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RESEARCH ARTICLE

The socioecology of Monk Parakeets: Insights into parrot social complexity

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ABSTRACT

In many species, individuals benefit from social associations, but they must balance these benefits with the costs of competition for resources. Understanding how these competing factors generate diversity in social systems is a major goal of behavioral ecology, but one that has been hampered by a lack of basic data quantifying many aspects of social structure and associations. Although parrots are generally assumed to have complex social groups, few studies have quantitatively examined these assumptions about parrot social structure. We critically assessed 4 assumptions about parrot socioecology using data from captive and wild groups of Monk Parakeets (*Myiopsitta monachus*). We evaluated (1) whether pairs are the fundamental unit of parrot social structure, (2) the patterns and extent of fission–fusion dynamics, (3) patterns of aggression and dominance hierarchy structure, and (4) whether individuals share foraging information. We found evidence that supported pairs as the fundamental unit of social structure, although these close associates were not always heterosexual breeding pairs and were sometimes trios. Fission and fusion of subgroups were common, and the amount of fission–fusion dynamics varied across flock types and by fission–fusion dimension, but the amount of variation among dimensions was consistent across replicate captive social groups. Despite these levels of fission–fusion dynamics, study of aggressive interactions in our 2 captive groups indicated that dominance hierarchies existed. Hierarchies were moderately linear (0.7) but not steep (<0.1). Finally, we found no evidence that Monk Parakeets share foraging information among groups through active vocal recruitment to foraging flocks. We compared these patterns with those documented for other species of parrots and other cognitively complex large-brained species. We consider the implications of our results for the study of the evolution of complex sociality and highlight several future directions for parrot socioecology research.

Keywords: aggression, dominance hierarchy, fission–fusion dynamics, *Myiopsitta monachus,* parrot, social complexity, social network analysis, social structure

Socioecología de *Myiopsitta monachus:* Revelaciones de la complejidad social de los loros

RESUMEN

En muchas especies, los individuos se benefician de las asociaciones sociales, pero deben balancear estos beneficios con los costos de la competencia por los recursos. Entender cómo estos factores que compiten entre sí generan diversidad en los sistemas sociales es un objetivo central de la ecología del comportamiento, pero uno que ha sido obstaculizado por la falta de datos básicos que cuantifiquen muchos aspectos dela estructura social y de las asociaciones. Aunque se asume generalmente que los loros tienen grupos sociales complejos, pocos estudios han examinado cuantitativamente estos supuestos sobre la estructura social de los loros. Evaluamos de modo crítico cuatro supuestos sobre la socioecología de los loros usando datos de grupos cautivos y silvestres de *Myiopsitta monachus*. Evaluamos: (1) si los pares son la unidad fundamental de la estructura social de los loros, (2) los patrones y el alcance de las dinámicas de fisión–fusión, (3) los patrones de agresión y la estructura jerárquica de dominancia, y (4) si los individuos comparten información de forrajeo. Encontramos evidencia que apoya la noción de que los pares son la unidad fundamental de la estructura social, aunque estos socios cercanos no siempre fueron parejas reproductivas heterosexuales, y a veces fueron tríos. La fisión y fusión de subgrupos fue común y la cantidad de dinámicas de fisión–fusión varió a través de los tipos de bandadas y por dimensión de fisión–fusión, pero la cantidad de variación entre dimensiones fue consistente a través de los grupos sociales cautivos replicados. A pesar de estos niveles de dinámica de fisión–fusión, el estudio de las interacciones agresivas en nuestros grupos cautivos indicó que existe una dominancia jerárquica. Las jerarquías fueron moderadamente lineales (0.7) pero no empinadas (<0.1). Finalmente, no encontramos evidencia de que *M. monachus* comparta información de forrajeo entre grupos mediante el reclutamiento vocal activo a las bandadas de forrajeo. Comparamos estos patrones con aquellos documentados para otras especies de loros y otras especies de cerebro grande cognitivamente complejas. Consideramos las implicancias de nuestros resultados para el estudio de la evolución de una sociabilidad compleja y subrayamos varias direcciones para futuras investigaciones de la socioecología de los loros.

Palabras clave: análisis de red social, agresión, complejidad social, dinámicas de fisión-fusión, estructura social, jerarquía de dominancia, loro, *Myiopsitta monachus*

INTRODUCTION

Social structure can fundamentally affect the fitness of individuals by influencing how they utilize space, gain access to resources, or interact with others. Social associations with conspecifics, such as shared group membership, can increase foraging efficiency (Smith et al. 1999), predator avoidance (Lima et al. 1999), and reproductive output of individuals (McComb et al. 2001, Silk 2007). Species display a wide range of social patterns, from largely solitary species in which pairs associate primarily during breeding seasons to more socially complex groups with many individuals, long-term bonds, and differentiated social relationships (Wilson 1975, de Waal and Tyack 2003, Whitehead 2008).

Parrots have long been thought to have complex social interactions and to exhibit complexity in their social organization. However, parrot sociality is poorly understood, largely because wild individuals are difficult to capture, individuals are difficult to observe consistently because of their high mobility (Eberhard 1998, Bradbury 2003, Salinas-Melgoza and Wright 2012), and many types of marks are readily destroyed (Meyers 1995, Bradbury 2003, Carlos Senar et al. 2012). In addition, group membership may be quite fluid in many species, although the extent of this fluidity is difficult to gauge, given the problems with marking and following individuals.

Despite these difficulties, understanding the social systems of parrots is critical to understanding social processes such as vocal learning and the spread of behaviors. Many parrot species are threatened or endangered, and increased understanding of how they structure their social interactions could improve our ability to manage these populations. Parrots also show evidence of cognitive complexity, and greater understanding of their social complexity may provide insight into how social and cognitive complexity evolved (Dunbar 1998, Freeberg et al. 2012).

Our existing knowledge of parrot social structure is based on a variety of approaches. Social structure has been directly observed in captive groups in non-natural laboratory settings (e.g., Masure and Allee 1934, Tebbich et al. 1996, Seibert and Crowell-Davis 2001), through tracking a small number of wild individuals (e.g., Bradbury et al. 2001, Salinas-Melgoza and Wright 2012), and through observing individually marked birds in the wild (e.g., Eberhard 1998, Berg et al. 2011). Social structure has been more indirectly inferred from natural-history observations of unmarked wild populations (e.g., Wyndham 1980), results of audio playback experiments in the wild and in captivity (e.g., Buhrman-Deever et al. 2008), the geographic structure of vocalizations in wild populations (e.g., Wright 1996, Bradbury et al. 2001, Baker 2003, Buhrman-Deever et al. 2007), and observations of social behavior in captivity (e.g., Brockway 1964, Trillmich 1976a, 1976b).

On the basis of these previous studies, several general assumptions have emerged and are widely cited. First, parrot sociality is widely assumed to revolve around the pair bond, with breeding pairs functioning as the "fundamental social unit," largely because wild parrots are often observed flying in groups of 2 (Juniper and Parr 1998, Bradbury 2003, Balsby and Adams 2011). However, to our knowledge, this assumption has not been quantitatively tested in any parrot species other than captive Budgerigars (*Melopsittacus undulatus*; Trillmich 1976b). Second, many parrot species are described as having fission–fusion social structures, largely on the basis of their variable flock sizes within and across days (Juniper and Parr 1998, Bradbury et al. 2001, Bradbury 2003, Cortopassi and Bradbury 2006, Buhrman-Deever et al. 2008, Scarl and Bradbury 2009, Balsby and Adams 2011). Species with fission–fusion social structure are characterized by groups that repeatedly split into separate subgroups and then merge again. Previous research suggests that parrot vocalizations, especially contact calls, may be used to mediate fission–fusion events (Vehrencamp et al. 2003, Balsby and Bradbury 2009, Scarl and Bradbury 2009, Balsby and Adams 2011, Balsby et al. 2012), although this has been difficult to test because the extent and characteristics of fission–fusion dynamics and the resulting social structure of groups have not been previously quantified for any parrot species. Referring to a species' social structure as "fission–fusion" without quantifying these dynamics does not provide much insight into the social dynamics of groups (Aureli et al. 2008). Third, there has been very little consideration of how dominance hierarchies might affect group dynamics in wild parrots. This may result from the purportedly high fission–fusion dynamics of wild parrots, as well as from a lack of obvious dominance structure in many captive groups. The structure of parrot dominance hierarchies has been described in only a few species, with varying results. Captive Budgerigars and Cockatiels (*Nymphicus hollandicus*) formed linear or mostly linear hierarchies (Masure and Allee 1934, Seibert

FIGURE 1. Monk Parakeet flocks (**A**) in flight and (**B**) perched. Photo credit: Steve Baldwin (brooklynparrots.com)

and Crowell-Davis 2001, Soma and Hasegawa 2004), whereas captive Keas (*Nestor notabilis*) formed a nonlinear hierarchy (Tebbich et al. 1996). Because dominance relations can greatly affect an individual's fitness and how resources are partitioned within a group (Drews 1993), the existence of dominance hierarchies could be an important structural feature in parrot groups. Finally, parrots are widely assumed to benefit from group membership through sharing or transferring information about foraging resources (Juniper and Parr 1998, Bradbury 2003, Salinas-Melgoza et al. 2013). The assumption that parrots share information stems from nocturnal social roosting, which occurs in many parrot species (Juniper and Parr 1998). These roosts could serve as information or recruitment centers in some species (Zahavi 1971, Ward and Zahavi 1973, Richner and Heeb 1995, 1996). Potential indications of information sharing have been found in Brown-throated Conures (*Aratinga pertinax*), based on differences in preferences for calling to other flocks that might function as direct recruitment signals (Buhrman-Deever et al. 2008). Information sharing has otherwise not been quantified or tested in parrot groups.

In the present study, we quantify aspects of the socioecology of the Monk Parakeet (*Myiopsitta monachus*), a common species in temperate South America that is notable for its highly social colonial and communal nesting behavior (Eberhard 1998; Figure 1). It is also widespread as an invasive species in temperate North America, Europe, and Asia (Van Bael and Pruett-Jones 1996, Sol et al. 1997, Domènech et al. 2003, Pruett-Jones et al. 2005, Muñoz and Real 2006, Strubbe and Matthysen 2009, Avery et al. 2012). Our study goal was to critically assess the evidence for some of the widespread assumptions about parrot sociality using data from both wild and captive Monk Parakeet groups. Specifically, we aimed to (1) evaluate the assumption that the pair is the fundamental unit of parrot social structure, (2) quantify the patterns and extent of fission–fusion dynamics, (3) describe and quantify patterns of aggression and dominance hierarchy structure, and (4) determine whether individuals share foraging information. We use our results to put Monk Parakeet social characteristics into context by comparing them to social patterns documented in other socially and cognitively complex species. Finally, we consider the implications of our results for the study of the evolution of complex sociality.

METHODS

Study Species

Monk Parakeets are found in abundant native populations in temperate southeastern South America. This species typically nests in colonial aggregations and often shares communal nest structures with several other pairs at year-round roost sites (Eberhard 1998, Forshaw 2006). Pairs are generally stable at least across several breeding seasons in the wild (Eberhard 1998), and individuals are long-lived in captivity (Young et al. 2012). The Monk Parakeet is one of the more tractable parrot species for a study of a marked population: Individuals are relatively easy to capture, abundant, and found in open habitat (Eberhard 1998). Monk Parakeets are also successful in colonizing new habitat: Populations have become established outside of their native ranges in the United States, Europe, and Japan as a result of accidental escapes and intentional releases of individuals in the pet trade (Muñoz and Real 2006, Pruett-Jones et al. 2007, Russello et al. 2008, Avery et al. 2012).

Wild Study Site, Population, and Observational Methods

We observed Monk Parakeets in wild populations in their native habitat during the austral winter from June to August 2007. Our study site was in northern Entre Ríos province, Argentina, on Estancia Santa Ana de Carpinchorí

(58°45′W, 31°25′S), a 5,508-ha cattle ranch and private wildlife preserve (Eberhard 1998). The ranch is composed of open pasture grazed by livestock (cows, sheep, and horses) and cultivated fields (sunflower, millet, sorgum, and corn), bordered by uncleared xeric native trees (*Acacia caven*, *Prosopis ajfinis*, and *P. nigra*). Non-native eucalyptus trees were also present along roads and near ranch buildings.

We conducted observations near nest colonies and adjacent to foraging sites and collected data on flying, foraging, and perched flocks. We used a chain rule (Wolf et al. 2007) to delimitate flocks; individuals were categorized as belonging to the same flock if they were within 10 m of others and behaving in a cohesive manner (e.g., flying at the same speed in the same direction). We designated individuals into separate flocks if the flocks were sighted at the same time but were separated by >10 m and were behaving as separate cohesive units (e.g., flying at different speeds or in different directions). For each flock, we counted the number of individuals present. Flock sizes ranged from 1 (a single individual observed alone) to many individuals. We also recorded whether individuals in the flock were calling and whether calling flocks received responses from other flocks. The primary author trained the second observer in the field prior to data collection to standardize observations.

Captive Study Site, Population, and Observational Methods

Our study of captive Monk Parakeets took place during June–August, 2008, at the U.S. Department of Agriculture National Wildlife Research Center in Gainesville, Florida, USA, where we worked with a colony of long-term resident Monk Parakeets. Prior to our study, Monk Parakeets were housed in groups of 1–6 individuals per cage; some were in visual contact, but direct physical contact between individuals in different cages was not possible. We randomly divided the total captive population into 2 replicate social groups (captive group 1, $n = 21$; captive group 2, $n = 19$). To facilitate visual identification of individuals, we marked each bird with a unique facial mark using colored permanent markers (Sharpie brand). These nontoxic markers have been successfully used in behavioral studies of other parrot species (e.g., Buhrman-Deever et al. 2008), and dye marks did not appear to adversely affect individual behavior or affiliative interaction rates between pair members. Each captive group was released sequentially into a 2,025-m^2 seminatural outdoor flight pen and observed over the course of 24 days by 1–4 observers (Hobson et al. 2013). We divided the flight pen into 25 quadrats, each approximately 10 × 10 m, using a visible grid of twine at ground level to facilitate collection of spatial data and to decrease interobserver differences in quadrat assignment.

We used a mix of scan and all-occurrence sampling procedures to record data on flock membership and behaviors (Hobson et al. 2013). To identify flock membership, we took a scan sample at least once every 10 min. We determined flock membership by identifying the location of each individual: Multiple individuals were categorized as in the same flock if they occupied the same quadrat or perching location. Large flocks that spanned >1 quadrat were identified as a single flock if they behaved as a cohesive group. In these cases, we assigned all members of the flock to the quadrat occupied by the majority of the flock. We also used all-occurrence sampling to record data on directed affiliative or agonistic behaviors. For directed behaviors, we recorded the identity of the actor and receiver during affiliative interactions such as allopreening events or copulations and during agonistic interactions such as aggressive displacements, bites, threats, and chases.

Evaluation of the Fundamental Social Unit

To evaluate whether the pair is the fundamental unit of Monk Parakeet social structure, we counted the numbers of Monk Parakeets in flocks in the wild and in both captive groups. For wild flocks, we used observations of naturally occurring flocks; experimentally provisioned foraging flocks were excluded from this analysis. We expected that if pairs were the fundamental unit of social structure, flocks of 2 individuals would be most common. For wild flocks, 1–2 observers were stationed in open areas with unobstructed views of colony areas and/or foraging sites. For captive groups, 1–4 observers were stationed in blinds within or adjacent to the flight pen. We counted the number of individuals in each flock, using the definition of "flock" provided above. All populations were sampled in nonbreeding conditions to avoid sampling flocks that contained family groups of newly fledged and still partially dependent offspring. Wild flocks were sampled during the austral winter (nonbreeding season), and captive flocks were sampled over a time span that precluded reproductive attempts.

We performed a cluster analysis with the flock membership data from our captive groups to determine the structure of overall group association patterns. If pairs are the fundamental social unit, we predicted that pairs would cluster together and that the clusters would be statistically significant. We used the R package "pvclust" version 1.2-2 (Suzuki and Shimodaira 2006, 2011) to run the cluster analyses and to assess the uncertainty of the observed clusters. We measured dissimilarity in raw group-membership patterns among individuals using the correlation method, and we used these distance measures to generate dendrograms using the average hierarchical clustering method (Suzuki and Shimodaira 2011). We measured the uncertainty of the resulting cluster patterns, obtaining bootstrap-based P values by 2 methods: bootstrap probabilities (BP) and approximately unbiased (AU) *P* values calculated through multiscale bootstrap resampling. Following recommendations, we used 10,000 bootstrap samples to calculate *P* values for both BP and AU methods (Suzuki and Shimodaira 2011). Clusters with high *P* values are strongly supported by the data; we rejected the null hypothesis that the cluster did not exist if the *P* value was >0.95 (Suzuki and Shimodaira 2011).

We also evaluated the strength of associations to determine whether individuals displayed preferential association patterns. If pairs are the fundamental social unit, we expected to find evidence that an individual maintained a strongly preferred association with 1 other individual and directed affiliative behaviors exclusively toward that preferred individual. To quantify dyadic association strength between individuals, we used observations of flock membership in captive groups. We pooled flock observations into 10-min sampling periods, and any individuals sighted in the same group during a sampling period were scored as "associated." We quantified association strength using the simple ratio index (SRI) in SOCPROG version 2.4 (Whitehead 2009). To determine variation in preferential association strengths in our 2 captive groups, we fitted a regression line to the ranked association strengths for each individual, examined the Cook's distances to determine influential points, and used the Grubbs test in the R package "outliers" (Komsta 2011) to test whether these points were statistical outliers. To quantify dyadic interaction strength between individuals, we constructed allopreening networks based on observations of allopreening behaviors whereby one individual preened another individual. We filtered the allopreening networks so that ties represented dyads that were observed allopreening at least twice during the study period.

Finally, we tested association strength networks and allopreening networks to determine whether they were significantly correlated in captive groups. We expected to find a significant positive relation between association strength and allopreening, whereby individuals with high association strengths would be more likely to allopreen partners than those with low association strengths. We constructed weighted networks of association strength in which tie strength was determined by dyadic SRI values. We compared these with allopreening networks in which ties indicated that the individuals were observed allopreening. We tested whether association strength was correlated with allopreening using the quadratic assignment procedure (QAP) correlation test (10,000 permutations; UCINET version 6.400). We also compared structural features of association strength networks and allopreening networks to test for a difference in the number and strength of ties. We measured network density to determine the proportion of existing ties compared to the total available ties in the population (Wasserman and Faust 1994); a high network density (i.e. near 1.0) indicates that the network is more interconnected, with many individuals associating with most of their potential social associates, whereas a low density (i.e. near zero) indicates that the network is more disconnected and that individuals associate with only a small proportion of their total available associates.

Quantification of Fission–Fusion Dynamics

We quantified variability in Monk Parakeet groups using 3 dimensions of fission–fusion dynamics: variation in flock size, variation in flock cohesion, and variation in flock membership, following recent recommendations (Aureli et al. 2008). We used coefficients of variation (CV) as unitless measures of variability to facilitate comparison among fission–fusion dimensions measured in different units. In wild populations, we quantified variation in flock size because we were unable to collect detailed data on individual locations or flock membership patterns. We quantified variation in the size of naturally occurring flocks by counting the numbers of individuals in flocks (following the methods above; experimentally provisioned foraging flock data were excluded). For each observation day, we quantified the mean and standard deviation of flock size, then used the CV to quantify variability across days. We determined whether there were significant differences in size and variability among wild flock types with analysis of variance (ANOVA) and Tukey's HSD tests (R Core Team 2013).

In our 2 captive groups, we quantified flock size, interindividual distances, and mean flock association strength to measure flock size, flock cohesion, and flock composition. For each dimension of fission–fusion dynamics, we quantified the mean and standard deviations for specific measures describing these dimensions for each observation day, as explained below. We then used the CV to quantify variability across days. First, we counted individuals in flocks to quantify mean daily flock sizes. Groups with low fission–fusion dynamics in flock size variability would have lower variation in flock sizes, but not necessarily larger or smaller overall flock sizes. Second, we quantified variation in flock cohesion using interindividual distances in our captive groups. We used an individual's quadrat location to quantify the Euclidean distance between all pairs of individuals identified during the same observation period, measured in quadrats. Individuals identified within the same quadrat were given a distance of "zero." A highly cohesive group would have low variability in interindividual distances. Third, we quantified variation in flock composition by determining each dyad's association strength (SRI, as above). For each identified flock, we quantified the mean dyadic association strength for all members present. For each observation day, we quantified the mean and standard deviation across all mean flock association strengths. Groups with highly consistent flock composition would have low variability across observation days. Finally, we compared flock size variability in wild Monk Parakeets to the variability we observed in our captive groups to determine whether this measure of fission–fusion dynamics differed between captive and wild groups.

Characterizing Patterns of Aggression and Dominance

We evaluated whether Monk Parakeets showed evidence of dominance hierarchies by using aggressive-interaction data from our 2 captive groups. We collected observations of clearly unidirectional aggressive events occurring between an aggressor and a target individual, in which the actions of the aggressor caused the target to be physically displaced or supplanted by the aggressor. We restricted our analysis of dominance to observations of these aggressive behaviors because they resulted in clear winners and losers. Of the 1–4 observers, only the primary observer collected aggression observations, in order to ensure standardization of data collection. We used these aggressive events to evaluate the patterns of aggression and the structure of group dominance hierarchies using SOCPROG. We quantified the direction of aggression among all individuals in the entire group to evaluate the directional consistency of aggression. We also evaluated directed aggression by sex to evaluate whether more aggressive events were directed toward same-sex individuals, which would provide evidence of separate sex-based dominance hierarchies. We used the Kr-test to test for relative reciprocity in the direction of aggression (10,000 permutations). The Kr-test evaluates the strength of correlation between a matrix of interactions and its inverse, under the null hypothesis that behaviors are unidirectional rather than reciprocal (Hemelrijk 1990).

To evaluate the group-level structure of the dominance hierarchy, we ranked individuals using the I&SI method (de Vries 1998). Dominance linearity was evaluated using the h' method (de Vries 1995; 10,000 permutations) and represents the degree to which individual dominance relations are transitive. A linearity score >0.9 is generally accepted as evidence of strong linearity, with the dominance hierarchy characterized by few directional inconsistencies in aggression patterns (Chase 1974, Martin and Bateson 1993, de Vries 1995, Lehner 1998, Vervaecke et al. 2000, Whitehead 2008). Finally, we quantified dominance steepness, or the degree to which higher-ranked individuals were likely to win aggressive encounters against lower-ranked individuals, corrected for chance (D_{ij} method, 10,000 permutations; de Vries et al. 2006). A steep hierarchy (steepness near 1.0) indicates that high-ranked individuals are very likely to win encounters against lower-ranked individuals, whereas a shallow hierarchy (steepness near zero) indicates that the outcome of these events is unpredictable (de Vries et al. 2006). If the captive individuals showed significant directionality in their patterns of aggression and low levels of reciprocation of aggression, and if captive groups had significantly linear and/or steep hierarchies, we would reject the assumption that Monk Parakeets do not have the potential to form dominance hierarchies.

Evaluation of Foraging Information Sharing

We tested whether wild individuals shared foraging information by using vocalizations to actively recruit others directly to foraging areas in wild groups in Argentina. We collected data on whether foraging or flying groups were vocalizing, the type of vocalization, whether foraging flocks vocalized to flying flocks, whether vocal exchanges took place, and whether flying flocks joined foraging flocks after vocal exchanges. Although we collected data on the occurrence of any vocalizations, we focused on the contact call because it is the most common call, is given in many contexts (during both foraging and flying), and has almost always been answered with a return contact call in previous playback experiments (Martella and Bucher 1990). In general, contact calls are widely recognized as important in facilitating group contact and movement patterns across species (reviewed in Berg et al. 2011). On the basis of previous studies, there is no indication that Monk Parakeets use specialized recruitment calls within a foraging context. We planned to record exchanges of contact calls between foraging and flying flocks with a Sennheiser ME66 short shotgun microphone connected to a Marantz PMD660 solid-state sound recorder at a sampling rate of 44.1 khz. We expected active vocal recruitment signals to be consistent with the pattern found in another small parrot species, whereby a flying flock calls, the foraging flock responds, and the flying flock responds and joins the foraging flock (Buhrman-Deever et al. 2008).

If foraging flocks actively recruited flying flocks, we expected that foraging groups would call to flying flocks and that flying flocks would be more likely to land with foraging groups if called to. We collected these data on natural foraging groups and compared them with group behaviors on experimentally manipulated foraging sites. We further tested recruitment behaviors by experimentally manipulating foraging resources. Foraging experiments were conducted from July 30 to August 11, 2007, in an open area where foraging flocks were commonly observed. We provisioned the site by spreading dried corn on the ground and then recorded observations of foraging and flying groups, following the methods above. If Monk Parakeets share information about foraging resources, we expected to observe more vocal flock recruitment signals (i.e. foraging flocks calling to flying flocks) in provisioned foraging groups than in unprovisioned groups because

TABLE 1. Summary of flock-size results in Monk Parakeets (captive group 1 = 21 individuals; captive group 2 = 19 individuals).

		Flock size						
Population	Flock type	*n*	Range	Mean	SD	Median	Mode	CV
Wild	All	9,828	1–95	3.97	5.33	2	2	1.3440
	Perched	2,012	1–26	2.76	2.06	2	2	0.7454
	Flying	6,452	1–60	3.37	3.88	2	2	1.1497
	Foraging all	1,364	1–95	8.57	10.14	5	2	1.1830
	Natural foraging	862	1–54	6.31	6.04	4	2	0.9580
	Provisioned foraging	502	1–95	12.45	13.89	7	2	1.1153
Captive	Group 1 all	10,117	1–20	3.24	2.80	2	2	0.8614
	Group 2 all	10,333	1–19	4.24	3.92	3	2	0.9235

provisioned areas would represent novel foraging resources and novel information that foraging flocks could share with flying flocks.

RESULTS

Fundamental Social Unit

We observed a total of 29,776 naturally occurring flocks in the wild and in captivity (Table 1; experimentally provisioned foraging flocks excluded), representing >550 hr of observer effort in the wild and >323 hr of observer effort in captivity. Of the 9,326 naturally occurring flocks we observed in the wild, flocks of 2 individuals were the most common, accounting for 32.3% of the total flocks observed. Single individuals were also commonly observed, accounting for 23.8% of total observations. Although flocks of ≤60 individuals were observed, flocks of ≥15 individuals accounted for only 2.4% of total flock observations. In captivity, we observed 10,117 flocks in captive group 1 and 10,333 flocks in captive group 2. Flocks of 2 individuals were most common and accounted for 30.4% of total flock observations in captive group 1 and 25.2% in captive group 2. Large flocks of ≥15 individuals accounted for 0.7% of flocks in captive group 1 and for 3.7% of flocks in captive group 2. Mean flock sizes were 3.24 ± 2.80 in captive group 1, 4.24 ± 3.92 in captive group 2, and 3.97 ± 5.33 in the wild.

Social association strengths among captive individuals differed across dyads, with individuals generally showing a marked preference for 1 individual (Figure 2). A small portion of associations could be categorized as influential data points (Cook's distances >1.0, percent dyads: captive group 1, 4.52%; captive group 2, 3.22%). Almost all of these influential points reflect a marked preference for the top-

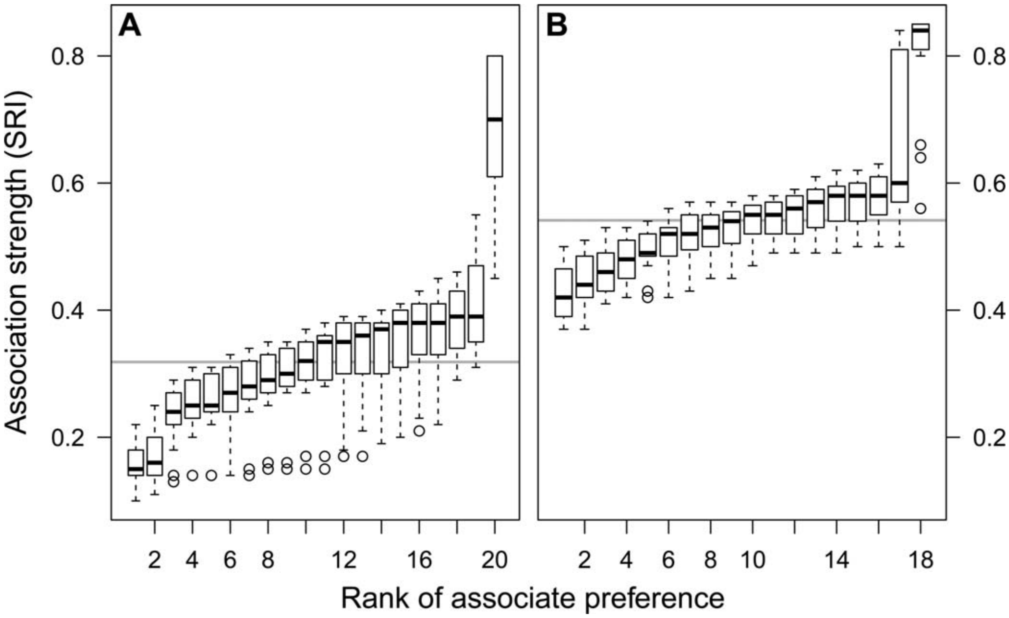

FIGURE 2. Association strength (SRI = simple ratio index) by ranked associate preference in Monk Parakeets. Ranks range from 1 (least preferred) to most preferred for all individuals in captive group 1 (**A**) and captive group 2 (**B**). Gray lines indicate mean association strength for each group.

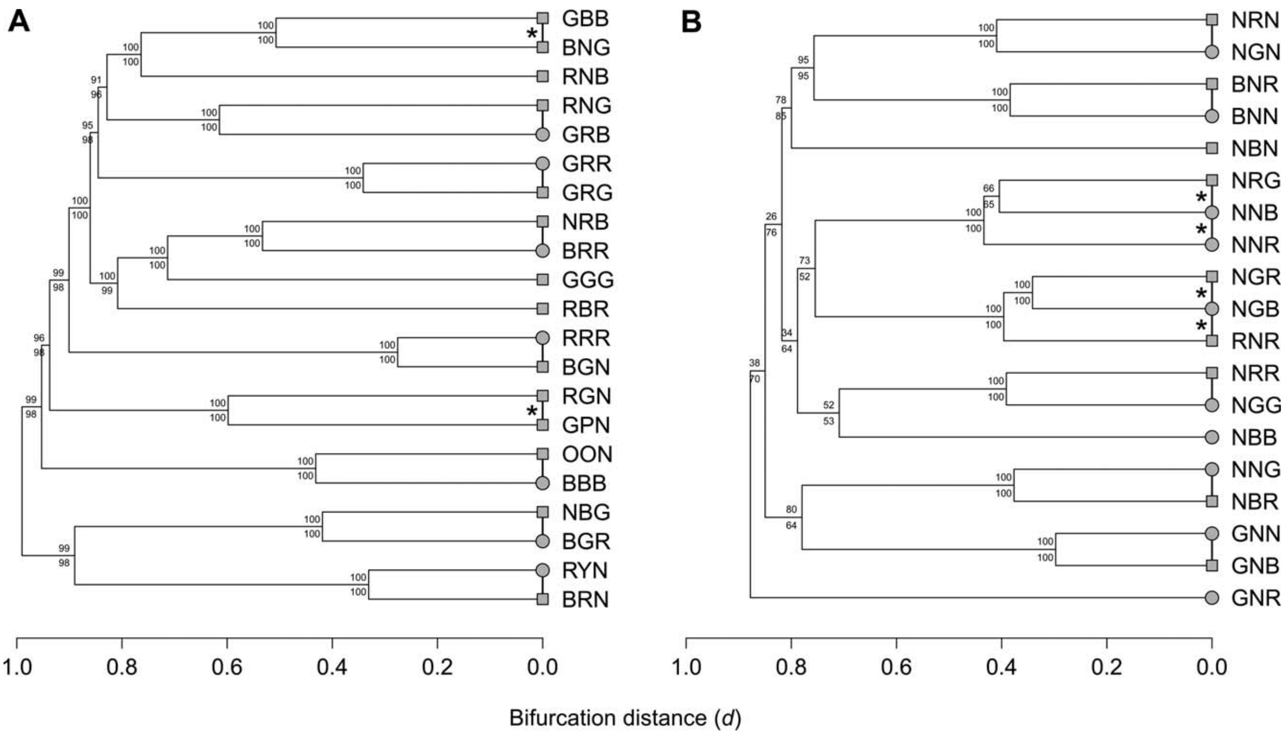

FIGURE 3. Dendrogram of association patterns in Monk Parakeets. Dendrogram depicting the results of cluster analyses of association patterns in captive individuals in captive group 1 (**A**) and captive group 2 (**B**). Bifurcation distances illustrate similarity; lower distances at branch bifurcations indicate higher similarity in group membership among individuals. Numbers at branch bifurcations show the results of bootstrap analyses; top numbers are approximately unbiased (AU) *P* values, and bottom numbers are bootstrap probabilities (BP); values >0.95 are strongly supported clusters. Labels at right indicate individual identification codes, and end-node shapes correspond to individual sex: Squares are males and circles are females. Thicker vertical lines connecting end nodes indicate well-supported preferred dyads or triads; male–male dyads and triads are highlighted with asterisks.

ranked associate, usually the pair-mate (captive group 1: 95%, $n = 18$; captive group 2: 100%, $n = 11$). All of the preferred partners were identified as significant outliers (Grubbs test: captive group 1, mean $P = 0.0063$, maximun $P = 0.0359$; captive group 2, mean $P = 0.0011$, maximum $P = 0.0082$), except for 1 nonsignificant dyad in captive group 1 ($P = 0.1225$), which represented the only bottom-ranked association that was identified as influential on the basis of Cook's distance.

Our cluster analysis of shared group membership patterns in captive groups found strong bootstrap support for relationships at the tips of the dendrogram (Figure 3). Cluster techniques generally identified strongly associated dyads, but we also found evidence of strongly associated trios in captive group 2. Not all of the strongly associated dyads were heterosexual pairs; we found 2 cases of highly associated male–male dyads in captive group 1. Deeper nodes in the captive group 1 dendrogram received high bootstrap support, whereas similar deeper nodes in captive group 2 received much lower support.

Individuals in captive groups generally allopreened a small number of their potential associates (number of partners: captive group 1, mean = 1.6, range: 0–5; captive group 2, mean = 2.1, range: 1–4). This selectivity in allopreening resulted in much lower tie density in allopreening networks than in association networks (Table 2 and Figure 4). We also found that an individual's allopreening effort was generally directed at a single other individual, not spread among many potential partners. In captive group 1, individuals directed a mean of 88% of effort toward their most preferred allopreening partner. In captive group 2, individuals directed most of their allopreening efforts to 1 preferred partner (mean = 79%), although 6 individuals that composed the 2 triads split their allopreening efforts between 2 preferred partners.

Finally, we found that social association strength was significantly and positively correlated with allopreening events, showing that dyads with higher association strengths were more likely to also engage in allopreening (QAP correlation test: captive group 1, $R = 0.66$, $P = 0.0001$; captive group 2, $R = 0.72$, $P = 0.0001$). However, we also found that structural patterns of networks differed when we compared networks composed of association strength ties with those composed of directed affiliative allopreening behaviors (Figure 4). Individuals were directly

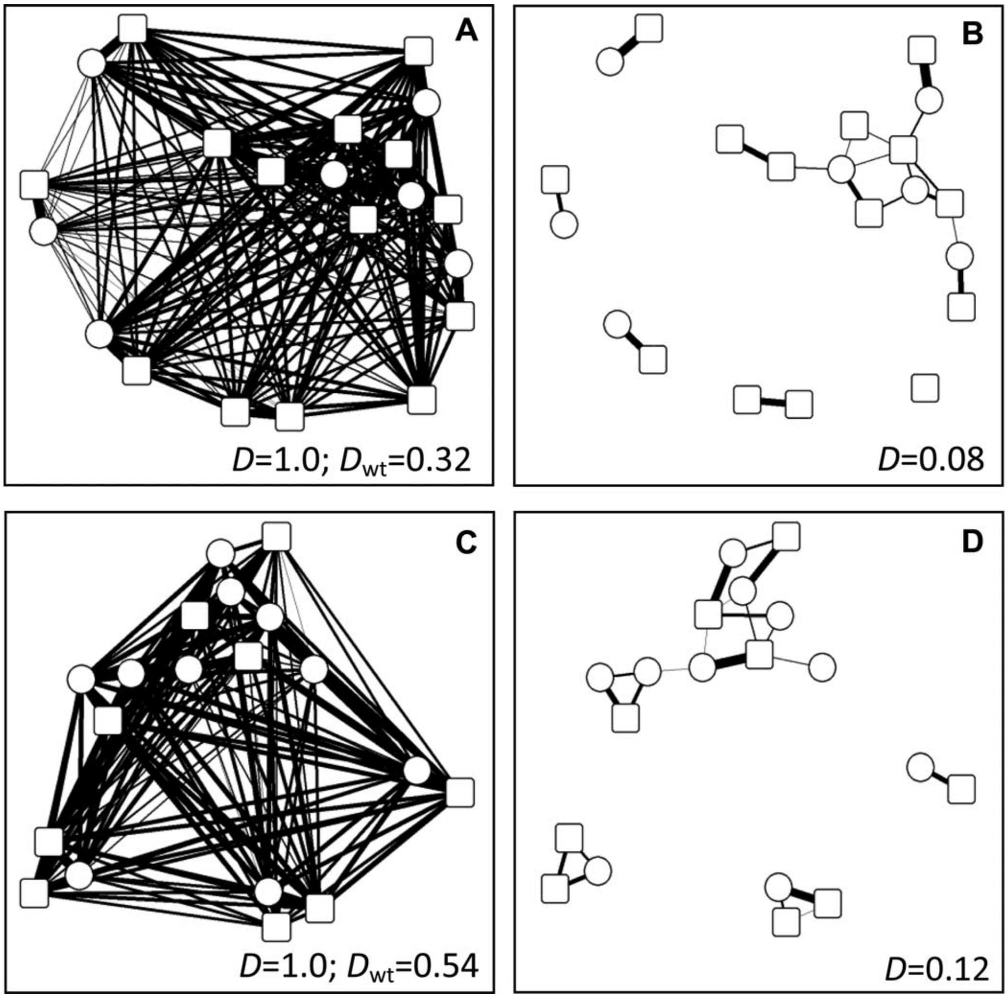

FIGURE 4. Association strength and allopreening networks in Monk Parakeets. Social network structure for captive group 1 (**A**, **B**) and captive group 2 (**C**, **D**). Networks depict group association strengths among individuals (**A**, **C**) and allopreening networks (**B**, **D**). Allopreening networks were filtered to exclude any ties based on a single occurrence of allopreening between individuals. Node shape indicates individual sex: Circles are females and squares are males. The widths of ties are proportionate to the strength of the relationships (either SRI association strength or the number of allopreening events). Density of networks (*D*) is given under each graph. In the case of networks of shared group membership (**A**, **C**), both binary network density (*D*) and weighted tie network density (D_{wt}) are shown.

associated with more individuals in networks of associations built on shared group membership data than in networks based on allopreening ties (Table 2). Association networks were perfectly connected in both captive groups 1 and 2, with all individuals associating at least once with all other individuals. Weighted association networks also had relatively high density (captive group 1, weighted density = 0.32; captive group 2, weighted density = 0.54), indicating that individuals frequently associated with a large proportion of the total potential associates within their groups. By contrast, networks built on allopreening ties were much less connected (captive group 1, density = 0.08; captive group 2, density = 0.12), indicating that individuals allopreened only a small proportion of their total available associates.

Fission–Fusion Dynamics

Parakeet flocks showed variability in group size, group cohesion, and group membership (Table 3). We evaluated a single dimension of fission–fusion dynamics, variability in flock size, in wild populations because we did not have enough marked individuals to estimate variability in group cohesion or group composition. In wild populations, the sizes of naturally occurring flocks (excluding experimentally provisioned foraging flocks) varied according to the activities of the flock (Table 1). Wild foraging, flying, and perched flock sizes all significantly differed in size (ANOVA: $P < 0.0001$; Figure 5A). Wild foraging flock size was significantly higher, and perched flock size was significantly lower (Tukey's HSD: P values for all comparisons <0.0001). We also found that variability in flock size differed by the

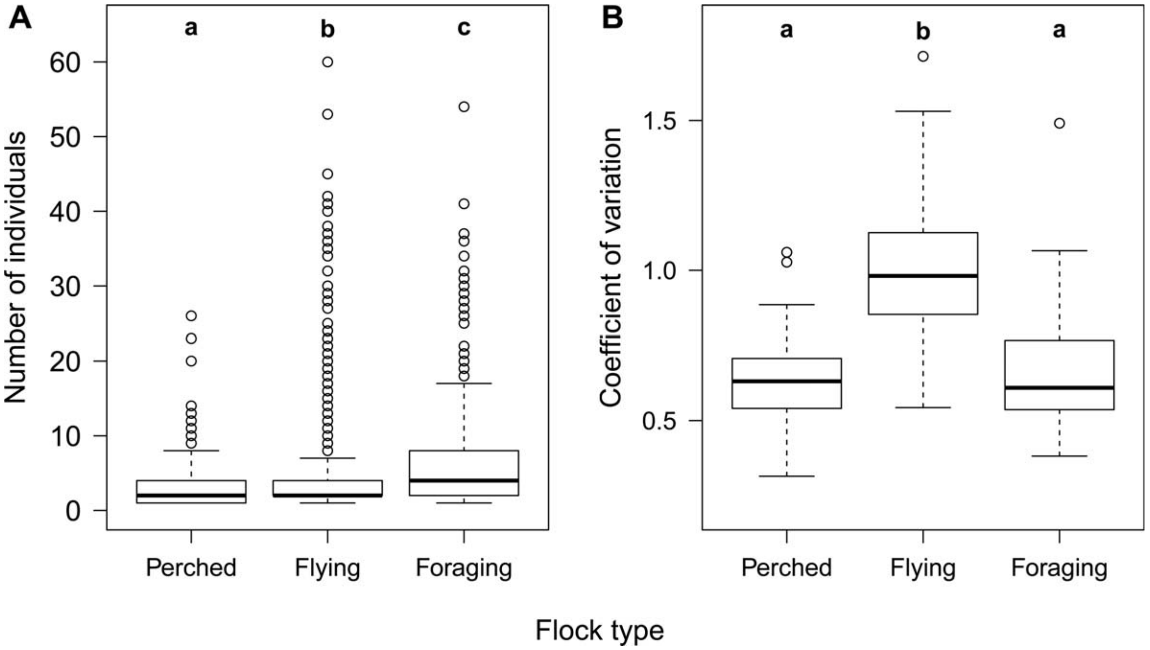

FIGURE 5. (**A**) Wild flock sizes by flock type and (**B**) variability of wild flock sizes of Monk Parakeets. Letters indicate significant differences among factors within plots ($\alpha = 0.05$, significant P values all <0.0001).

activity of the flock (ANOVA: $P < 0.0001$; Figure 5B). When we considered the variability of flock sizes by flock activity, we found that flying flock sizes were significantly more variable than foraging or perched flocks (Tukey's HSD: $P < 0.0001$), but that foraging and perched flocks did not significantly differ in variability (Tukey's HSD: $P = 0.3018$).

In captive groups, we evaluated all 3 dimensions of fission–fusion dynamics. Captive group 1 had slightly lower mean flock size, higher interindividual distances, and lower mean flock association strength than captive group 2 (Table 3). We found consistent differences in the variability of fission–fusion dimensions across replicate social groups. In both captive groups, flock size was most variable, flock spatial cohesion was moderately variable, and flock composition was least variable (Figure 6).

Aggression and Dominance

We observed 1,013 aggressive events in captive group 1 and 1,360 events in captive group 2, although the severity of aggression was relatively low and observed injuries rare in each group. Levels of aggression varied across individuals, but no individual in either group was responsible for >16% of total observed aggressive events (Figure 7). We found no evidence that males and females had separate dominance hierarchies. Overall levels of aggression did not differ by sex in either group (Welch's two-sample t-test: captive group 1, $t_{10.65} = 0.1599$, $P = 0.876$; captive group 2, $t_{13.11} = -0.7409$, $P = 0.4718$). We also found no evidence that sex had any effect on the target of aggression; individuals did not direct more aggression toward same-sex individuals than toward other individuals (Kr-test: captive group 1, male–male: $P = 0.9999$, female–female: $P = 0.9365$; captive group 2, male–male: $P = 0.9988$, female–female: $P = 0.9852$).

We found evidence that Monk Parakeet groups are structured by dominance hierarchies (Table 4). Both captive groups could be ranked into a linear dominance hierarchy: Captive group 2 showed minor uncertainty in

TABLE 2. Network structure for association and allopreening networks in Monk Parakeets. "Mean ties" indicates the mean number of ties present for binary networks or the mean tie strength for weighted networks. Allopreening networks are based on allopreening behaviors observed more than once during the study periods; ties that represent a single instance of allopreening between 2 individuals were excluded from the analysis.

	Captive group 1			Captive group 2		
	Mean ties	Range	Density	Mean ties	Range	Density
Binary association networks	20	–	1.00	18	–	1.00
Weighted association networks	6.7	4.1–7.4	0.32	9.7	8.4–10.6	0.54
Binary allopreening networks	1.6	0–5	0.08	2.1	1–4	0.12

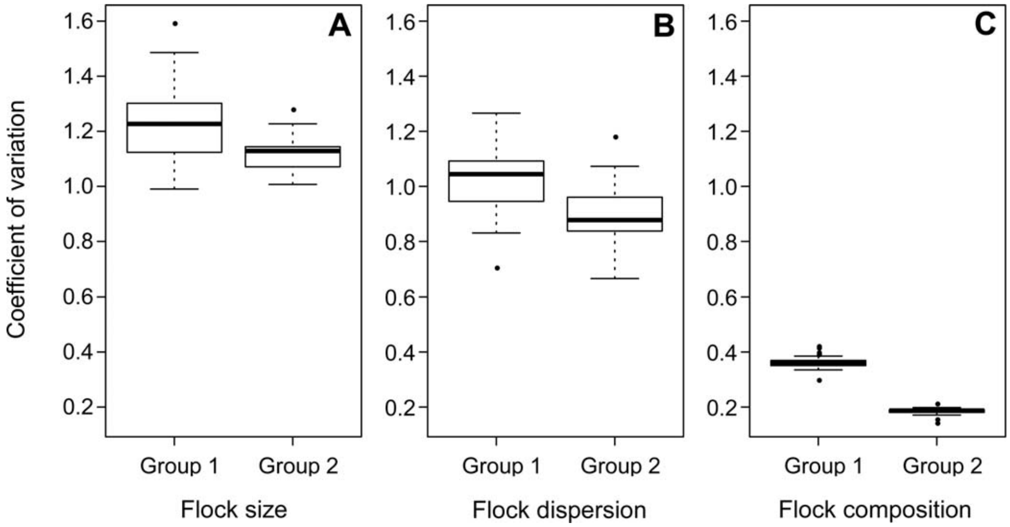

FIGURE 6. Variability in fission–fusion dynamics in captive groups of Monk Parakeets. Variability in captive groups 1 and 2 in flock size (**A**), flock dispersion (**B**), and flock composition (**C**).

the relative rank of 2 individuals, whereas captive group 1 showed no alternative rankings (Figure 7). We also found no evidence of reciprocity in aggressive events between individuals, which indicates that aggressive events between individuals were unidirectional (Kr-test: $P = 1.0$ for both captive groups 1 and 2). Although dominance hierarchies in both captive groups were significantly linear and aggression was unidirectional, linearity values were moderate (Table 4). Dominance steepness values were very low in both captive groups, and only captive group 1 had a significantly steep hierarchy (Table 4).

Foraging Information Exchange

We used observations of flock call-and-response patterns to evaluate whether foraging flocks displayed vocal recruitment behaviors to actively recruit flying flocks directly to foraging resources. We collected data on calling patterns in 4,035 wild flocks, 3,158 flying flocks, and 862 natural foraging flocks. Of these flocks, 92.2% vocalized in flight, whereas only 10.9% of foraging flocks vocalized while foraging. We collected data on response patterns for 2,295 flying flocks that called during flight and found that 15.7% of flying flocks received vocal responses from other flocks. In foraging flocks that vocalized, we observed only 2 cases in which vocalizations appeared to be contact calls directed to other flocks, which amounted to a response rate of 2.1%. We did not observe any instances that followed the predicted contact-call-exchange behavior of foraging flocks calling to flying flocks that resulted in flying flocks landing with foragers. Although flying flocks frequently joined foraging flocks, none of these arrivals was preceded by vocalizations from the foraging flocks.

We observed a total of 1,364 foraging flocks in the wild: 862 natural unprovisioned flocks and 502 flocks foraging on experimentally provisioned areas. Flock sizes were significantly larger in experimentally provisioned flocks than in natural unprovisioned flocks (Table 1; Welch's two-sample t-test: $t_{613.14} = 9.4125$, $P < 0.00001$). Despite increased resource availability, the larger flock sizes observed in provisioned sites do not appear to be due to direct recruitment to foraging sites. We found no evidence of direct recruitment through call exchanges in either natural or provisioned foraging groups. Foraging groups showed slightly higher rates of calling in natural foraging

TABLE 3. Fission–fusion measures and variability in captive groups of Monk Parakeets. Summary of results of quantification of fission–fusion dynamics by observation day ($n = 24$ days for each captive group). Mean values (± SD) are listed for each group: mean of mean daily flock size (number of individuals in each flock), mean of mean daily interindividual distance (distance between birds measured in quadrats), and mean of mean daily flock association strength (mean flock simple ratio index).

	Captive group 1		Captive group 2	
Fission–fusion measure	Mean	Mean CV	Mean	Mean CV
Flock size	3.228 ± 2.688	1.228 ± 0.153	4.302 ± 3.873	1.119 ± 0.069
Interindividual distance	1.042 ± 1.013	1.021 ± 0.132	0.957 ± 1.064	0.896 ± 0.123
Flock association strength	0.467 ± 0.170	0.365 ± 0.293	0.628 ± 0.116	0.185 ± 0.014

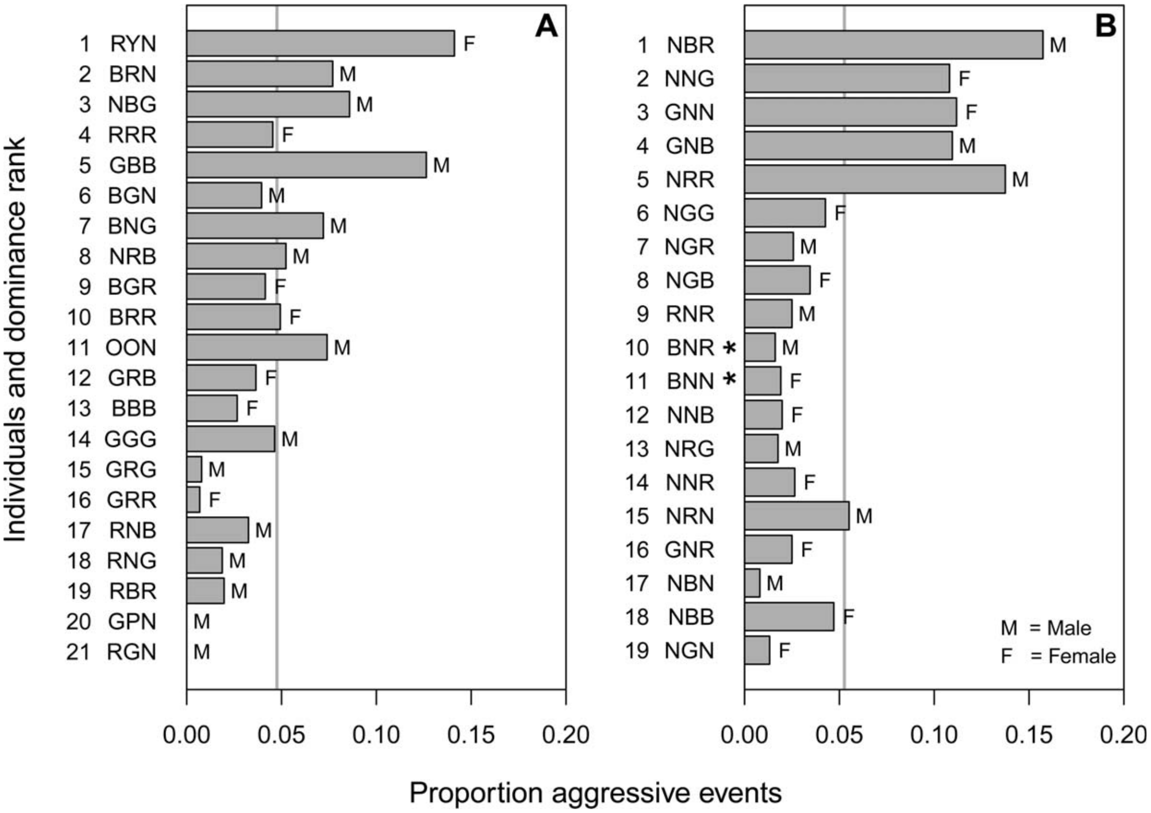

FIGURE 7. Rank and aggression in captive groups of Monk Parakeets. Bars show the proportion of total group aggressive events by individual for captive group 1 (**A**) and captive group 2 (**B**). Individuals are shown in order of dominance rank, where rank 1 is the most dominant individual. The gray vertical line shows the mean proportion of aggressive events for each group. Individuals for which rank order was indeterminate are highlighted with asterisks: Alternative rank order was 10 BNN, 11 BNR.

groups (12.7%, $n = 71$ flocks) than in provisioned groups (7.8%, $n = 25$ flocks), although calling during foraging was not frequently observed in either case. We also examined the types of calls that foraging groups used. In natural foraging groups, 16.9% of calls given by vocalizing groups were long-range contact calls, whereas 0% of calls in provisioned groups were long-range contact calls. We again did not observe any instances of active vocal recruitment that were consistent with our predicted pattern (i.e. active vocal exchanges between a flying flock and a foraging flock that concluded with the flying flock joining the foraging flock). Although we were prepared to record potential vocal recruitment calling, we were unable to obtain any call–response vocal sequences during foraging because these behaviors were never observed.

DISCUSSION

We used data from wild and captive populations of Monk Parakeets to examine several common, but largely untested, assumptions about parrot sociality. We assessed whether (1) pairs are the fundamental unit of social structure, (2) fission–fusion dynamics are high, (3) dominance hierarchies occur in parrot groups, and (4) individuals actively share foraging information. We found evidence that supported pairs as the fundamental unit of social structure, although these close associates were not always heterosexual breeding pairs and were sometimes trios. Fission and fusion of subgroups were common, and these dynamics were consistent across replicate captive social groups. Despite these high levels of fission–fusion

TABLE 4. Summary of dominance results in Monk Parakeets (values in bold are significant at alpha = 0.05).

	Number of aggressive events by individual			Interacting dyads	Linearity			Steepness	
Captive group	Mean	Median	Range	%	h′	*P*	P_{ij}	D_{ij}	*P*
1	48.24	42.0	0–143	88.6	0.673	<**0.001**	0.132	0.086	**0.012**
2	71.58	41.5	11–214	91.8	0.676	<**0.001**	−0.047	−0.025	0.702

dynamics, moderately linear dominance hierarchies formed in both captive groups. Finally, we found no evidence that Monk Parakeets shared foraging information among groups through direct recruitment to foraging flocks. This evaluation of Monk Parakeet socioecology provides methods that can be used to quantitatively understand social structure in other parrots and other social species in general. Below, we describe how increased understanding of parrot social structure could provide insight into the evolution of social complexity in other species and discuss potential future directions for parrot social research.

Fundamental Social Unit

Our evidence supported the assumption that the pair is the fundamental unit of Monk Parakeet social structure. The modal flock size was 2, although mean flock sizes were >2 in both wild and captive groups. We also found that individuals in captive groups generally had highly connected networks based on flock membership, with very strong associations with 1 or 2 other individuals, multiple moderate associates, and only a few weak associates. By contrast, networks of allopreening relationships were much less connected, and individuals were more selective in their choice of allopreening partners than in their choice of flock members. These patterns of flock size, preferred association strength, and highly selective allopreening partners support the pair as the fundamental unit of social structure in Monk Parakeets.

Although we found evidence that pairs are important in Monk Parakeets, these relationships did not always reflect potential breeding pairs and sometimes included >2 individuals. Preferred association partners were generally individuals of the opposite sex, but we observed 2 strong associations between same-sex individuals. In addition, allopreening, purported to be behavior used to reinforce the pair bond, was not exclusively observed in heterosexual breeding pairs. Furthermore, we found evidence for 2 strongly associated trios in captive group 2. Trios have been previously observed in captive Monk Parakeet groups (Emlen 1990) and in wild Monk Parakeet populations despite equal sex ratios, although they appear to be relatively rare in the wild (Eberhard 1998). In our case, the captive conditions, especially restrictions on available partners, may have affected natural patterns.

Across parrots, flock sizes of 2 are commonly observed (Juniper and Parr 1998). However, because few studies involve identifiable individuals, we currently know little about the stability of pair associations or the benefits of associating with specific individuals for most species in the wild. Future research focused on studies of how individuals interact with other individuals will be critical in answering these questions.

Fission–Fusion Dynamics

We developed a method to quantify 3 dimensions of fission–fusion dynamics, based on previous recommendations (Aureli et al. 2008). We quantified variability in flock size, variability in flock spatial cohesion, and variability in flock membership in captive groups; and variability in flock size for several types of flocks in the wild. We found evidence that captive Monk Parakeet flocks vary in their size, cohesion, and membership but that the degree of variability, as assessed by the CV of daily flock measures, differed among the fission–fusion dimensions. We found the most variability in flock size, moderate variability in flock spatial cohesion, and the lowest variability in flock membership. Naturally occurring flocks in the wild ranged in size from single individuals to large flocks almost certainly composed of individuals from several separate nests. In some cases, these large flocks may represent individuals from several separate colonies fusing together. In the wild, flock sizes were significantly different, depending on whether the flock was perched, flying, or foraging. These differences in flock sizes indicate that flock dynamics, or the patterns of merging or splitting, differed depending on the flock activities. We found that mean foraging flock size was largest, and these flocks probably represented the fusion of several smaller flying flocks.

Across parrots, different species are likely to exhibit varying levels of fission–fusion dynamics, and these dynamics may not be tied directly to gregariousness (i.e. the propensity of individuals to flock together). Differences in fission–fusion group dynamics are hypothesized to drive some of the differences observed between species, such as geographic variation in parrot vocalizations (Cortopassi and Bradbury 2006). Parrots are also likely to exhibit seasonal shifts in fission–fusion dynamics because many species reduce communal roosting behaviors during the breeding season (Juniper and Parr 1998, Harms and Eberhard 2003, Cougill and Marsden 2004, Matuzak and Brightsmith 2007, de Moura et al. 2010). Future research into the costs and benefits of fission–fusion patterns may provide insight into the factors driving fission–fusion dynamics and social structure.

Characterizing social structure is especially challenging in species with high fission–fusion dynamics (Aureli et al. 2008) because group membership can change frequently, as groups form and then subsequently dissolve or merge with others to form new groups (Cross et al. 2005). Species differ in the level of fission–fusion dynamics, from stable groups with low levels of fission–fusion dynamics to dynamic groups in which membership is much more fluid. Species that exhibit very high fission–fusion dynamics, whereby group membership changes on a time scale of minutes, make characterization of social structure and the nature of social interactions frustratingly difficult. However, a quantitative understanding of the social structure of a species will help us better understand social behavior and selection pressures, and recent research has documented high levels of social organization in groups with very fluid fission–fusion dynamics (Carter et al. 2013). Because no other study has used a CV-based method to quantify the amount of variability in all 3 of the hypothesized fission–fusion dimensions of group size, group spatial cohesion, and group membership, we are currently unable to determine where Monk Parakeets fit on a fission–fusion dynamics continuum in relation to other species. The previous lack of a generalizable method for quantifying fission–fusion dynamics has hampered comparison of intraspecific and interspecific variation in fission–fusion dynamics. We believe that our methods will enable cross-species comparisons of fission–fusion dynamics, although they require a population in which all individuals can be identified and geolocated (e.g., Mennill et al. 2012, Krause et al. 2013).

Aggression and Dominance

Our work provides the first detailed quantitative study of parrot dominance hierarchies under more natural housing and social conditions. Both groups of Monk Parakeets developed moderately linear hierarchies over a relatively short time span in seminatural captive conditions. We found no evidence that sex affected either the overall levels of aggression or how aggression was directed at others. These results indicate that Monk Parakeet groups had integrated dominance hierarchies, rather than the sex-separated hierarchies observed in some mammal groups, such as hyenas (Holekamp et al. 2012). These results demonstrate that Monk Parakeets have the potential to develop linear and transitive dominance hierarchies, but whether dominance structure forms or is important in wild groups remains an open question.

Previous studies of captive parrots have provided some evidence of dominance hierarchies, but unnatural social-grouping conditions and differences in dominance hierarchy construction and analysis methods limit the utility of comparisons to our data. These studies found evidence for linear dominance hierarchy structure in small groups of captive Budgerigars (Masure and Allee 1934, Soma and Hasegawa 2004) and Cockatiels (Seibert and Crowell-Davis 2001), whereas dominance in a small group of captive Keas was nonlinear, with several rank reversals (Tebbich et al. 1996). There was also evidence of seasonal variation in Budgerigars: Females dominated males in the nonbreeding season, whereas males dominated females during the breeding season (Masure and Allee 1934). Our study of Monk Parakeet hierarchies took place during the summer, when breeding in wild and feral populations occurs, but our captive population was not actively breeding. In contrast to Budgerigars, our results from Monk Parakeets indicate that they form sexually integrated hierarchies; more research is required to determine whether this pattern varies seasonally. More study of groups interacting in more natural conditions and with modern dominance hierarchy analysis methods is needed before any generalizations can be made about the prevalence and strength of dominance hierarchies in parrots.

Although both captive groups of Monk Parakeets developed hierarchies that were moderately linear, steepness values for both groups were very low, indicating that the outcome of aggressive interactions between adjacently ranked individuals was relatively unpredictable (Whitehead 2008). In comparison to other groups, Monk Parakeets have some of the lowest dominance steepness measures currently reported (Figure 8). Methods to measure dominance steepness were developed only recently (de Vries et al. 2006), and few steepness measures have been reported so far. Those that have been reported are largely from primate groups. This study is one of the first to quantify dominance steepness for any avian species. Despite captive conditions, which may increase dominance steepness (Stevens et al. 2007), our captive Monk Parakeets had moderately linear dominance hierarchies with very low steepness values. Solely on the basis of these low steepness values, our 2 captive groups of Monk Parakeets would be classified on the egalitarian side of the egalitarian–despotic continuum (van Schaik 1989, de Vries et al. 2006).

Egalitarian species tend to forage on dispersed food resources that are difficult for individuals to monopolize and are generally characterized by low monopolization of reproductive opportunities (Vehrencamp 1983). Parrot natural-history information provides indications that foraging and reproductive resources may be costly, difficult, and, in some cases, unfeasible for individual parrots to monopolize. For example, parrots typically range widely in search of food, such as ephemeral fruiting crops, that may be difficult to defend or monopolize (Juniper and Parr 1998). Future research into the dominance structures and resource monopolization opportunities in parrots may provide important insight into the evolution of dominance hierarchies, especially if they occur under conditions that do not normally favor resource monopolization.

Alternatively, the formation of a linear dominance structure with low steepness values could be an indication that existing steepness measures are not appropriate methods to determine rank-related differences in the ability to win contests in a species with pair-based social structure or strong affiliative bonds that offset aggression. Our study showed that individuals formed affiliative relationships with other group members, both at and beyond the level of the most preferred partner. If preferred associates have similar ranks, currently available steepness

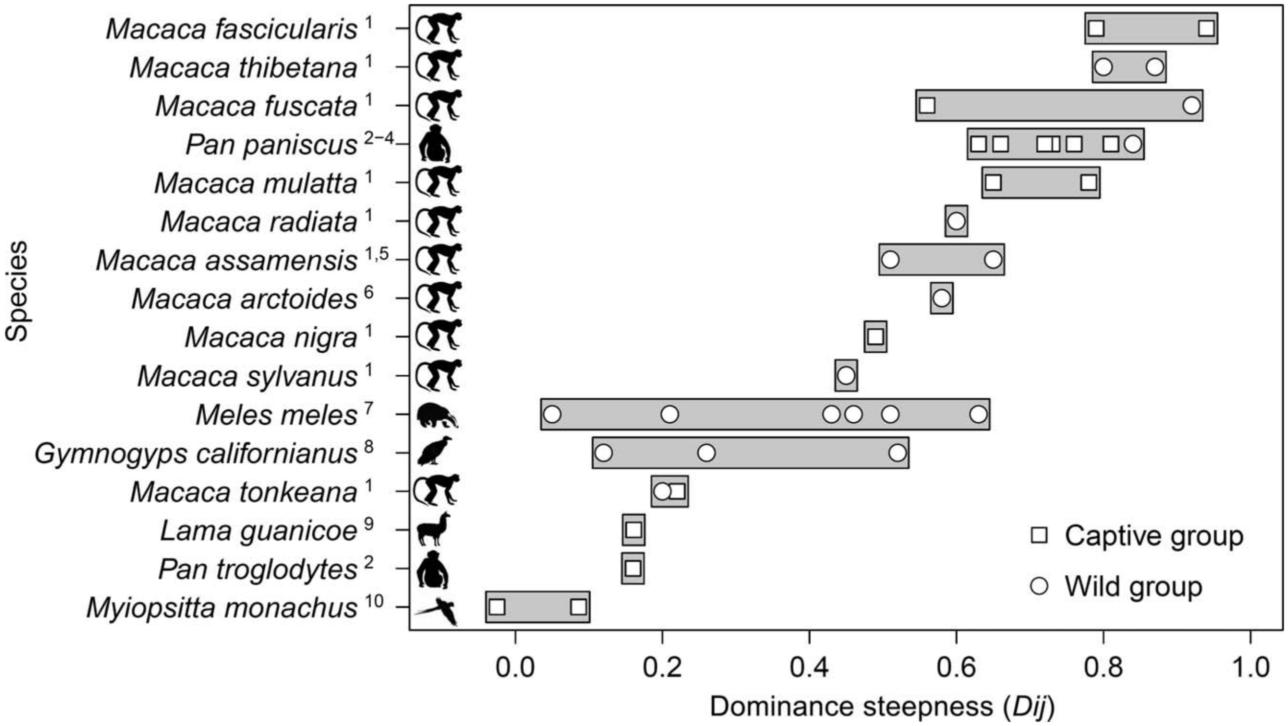

FIGURE 8. Dominance steepness across species. Dominance steepness (D_{ij}) measures reported for wild and captive adult groups, with species ordered by mean reported steepness values. Silhouettes indicate the type of animal. Superscripts indicate data sources: [1] Balasubramaniam et al. 2012; [2] Jaeggi et al. 2010; [3] Stevens et al. 2007; [4] Surbeck et al. 2011 (D_{ij} method, corrected value = 0.84, pers. comm.); [5] Ostner et al. 2008 (D_{ij} method, pers. comm.); [6] Richter et al. 2009; [7] Hewitt et al. 2009; [8] Sheppard et al. 2013; [9] Correa et al. 2013; [10] present study.

measures may be inappropriate for describing characteristics of the overall group dominance structure, because they are focused on differences in winning between adjacently ranked individuals. Reanalysis of species with a combination of significantly linear but shallow hierarchies is likely to provide insight into the relationship between hierarchy structure and affiliative ties. For groups in which strong affiliative ties exist along with dominance rank, alternative measures of dominance steepness may need to be developed.

Exchange of Foraging Information

During our observations in the austral winter, we found no evidence that wild individuals shared foraging information by active vocal recruitment of others directly to foraging resources. Although the majority of flying flocks called during flight, they elicited very low response rates in general and were never responded to by foraging groups during our observations. Foraging flocks were much less vocal than flying flocks and rarely gave contact calls while foraging. We also found no evidence that the presence of a novel food resource increased information-sharing behaviors. Natural foraging flocks occasionally gave contact calls while foraging, but experimentally provisioned foraging flocks were never observed contact-calling in return.

By contrast, another parakeet species of similar size, the Brown-throated Conure, displays calling behaviors that may function as a means of active information sharing (Buhrman-Deever et al. 2008). Individuals in flocks flying past a foraging group were more likely to land and join a group foraging in a tree if a member of the foraging group called to the flying group. However, Brown-throated Conure foraging groups did not call to all flying groups, which indicates that individuals may selectively share information (Buhrman-Deever et al. 2008). In wild Monk Parakeets, flying groups frequently landed with foraging groups despite the lack of vocal recruitment. Targeted information sharing may not be necessary for information to be shared with others in Monk Parakeets: Flying flocks are apparently able to easily notice foraging flocks and scrounge foraging information. The difference in recruitment behaviors and information sharing may be due to differences in habitat and foraging preferences between the 2 species. Short grass is a preferred feeding habitat for Monk Parakeets (Bucher and Aramburú 2014), and during our observations in the austral winter the Monk Parakeets spent the majority of their time foraging on the ground in low grass. By contrast, Brown-throated Conures forage in thickly vegetated trees, where they are much less visible to passersby. This more cryptic foraging style likely makes scrounging foraging information from observations more difficult for flying flocks, and reciprocal sharing of foraging information may be more important for locating suitable foraging resources in this species than in the Monk Parakeet. Further research, across more species, into foraging behavior and the propensity to share information is needed to determine whether information sharing is common or rare in parrots.

Parrot Socioecology and the Evolution of Social Complexity

Future research on social structure and social interaction patterns in parrots and other highly social avian taxa could provide insight into the evolution of complex sociality, cognition, and intelligence in other species. Hypotheses such as the social intelligence hypothesis (Humphrey 1976), the Machiavellian intelligence hypothesis (Byrne and Whiten 1988), the social brain hypothesis (Dunbar 1998), and the social complexity hypothesis (Barton 1996) all propose that large brains are adaptations to perceive and process the complex social relationships that are characteristic of many primate species. Although research into the evolution of social complexity originally focused on primates, other species are also unusually large-brained and cognitively advanced, such as elephants, cetaceans, and pack-hunting carnivores among mammals, and corvids and parrots among birds (Emery 2006, Barrett and Würsig 2014).

Parrots represent an intriguing possibility for comparative research on the origin and evolution of social complexity because they share many characteristics with hominids and other primates. Both parrots and primates have similar relative brain volumes (Iwaniuk et al. 2005), are long-lived (Austad and Fischer 1992, Munshi-South and Wilkinson 2006, Young et al. 2012), have extended developmental periods (Iwaniuk and Nelson 2003, Emery 2006), live in complex social groups (Dunbar and Shultz 2007, Hobson et al. 2013), and show evidence of advanced cognition (Iwaniuk et al. 2005, Roth and Dicke 2005). Parrots also share additional characteristics with humans, which display the highest social and cognitive complexity of any species (Wilson 1975, Herrmann et al. 2007). Parrots are among the few taxa that display vocal learning, which is a defining characteristic of humans but is not widespread in nonhuman primates (Jarvis 2004). The structure of socially learned parrot vocalizations often varies regionally (Wright 1996, Bradbury et al. 2001, Buhrman-Deever et al. 2007, Wright et al. 2008), and social factors are known to have a strong influence on vocal learning (Snowdon and Hausberger 1997, Bradbury et al. 2001, Salinas-Melgoza and Wright 2012). Because vocal learning is fundamentally a socially driven phenomenon, deeper understanding of why parrots learn calls from certain individuals could provide insight not only into factors that affect vocal learning in parrots, but also into the evolution of vocal learning and social complexity. The high fission–fusion dynamics likely present in many parrot species may also more closely resemble the high fission–fusion dynamics of human groups (Aureli et al. 2008) and may provide insight into the selection processes that drive sociality in our own species.

The present study of Monk Parakeet socioecology provides the first detailed account of social structure in any parrot species. Our results showing that Monk Parakeet social structure is built on the basis of preferred dyadic bonds, and linear, but shallow, dominance hierarchies are evidence that Monk Parakeets have individualized relationships. These individualized relationships are maintained despite potentially high fission–fusion dynamics. Individualized relationships also extend past the preferred pair bonds to involve other group members (Hobson et al. 2013). We found evidence that Monk Parakeet association patterns could be divided into larger clusters beyond that of the pair. In the wild, we observed large flocks that likely represented secondary associations among multiple pairs and that potentially represent the fusion of individuals from multiple nests or colonies. In captive groups, several pairs were often observed perching or foraging together. These results may indicate the presence of additional tiers or units of social structure, potentially similar to social levels documented in elephants (Wittemyer et al. 2005, de Silva and Wittemyer 2012), sea lions (Wolf et al. 2007), and dolphins (Lusseau et al. 2006). Further study of Monk Parakeet social structures beyond the pair, especially in wild populations, in which maximum flock size and movements are not constrained by captive conditions, is needed to determine whether additional levels of social organization exist in Monk Parakeets and other parrot species.

These results provide intriguing insight into parrot social complexity. Some aspects of Monk Parakeet socioecology are similar to characteristics of social corvids such as Rooks (*Corvus frugilegus*). Like Monk Parakeets, Rooks form preferential pair-based relationships and appear to use allopreening almost exclusively between pair members to maintain these bonds (Emery et al. 2007). More study is needed to determine whether Monk Parakeets show similar postconflict affiliation, cooperative alliances, and problem-solving skills. Comparisons of parrot and corvid social structure have the potential to provide insight into the evolution of social complexity in birds and mammals. The similarities between parrots and other socially complex groups such as corvids and primates make parrots a taxon of potentially great value in the broader study of the costs, benefits, and drivers in the evolution of social complexity.

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CORRECTION

Erratum: The socioecology of Monk Parakeets: Insights into parrot social complexity

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ABSTRACT
Our recent work on Monk Parakeets (*Myiopsitta monachus*) reported dominance steepness values that were inaccurate because of a bug in the analysis program. Updated steepness values are more moderate than initially reported, which places captive Monk Parakeet groups midway between egalitarianism and despotism.

Keywords: dominance hierarchy, SOCPROG, steepness

Errata: Socioecología de *Myiopsitta monachus*: Perspectivas sobre la complejidad social de los loros

RESUMEN
Nuestro trabajo reciente sobre *Myiopsitta monachus* presentó valores incorrectos de pendiente de dominancia debido a un error en el programa de análisis. Los valores actualizados de pendiente son más moderados que los presentados originalmente, lo que ubica a los grupos cautivos de *M. monachus* a medio camino entre igualitarismo y despotismo.

Palabras clave: jerarquía de dominancia, pendiente, SOCPROG

The dominance steepness results for captive Monk Parakeets (*Myiopsitta monachus*) we reported (Hobson et al. 2014) were inaccurate because of a bug in the program we used for dominance hierarchy analyses. SOCPROG version 2.4 (Whitehead 2009) had an error in how steepness was calculated (H. Whitehead personal communication). We reanalyzed aggression for our captive Monk Parakeet groups using the R package 'steepness' (Leiva and de Vries 2014; 10,000 permutations). Dominance linearity was consistent with our originally published values. Steepness values are more moderate than previously reported (Table 1; steepness values replace those in Hobson et al. 2014: table 4). The D_{ij} steepness values are no longer on the extremely egalitarian end of the egalitarian–despotic continuum as previously reported (Hobson et al. 2014: figure 8). Rather, the updated values are now moderate for both captive groups, putting both groups in the middle of this continuum (Figure 1). Because captive conditions are likely to increase the chances of a steeper hierarchy (Stevens et al. 2007), dominance hierarchies for Monk Parakeets in the wild are still likely to be less steep, and more egalitarian, than those observed in captivity (Hobson et al. 2014).

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TABLE 1. Corrected dominance steepness values for captive groups 1 and 2.

Captive group	Steepness (P_{ij})	Steepness (D_{ij})
1	0.7462 ($p = 0.0001$)	0.5484 ($p = 0.0001$)
2	0.6603 ($p = 0.0001$)	0.5279 ($p = 0.0001$)

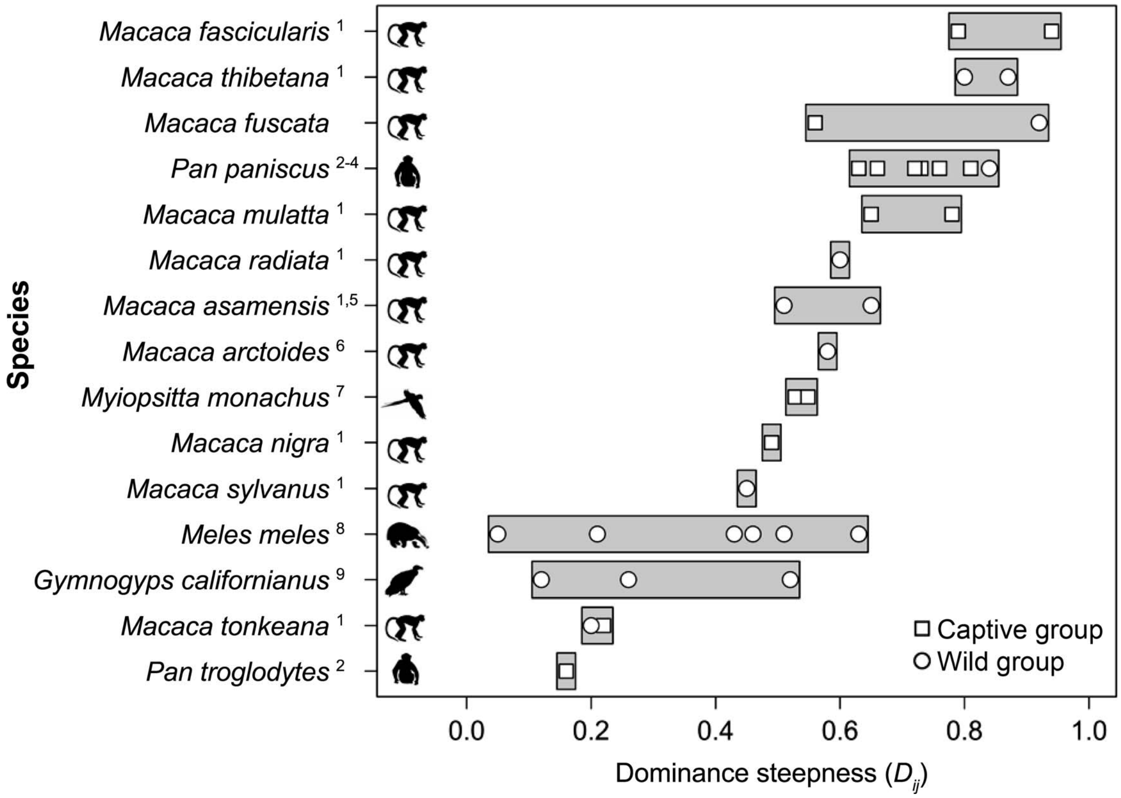

FIGURE 1. Dominance steepness across species. Dominance steepness (D_{ij}) measures are reported for wild and captive adult groups, with species ordered by mean reported steepness values. Silhouettes indicate the type of animal. Superscripts indicate data sources: [1] Balasubramaniam et al. 2012; [2] Jaeggi et al. 2010; [3] Stevens et al. 2007; [4] Surbeck et al. 2011 (D_{ij} method, corrected value = 0.84; personal communication); [5] Ostner et al. 2008 (*Dij* method, personal communication); [6] Richter et al. 2009; [7] Hobson et al. 2014 (revised steepness values); [8] Hewitt et al. 2009; [9] Sheppard et al. 2013. Steepness values for adult *Lama guanicoe* (Correa et al. 2013) that were reported in Hobson et al. (2014) were omitted from this revised version because that study reported using SOCPROG version 2.4 to calculate steepness.

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