individual identification and then randomly allocated to two replicate social groups (Group 1 $n = 21$; Group 2 $n = 19$; marks did not measurably affect interactions, unpub. data). Each group was introduced sequentially into a large 2,025 m² outdoor semi-natural flight pen that was visibly delineated into approximately 10 m² quadrats to facilitate collection of spatial location data. Each group occupied the flight pen for 24 days (Group 1: 14 June–07 July; Group 2: 08–31 July). All activities conducted during this study were approved by New Mexico State University Animal Care and Use Committee protocol #2006-027 (additional details available in (Hobson et al., 2013; Hobson et al., 2014)).

1.2 Observation methods & data restrictions

Observations of social behavior were made from blinds by 1 to 4 observers between 07:00 and 19:00 using a mix of scan and all-occurrence sampling methods (Whitehead, 2008; also see Hobson et al., 2013;

Hobson et al., 2014). In this study, we focused on observations of directed aggression and affiliative nearest neighbor identities. Using all-occurrence sampling, we recorded the identities of individuals involved in unidirectional dyadic aggression events, in which one individual physically supplanted or displaced another individual, to determine the winner (aggressor) and the loser (target of aggression) for each interaction (as in Hobson et al., 2014). Using scan sampling, we completed a scan at least every 10 min that identified the location of each individual within the flight pen, and recorded the identities of each individual’s nearest neighbor within a single quadrat (individuals alone in a quadrat had no nearest neighbors).

For this study, we restricted the affiliation and aggression data to periods following relationship stabilization. For aggressive events, we restricted our aggression data to include only the final 3 weeks of observations for each replicate group because previous results showed that aggression patterns stabilized in both groups following the first week of interactions (Hobson et al., 2013; unpublished data). For affiliative nearest neighbor observations, temporal data restrictions were not necessary because nearest neighbor dyadic tie strength stabilized quickly within the first days of group occupancy in the flight pen (Hobson et al., 2013).

1.3 Quantification of dyadic social relationships

We quantified dyadic social relationship strength in affiliative and agonistic social contexts using our observations of aggression and nearest neighbors. Both aggression events and nearest neighbor observations could only occur when individuals were in spatial proximity. For aggression networks, we used observations of aggressive events to determine the proportion of total aggression each individual directed towards each other individual. We used observations of nearest neighbors to determine affiliative tie strength. Grooming and proximity are often used as proxies to determine affiliative relationship strength (Von Rohr et al., 2012); because monk parakeets are highly selective in their allopreening, and generally groom only their partners (Hobson et al., 2014), we focused on close spatial proximity between neighbors to estimate affiliative association strength. We determined which individual was nearest to each focal individual within the same quadrat. These observations resulted in directional measures of nearest neighbors, because individuals were not always nearest to each other (individual A could be nearest B from the perspective of B, even though individual B is nearest C from the perspective of C). We used only nonaggressive

observations of nearest neighbors (peaceful proximity) to determine the proportion of observations for which each individual was nearest to each of its potential social associates.

We constructed an aggression network and an affiliation network for each of the two replicate groups. These networks were weighted, directed, and asymmetric, and relationship strength between any two individuals reflected the proportion of an individual's total affiliative or agonistic effort directed at each other individual in the group. To determine how relationships at the dyadic social scale were correlated across social contexts, we correlated aggression proportion and neighbor proportion using the Quadratic Assignment Procedure (QAP) in the program UCInet 6.519 (Borgatti et al., 2002; 10,000 replicates).

1.4 Quantification of emergent social properties

We quantified two emergent social properties, dominance and popularity, by measuring each individual's centrality within agonistic and affiliative networks. Here, we define 'dominance' and 'popularity' as emergent social properties based on an individual's centrality in agonistic networks and affiliative networks, respectively. We quantified dominance and popularity using eigenvector centrality, which determines an individual's position within a social group through a recursive process that uses both direct and indirect dyadic interactions (Bonacich, 1987; Newman, 2001; Newman, 2004; Bonacich, 2007). Eigenvector centrality is one of the primary algorithms for determining consensus beliefs such as rank within a network (Flack and Krakauer, 2006; Brush et al., 2013). We used the matrices of counts of observations of aggression and nearest neighbors for all individuals in each of the two groups. We restricted the neighbor data to exclude observations where an individual was nearest neighbors to its primary partner (or partners, in the case of two closely associated triads in Group 2), because previous results showed that the pair is the fundamental unit of social structure (Hobson et al., 2014). Including only observations of non-partner neighbors allowed us to focus on popularity among non-partnered individuals, which better reflected an individual's emergent popularity.

None of these matrices contained completely isolated individuals. We normalized the count matrices to reflect probabilities of interactions and added a very small regularizing term (10^{-12}) to ensure that all individuals had a nonzero probability of both acting and receiving an aggression or neighbor. We used these transition matrices to calculate eigenvector centrality in the R pack-

age igrph for directed and weighted ties (Csardi and Nepusz, 2006). This analysis provided a continuous measure of dominance and popularity centrality and allowed us to differentiate between adjacently-ranked individuals that had similar levels of dominance or popularity centrality versus those which exhibited larger differences in centrality measures.

We used these centrality measures to determine the rank order of individuals for both dominance and popularity. For dominance, centrality measures were lowest for the highest-ranked individuals: an individual with a high dominance centrality was considered a low-ranked subordinate while an individual with a low dominance centrality was high-ranked as a dominant individual. For popularity, centrality measures were highest for the highest-ranked individuals, as these were often the nearest neighbor for many other individuals. Within Groups 1 and 2, we investigated the association between these emergent social properties by testing the correlation between an individual's dominance rank and popularity rank (Spearman rank correlation test, R 3.1.1, R Core Team 2014). We expected that if dominance rank was positively associated with popularity rank, individuals that attained high dominance would also be most popular.

1.5 Attribute-ordered network visualization

Patterns among different types of networks can be visually compared by plotting connections among individuals in network graphs. Network graph layout is a multiobjective optimization problem, where many methods optimize for aesthetic graphs that minimize edge crossings and maximize symmetry (Coleman and Parker, 1996; Purchase, 2000). However, these methods are often inherently unpredictable, inconsistent, lack perceptual uniformity, and result in graphs that resemble "hairballs" that are difficult to interpret or compare (Krzywinski et al., 2012). Many popular layout methods are especially ineffective at plotting dense, highly-connected networks with many bi-directional weighted ties. Emergent social properties may be included in network diagrams through varying node size with individual attribute, but this method cannot effectively depict ordered attributes in a way that is easily comparable across graphs. Here, we develop a new network visualization method, "attribute-ordered networks", inspired by the hive plot (Krzywinski et al., 2012) and arc diagram (Wattenberg, 2002) layout methods.

We designed our attribute-ordered network layout with the goal of plotting weighted bi-directional asymmetric association networks along with attribute-ordered individual attributes in a manner that facilitated

comparison of the same set of individuals across different social contexts. We plotted three attribute-ordered networks for each of our two replicate groups: aggression-dominance (Fig.1A, 2A), affiliation-popularity (Fig.1B, 2B), and response-response strength (Fig.1C, 2C).

1.6 Call recording and processing

We recorded contact calls from all individuals to use as the auditory stimulus during playback trials. We focused on these calls because parrots are thought to use contact calls to maintain or regain contact with group members (Vehrencamp et al., 2003; Balsby and Bradbury, 2009; Scarl and Bradbury, 2009; Balsby and Adams, 2011; Balsby et al., 2012). Although we do not currently have data on whether monk parakeets can recognize individuals by contact call, previous work in other parrot species has shown that contact calls are individually recognizable and that individuals respond preferentially to the calls from specific associates (Brown

et al., 1988; Wanker et al., 1998; Buhman-Deever et al., 2008; Balsby and Adams, 2011; Berg et al., 2011).

We recorded calls from all individuals after completion of social observation in the flight pen: individuals in Group 1 were recorded on 08–09 July 2008 and Group 2 during 03–06 August 2008. Individuals were isolated in small groups in an open-walled building visually separated from the rest of the flock for vocal recording. Vocalizations were recorded with a Sennheiser ME66 short shotgun microphone to a Marantz PMD660 solid state sound recorder at a sampling rate of 44.1 khz and saved as .wav files. Only high-quality contact calls with little background noise were candidates for selection for playback trials. All high-quality calls were batch processed with the sound analysis program Raven 1.3 (Bioacoustics Research Program, 2008) with a bandpass filter of 500–14,000 Hz and amplified to 10,000 Hz to standardize playback stimuli. We selected

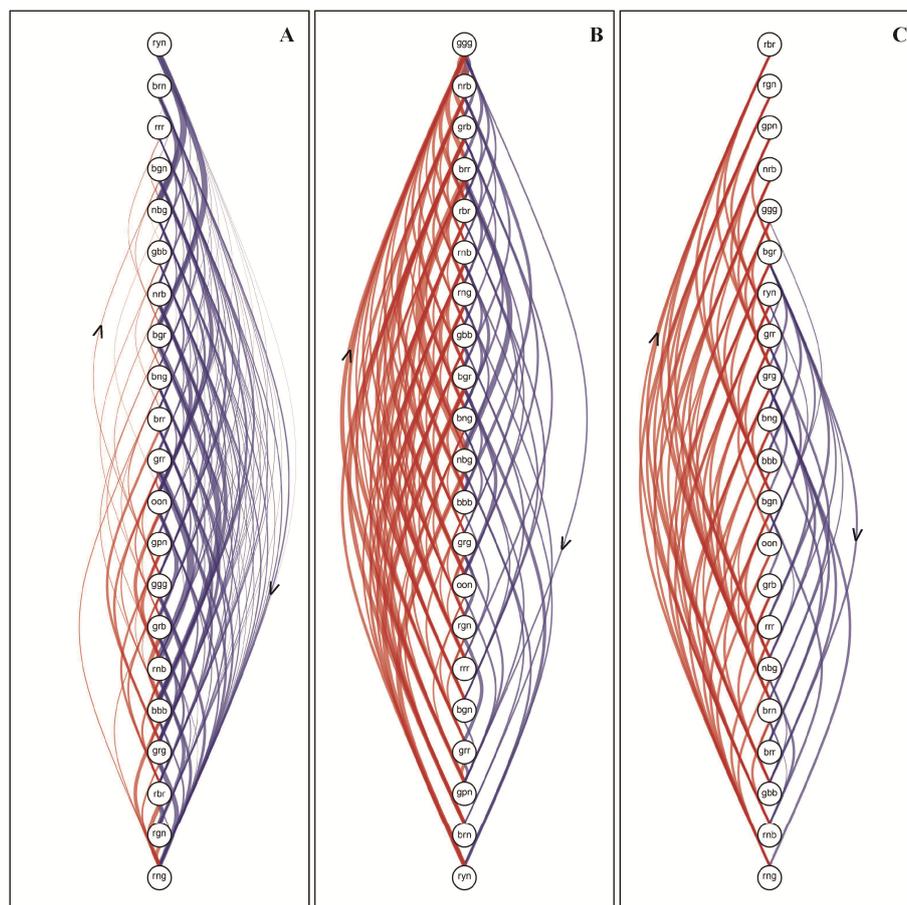


Fig. 1 Group 1 attribute-ordered networks depict the flow of network ties based on individual rank order for (A) aggression-dominance, (B) affiliation-popularity, and (C) response-response strength networks

Nodes indicate individuals and are ranked in order of (a) dominance, (b) popularity, and (c) mean elicited response strength, with the highest ranked individual at the top. Ties indicate relationships between individuals; tie width indicates (a) proportion directed aggression, (b) proportion non-partner neighbor observations, and (c) response strength. Carets (>) indicate the direction of ties: ties to the right side of networks (in blue) show how higher-ranked individuals interacted with lower-ranked individuals, while ties to the left side of networks (in red) show how lower-ranked individuals interacted with higher-ranked individuals. Attribute-ordered networks were drawn with igraph.

5 calls from each individual and randomly chose 3 to construct a stimulus call series for each playback trial. One individual in Group 2 (RNR) only provided 2 usable contact calls; we repeated the first stimulus call at the end to form a three-call series for this individual.

1.7 Playback design and presentation

We constructed unique playback trials for each test subject that contained calls from each of the test subject's social group members. We randomized both the order of presentation of stimulus individuals to each test subject and the order of testing for subjects. We used the program Audacity® 1.3.10 (<http://audacity.sourceforge.net>) to construct unique playback sound tracks for each test subject. For each track we used three contact calls from each stimulus individual, spaced 2 seconds apart to mimic natural call spacing patterns (E. Hobson, unpublished data). Call series from each stimulus individual were spaced 1 minute apart (or longer due to breaks, see below). Once constructed, the playback tracks allowed for the controlled presentation of stimulus calls in a manner that mimicked natural calling patterns, but was standardized across playback trials and avoided potential sources of researcher bias in playback delivery, as researchers were blind to the identity of stimulus individuals and did not control the rate of call delivery.

Playback trials were conducted in an open-walled roofed building during August 07–11, 2008. All test subjects were habituated to playback test conditions prior to the experiment. We visually isolated individuals from the rest of the group during playback trials to reduce chances of social calling and promote contact calling in response to playback stimuli. Each test subject received stimulus call series from all of its group members: Group 1 individuals ($n = 21$) were presented with stimulus series from 20 group members and Group 2 individuals ($n = 19$) were presented with stimuli from 18 group members. In order to reduce the chances of habituation to multiple stimuli, we divided playbacks into two parts, presented on two different days. In Part 1, test subjects were presented with calls from one quarter of potential social associates (Part 1A) followed by a 3 minute break of silence where the speaker position was changed from one randomly selected side of the test room to the other. After the break we presented the second quarter of social associates (Part 1B). On the second day of testing, we presented the third (Trial Part 2A) and fourth (Trial Part 2B) quarters of social associates in the same manner. Trials were recorded with the same audio recording system as for the stimuli.

1.8 Measuring playback responses

We quantified response strength using on-screen analysis of playback trial recordings with Raven 1.3. During analysis we were blind to the identity of stimulus individuals within playback tracks. We defined a 3 second response window within which we considered vocalizations to be responses to stimulus calls. Calls from test subjects were scored as responses if they occurred a maximum of 3 seconds after any of the three stimulus calls within each call series. We also counted the number of calls given during playback trials to determine if Groups 1 and 2 differed in their overall responsiveness (calls given in response to playback stimuli) and/or overall vocalness (calls given during trials but outside of the allotted response window).

If the subject responded with a contact call during the response window, we measured the speed of the response as the amount of time from the start of the stimulus call to the start of the response call. We quantified response strength as the difference between response lag times and the allowed response window (3 sec). Quantifying response strength in this way allowed us to include 'no response' as response strength of 0, which was a more appropriate format for use in our statistical tests. We also quantified mean response strength for each focal individual, which indicated the mean strength with which tested individuals responded to stimulus calls from focal individuals, and ranked individuals from strongest mean elicited response strength to weakest mean elicited response strength.

1.9 Testing perceptions via response patterns

We tested whether dyadic or emergent social relationships predicted playback response strengths using a network-based permutation-driven regression test, the Multiple Regression Quadratic Assignment Procedure (MRQAP, Dekker et al., 2003; Dekker et al., 2007). MRQAP allows simultaneous testing of multiple explanatory variables on a single response variable in a single model while controlling for the potential effects of stimulus habituation (Wey and Blumstein, 2010; Croft et al., 2011; Mann et al., 2012; Pinter-Wollman et al., 2014). We used the "Double Dekker Semi-Partialling MRQAP" approach, which is robust against multicollinearity among the explanatory variables (Dekker et al., 2003; Dekker et al., 2007). We chose to use MRQAP over other methods such as exponential random graph modeling (ERGM, as in Dey et al., 2015) and joint network modeling (as in Beisner et al., 2015) because both our predictor networks and our response network were continuous and weighted. ERGM is currently un-

der development to expand its use to continuous data (Desmarais and Cranmer, 2012) but current routines can only handle a response network that is either binary or count data. The recently developed joint network modeling method (Chan et al., 2013; Fushing et al., 2014) is also currently only available for binary network ties. We chose to use the weighted data because dichotomization of weighted ties can result in the loss of important socially-relevant detail (Croft et al., 2011; Farine, 2014).

We constructed our MRQAP model including three dyadic social factors (Affiliation (all), Affiliation (non-partner), and Aggression), four emergent factors (Dominance difference, Dominance rank difference, Popularity difference, and Popularity rank difference), and two controls for habituation (Trial part and Call order), with response strength as the dependent variable. Dyadic affiliative matrices contained the proportion of peaceful proximity neighbor observations; one matrix (all) included partner observations while one matrix (non-partner) excluded partner observations. Dyadic aggression matrices contained the proportion of aggression was directed at each potential target. For emergent social factors, we transformed individual attributes into dyadic difference matrices for all potential dyads for each of our two groups. We quantified the difference in centrality and rank between all individuals to get dyadic difference in dominance centrality, dominance rank, popularity centrality, and popularity rank. A positive value indicates that individual A had higher centrality or rank than individual B. We also constructed matrices with information on playback trial part and call order to control for the potential effects of habituation to the playback stimuli. Trial part matrices contained '1' for stimulus calls presented to an individual in part 1 of the trial, and '2' for stimulus calls presented in trial part 2. Call order matrices were based on the order in which stimulus calls from each individual were presented to each focal individual within trial parts, and were indicated as 1–10 for Group 1 and 1–9 for Group 2. Finally, we compiled a matrix of response strengths for all dyadic combinations, where rows indicated response strength of tested birds to stimulus individuals in columns. We conducted our MRQAP tests using the program UCInet 6.519 with 10,000 replicates.

2 Results

2.1 Relationship structure across social context and social scale

We collected data on aggressive events and nearest

neighbor occurrences for the two monk parakeet groups during > 323 hours of observer effort. We used these data to quantify dyadic relationship strengths for affiliative and agonistic social contexts as well as emergent dominance and popularity for each individual. We plotted these as attribute-ordered networks for agonistic and affiliative social contexts for both groups (Fig. 1, 2).

We collected 1,013 observations of aggressive events in Group 1 and 1,360 in Group 2. Aggression networks were highly but not perfectly connected (Fig. 1A, 2A). Although a small percent of total dyads did not interact (non-interacting dyads: Group 1= 11%, Group 2=8%), no individual was completely isolated. Most observations of aggression involved higher-ranked individuals aggressing against lower-ranked individuals (Fig. 1A, 2A, blue ties) but rank opportunism was observed in both groups, as lower-ranked individuals occasionally aggressed against higher-ranked birds (Fig. 1A, 2A, red ties).

We collected a total of 17,890 nearest neighbor observations in Group 1 and 28,875 in Group 2. Full affiliation networks including the most preferred associates (partners) were perfectly connected in both Group 1 and Group 2, with all individuals observed as neighbors of all other individuals at least once. Within the full affiliation networks, focal birds were nearest an individual other than their partner(s) in 8,674 (48.4%) observations in Group 1 and 13,747 (47.6%) observations in Group 2 (Fig. 1B, 2B). Most non-partner affiliative network ties involved less popular individuals in proximity to more popular individuals (Fig. 1B, 2B, red ties), but more popular individuals were also frequently neighbors to less popular individuals (Fig. 1B, 2B, blue ties).

At the dyadic scale, we found a significant negative correlation between aggression and affiliation (including partner observations) in Groups 1 and 2 (QAP correlation test, Group 1: $R = -0.0632$, $P = 0.0475$; Group 2: $R = -0.0885$, $P = 0.0060$). This effect reversed when we excluded the partner observations, and the amount and direction of aggression and non-partner neighbor affiliation were significantly positively correlated (Fig. 1A vs. 1B, Fig. 2A vs. 2B; QAP correlation test, Group 1: $R = 0.1649$, $P = 0.0032$; Group 2: $R = 0.1384$, $P = 0.0205$). These results indicate that individuals directed less aggression towards those with which they had strong affiliative relationships (their partners), but more aggression towards frequent non-partner neighbors.

At the emergent social scale, the relationship between dominance and popularity was variable across individuals. We did not find a significant correlation

MRQAP, we were able to detect response strengths that were driven by social factors above and beyond this habituation effect.

Response strength was driven by a mix of dyadic and emergent social factors in Group 1, but only dyadic factors in Group 2. At the dyadic social scale, affiliative

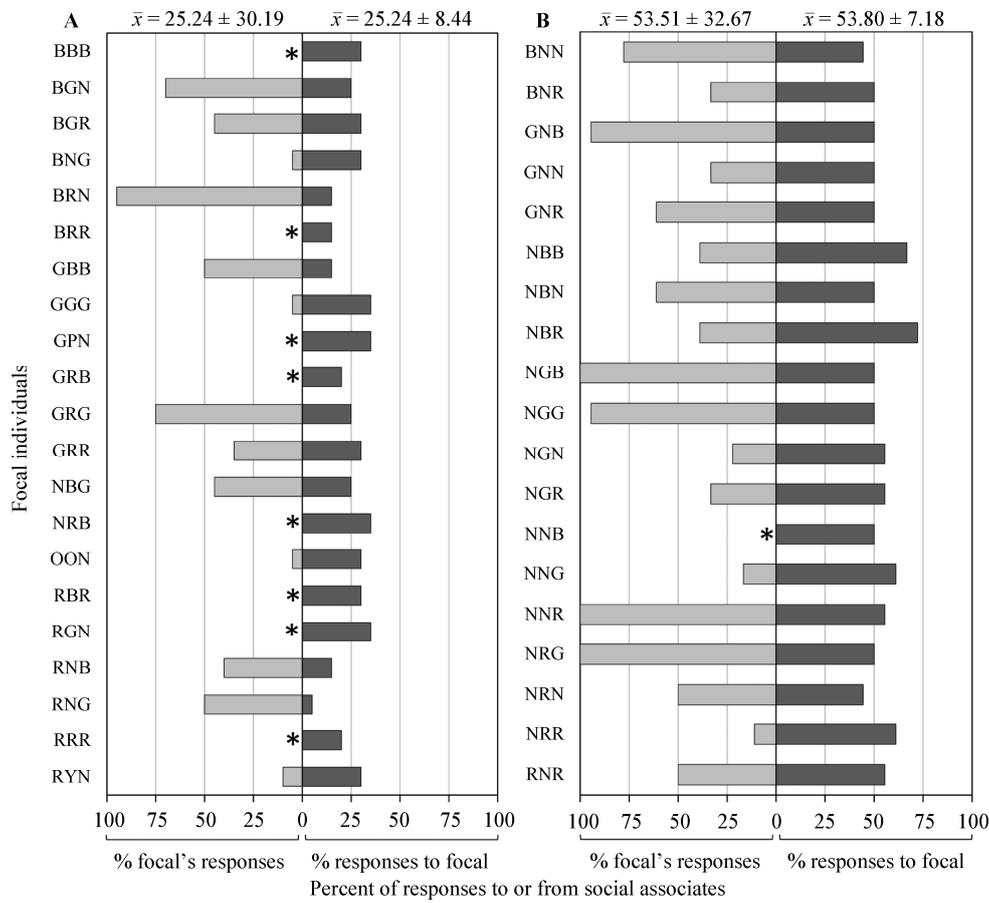


Fig. 3 Playback responsiveness differed across individuals

Graphs display the percent of binary responses for individuals responding to any call in a stimulus series for (A) Group 1 and (B) Group 2. Individuals labeled on the y-axis are “focal individuals”. The light grey bars show the percent of stimulus individuals that each of the focal individuals responded to during playback trials; dark grey bars show the percent of tested individuals that responded to stimuli from each of the focal individuals during playback trials. Stars indicate individuals that did not respond to any stimulus calls during playback trials. Mean percent responses given by and received by focal individuals in each group are indicated at the top of each graph.

Table 1 Response strength MRQAP results

Variable	Group 1			Group 2			
	Coefficient	SE	P	Coefficient	SE	P	
Dyadic factor	Aggression	0.04189	0.68515	0.18748	-0.02558	0.66447	0.33227
	Affiliation (all)	-0.06069	0.3355	0.0408	0.16213	0.47425	0.0002
	Affiliation (non-partner)	-0.07312	1.44628	0.06499	0.04905	1.27214	0.14549
Emergent factor	Dominance difference	1.07014	5.14545	0.06659	-0.14727	2.16923	0.33817
	Dominance rank difference	1.18534	0.10993	0.05629	-0.04869	0.05217	0.43246
	Popularity difference	-0.62401	4.27224	0.0231	-0.04185	6.40773	0.45925
Controls	Popularity rank difference	0.64477	0.05618	0.0419	-0.04951	0.0628	0.44246
	Trial part	-0.02058	0.08375	0.29697	-0.18816	0.10432	0.0001
	Call order	-0.07092	0.01424	0.026	-0.19941	0.02026	0.0001
Model fit	0.070362		0.002	0.104539		0.0001	

Response strength based on the strongest response to any of the three stimulus calls in the stimulus series. Coefficients are standardized regression coefficients. Model fit coefficient is the adjusted R² (corrected for multiple factors). Significant results ($\alpha < 0.05$) are indicated in bold.

neighbor networks significantly predicted response strength in both groups, but only for the full neighbor networks that included observations of partners. The direction of this effect differed between the two groups: in Group 1, neighbor effort was negatively associated with response strength, while in Group 2, it was positively associated with response strength. Aggression and non-partner affiliation networks did not predict response patterns in either group. At the emergent social scale, we found mixed results for the effect of emergent social properties on response patterns. In Group 1, popularity difference and popularity rank difference each predicted response strengths. However, neither measure predicted response strengths in Group 2. We were unable to test for interaction effects in our models because the development of network statistics is still underway, and there is not currently a statistical procedure that allows for examination of interactions among factors using MRQAP (Mann et al., 2012).

3 Discussion

We investigated how different types of social relationships affected individual responses during playback experiments with two groups of captive monk parakeets. We found that social context affected patterns of dyadic relationships but did not affect patterns of emergent relationships. We also found that affiliative relationships at the dyadic scale and, to a lesser degree at the emergent scale, affected playback response patterns, but the ways in which monk parakeets responded to these relationships differed across our two replicate groups. We discuss the extent to which these results allow us to draw inferences about how individuals perceive the importance of different relationships.

3.1 Relationship structure across social context and social scale

At the dyadic level, monk parakeets formed agonistic relationships with some individuals and affiliative relationships with others. We found that strong affiliative partners were not strongly agonistic with one another. These results indicate a separation between strong agonistic relationships and strong affiliative relationships. However, weaker affiliative relationships were positively associated with aggression, indicating that individuals that were often neighbors were more often aggressive with one another than with individuals with which they were rarely neighbors. Because individuals must be in close spatial proximity for aggression to occur, a moderately strong neighbor relationship, even based on peaceful proximity observations, may provide

individuals with greater opportunities for aggression against these frequent neighbors. At the emergent level, we found no association between dominance rank and popularity rank. Dominant individuals were no more or less likely to be popular, and popular individuals were no more or less likely to be dominant.

We developed a network layout that more effectively visualizes the structure of directed dyadic relationship networks and individual rank attributes. Our attribute-ordered network layout allows dyadic and emergent social information to be presented in a combined manner that reduces the cognitive load of interpreting and comparing these graphs across social contexts. Because this method is flexible and can be used to display and compare different types of social information, we expect it to be useful in a wide range of applications (R code available upon request).

3.2 Playback response patterns by social context and scale

Our overall model of social factors significantly predicted response strengths in both social groups. Habituation to playback stimuli affected response patterns, but this effect was controlled in the full statistical model. The regression coefficients from our model, although statistically significant, were relatively small, indicating that some amount of additional variation was unaccounted for in our model. The coefficient sizes can be partially attributed to the statistical approach we used (MRQAP) which is known to have lower regression coefficients than those from ordinary least squares regression (Krackhardt, 1988; Mann et al., 2012).

Within the full model, monk parakeet responses during playback trials were predicted by dyadic affiliative relationships, but only when observations of partners were included. The direction of this association between response and affiliative association strength differed between replicate social groups: Group 1 individuals were less likely to respond to stimulus calls from their strongest affiliative associates (partners), while in Group 2, playback responses were positively associated with affiliative relationship strength. Dyadic affiliative relationship strength did not predict playback responses when observations of affiliative partners were excluded, indicating that individuals were no more or less likely to respond to calls from a stimulus individual regardless of the amount of time it spent in proximity with non-partner neighbors. Agonistic relationships at the dyadic scale did not predict playback response patterns in either of the two groups; playback subjects were no more likely to respond to calls from a stimulus individual with

which it had a strong or weak agonistic relationship. At the emergent level, monk parakeet playback responses were significantly predicted by emergent popularity, but only in Group 1. Responses were not predicted by difference in dominance centrality or difference in dominance rank in either Group 1 or Group 2.

3.3 Inferring individual perception of relationships

Overall, the lack of general consistency in our results limited our ability to conclusively assess how individuals perceived their social relationships. However, we can use the playback response patterns to draw preliminary inferences about the perception of importance of social relationships. Response patterns in both Groups 1 and 2 were significantly driven by strong affiliative dyadic relationships when partner observations were included. If we define perception of importance of relationships based on significant predictors of playback responses, our results indicate that strong relationships in affiliative social contexts at dyadic social scales were important in driving response patterns, although the direction that responses were driven differed between our two social groups. Individuals in Group 2 appeared to perceive strong affiliative relationships as more important than weaker relationships, while this effect was reversed in Group 1 and individuals responded less strongly to those with which affiliation was stronger. Individual responses were also predicted by relationships within an affiliative social context at the emergent social scale, but only in one of the two replicate social groups: Group 1 playback responses were significantly associated with popularity difference. These results indicate that parakeets may be able to perceive emergent affiliative rank but it was not universally an important driver of playback responses.

We found no evidence that individual response patterns were driven by the strength of relationships within an agonistic social context, regardless of the social scale of those relationships. Neither dyadic aggression nor differences in emergent dominance affected playback response patterns. With our definition, these results indicate that both dyadic aggression and emergent dominance relationships may be perceived as less important than affiliative relationships. Interestingly, previous research in other species has demonstrated that individuals can recognize an individual's emergent social attributes, especially within agonistic social contexts, where individuals recognize and respond to relative differences in dominance rank and rank reversal events (Cheney et al., 1995; Bergman et al., 2003; Massen et al., 2014a).

In the monk parakeets, the apparent perceived importance of dyadic affiliative relationships occurs despite the parallel formation of moderately linear dominance hierarchies in the same social groups (Hobson et al., 2014). Traditionally, studies of social structure within animal groups, particularly in birds, have focused primarily on the influence of aggression and dominance on groups (Schjelderup-Ebbe, 1922; Chase, 1974; Banks and Allee, 1975; Ketterson, 1979; Chase, 1982; Lamprecht, 1986; Bond et al., 2004; Schubert et al., 2007; Chiarati et al., 2010; Sheppard et al., 2013; Dey and Quinn, 2014; Massen et al., 2014a). Much less work has focused on the quality or benefits of affiliative relationships at both the dyadic and emergent scales, even though dyadic affiliative relationships outside of pair bonds are present and likely important in a wide range of taxa (Seyfarth and Cheney, 2012) and affiliative relationships can have large impacts on fitness (Silk et al., 2003; Silk et al., 2006a; Silk et al., 2006b; McDonald, 2007; Ryder et al., 2008; Silk et al., 2009). Many birds show a strong pair-based social structure (Emery, 2006; Emery et al., 2007) and the quality of social relationships has been shown to be important in ravens (Fraser and Bugnyar, 2010), suggesting that a mix of affiliative and agonistic relationships are likely important structural features in social avian species.

However, our results could also suggest that other processes or mechanisms may be driving response patterns, rather than perception of the importance of different types of relationships. In particular, we were unable to determine whether call recognition processes may have affected response patterns. We focused on contact calls as stimuli during playback experiments, but we did not directly evaluate whether individuals were able to recognize others solely by contact call. Based on previous results in other parrot species, it is likely that monk parakeets can recognize non-pair individuals by contact calls: brown-throated conures *Aratinga pertinax*, green-rumped parrotlets *Forpus passerinus*, spectacled parrotlets *Forpus conspicillatus*, and budgerigars *Melopsittacus undulates* have all shown evidence for individual recognition by contact call (Brown et al., 1988; Wanker et al., 1998; Buhrman-Deever et al., 2008; Berg et al., 2011). Our results suggest that individuals can recognize their partners by call alone. However, it is unknown whether less closely associated individuals can also be recognized solely by vocal structure. Even if monk parakeets recognize all social associates by contact call, the timing of our playback experiment could have contributed to the variability in response patterns.

While Group 2 individuals were recorded and then tested in playback trials within the same week, Group 1 had a longer lag between recordings and trials (recordings: Group 1: 08–09 July; Group 2: 03–06 August; playback trials: both groups: 07–11 August). If monk parakeets alter their contact calls over time, this lag of about 1 month for Group 1 may have been enough time for individuals to alter their own calls and to learn the new calls of their social associates. If this was the case, the playback stimuli would represent ‘outdated’ contact calls, which may be a reason that they did not elicit strong responses. Further study is currently underway to determine if contact call structure changes over time in monk parakeets, as is commonly found in budgerigars (Brown et al., 1988; Farabaugh et al., 1994; Hile et al., 2000).

In addition to call recognition effects, several social factors could also have contributed to the variable response patterns. Memory and forgetfulness cause human perception of social relationships to vary from measures based on observational methods (Brewer, 2000; Bell et al., 2007) and social context and individual personality can also affect a person’s level of accuracy in recalling social associates (Casciaro, 1998). A similar mismatch between interaction events and perception of relationships may have contributed to the variable responses we observed during playback experiments with our parakeets. Differences in response rates and general association patterns between the two groups may also help explain the inconsistent response patterns between groups. Group 2 had higher response rates than Group 1, and also had significantly higher association strengths than Group 1 (Hobson et al., 2014). If the function of the contact call is to regain contact with group members, there may have been little incentive or biological reason for individuals to respond preferentially to only their closest associates. Instead, Group 2 individuals may have benefitted equally from contacting any member of their group because most individuals in Group 2 had moderately strong association strengths. Additional measures, such as physiological responses, may provide additional insight into the perception of relationships when used in conjunction with vocal response playbacks. Finally, our statistical approach was designed to detect consistency in overall response patterns within groups. However, if individuals within groups differ in which relationships they perceive as important, their response patterns may also differ, causing inconsistencies at the group level that would be difficult to detect with our current methods.

3.4 Importance of understanding relationships across contexts and scales

Many species form dyadic and emergent social relationships across both affiliative and agonistic social contexts, and individuals may gain fitness benefits from a combination of different types of relationships. In primates, individuals may invest in dyadic relationships with specific individuals in one context to gain a benefit from their relationship with that individual in a different social context. For example, female baboons with young infants form dyadic affiliative relationships with males, and then benefit from reduced aggression as the males then defend the females and their offspring against aggression from other males in the population (Nguyen et al., 2009). In this case, stronger dyadic affiliative relationships serve as a buffer against the formation of dyadic agonistic relationships. In another example, subordinate females in several primate species preferentially groom higher-ranked females (thus investing in dyadic affiliative relationships) and are then more likely to receive benefits from those individuals such as support during agonistic encounters (thus receiving a benefit in dyadic agonistic relationships, Seyfarth 1977; Schino 2001). Recent work with ravens has shown that individuals may strategically intervene in affiliative interactions among others, possibly to prevent individuals from forming alliances and becoming stronger competitors (Massen et al., 2014b). In this case, individuals use dyadic agonistic relationships to disrupt the dyadic affiliative relationships that the target of aggression can form with others. Because the benefits from relationships can differ depending on the social context and social scale, individuals may be able to employ different social strategies in order to gain access to similar benefits.

Understanding how dyadic relationships and emergent social properties form across affiliative and agonistic social contexts, and how individuals perceive their social landscape, are crucial to understanding selection pressures on sociality and the evolution of complex sociality across a broader range of taxa. The analysis and visualization methods developed here could be used in a wide range of social species, and comparative analyses among diverse taxa could provide important insight into the perception of social relationships across context and scale.

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