Inferring the identifying features underlying association preferences in wild mixed species parrot groups

Vanessa Ferdinand[a], Elle Pattenden[a], Donald Brightsmith[b], and Elizabeth A. Hobson[c]

[a] *University of Melbourne;* [b] *Texas A&M University;* [c] *University of Cincinnati*

Abstract

Many animals participate in mixed-species aggregations for a variety of reasons, leading to species specific differences in benefits and costs, resulting in a variety of community assemblage patterns and dynamics based on what information individuals use to make joining decisions. Current research tends to focus specifically on "species" as a defining factor affecting joining decisions. However, we still have little understanding of how species perceive each other when making these decisions and what categories of perception are important (e.g., colour, group size). We propose a new approach: instead of assuming species recognition, we test what kind of information each species may use about others to make decisions about which mixed-species aggregations to participate in. We used data on mixed-species aggregations of 12 species of parrots, where the species vary widely in their overall size, colours, and potential motivations for joining different groups. We used co-occurrence and joining patterns with new computational methods to test how these parrot species make grouping decisions. Our results show that using these two perspectives, static co-occurrences and dynamic joining, provided very different insight into the ways species interact with each other. While some species used a more complex categorization system (based on 12 species), the majority of species (7 of 12) used simpler category systems based on two or three categories. We found that not only does this approach provide a framework to test hypotheses about why individuals join or leave mixed species aggregations, it also provides insight into what features each parrot likely used to make their decisions. In doing so, our approach goes farther than previous approaches and provides a link to the perceptive and cognitive abilities of the animals making these minute-by-minute decisions.

Keywords

Categorization, coarse-graining, social decision-making, species co-occurrence, social interactions

Introduction

Many species form mixed species animal groups through interspecific attraction [16]. These groups bring individuals from multiple species into close contact and can often help individuals increase their foraging efficiency or decrease their risk of predation [16, 17, 21]. Understanding

1

why species associate with other species can provide insight into the resource needs of each species, the competitive dynamics operating within a community, and the relative costs and benefits of being in close proximity to other species. Some mixed species groups can be quite stable, either involving the same mix of species, or the same individual members of the group [12, 13], with individuals remaining together over weeks, months, or years. Other mixed species groups form and break apart on a much shorter timescale over minutes to hours.

Ephemeral associations could provide insight into the types of information individuals use to make decisions about the composition of the mixed-species groups with which they associate. When studied, this has usually been analyzed as either interaction rules each species uses to make collective decisions which can be based on simple rules of attraction based on group size (e.g., [12]) or attraction or repulsion between each species (e.g., [16, 17]). These patterns are each based on different information: a species using a simple rule of attraction may only need to perceive the number of individuals in a group, while a species which changes its behavior depending on the presence of individuals of other species needs to recognize each different species, resulting in species-level relationships that predict individual co-occurrences. However, the species-level characteristics that we often use as researchers may not accurately represent the different ways animals themselves categorize each other. Species may use varying types of information about each other to decide whether to join, remain in, or leave a mixed-species aggregation. Individuals may not focus on which particular species is present, but potentially on physical characteristics like size or color of group members, especially if dilution of predation risk drives these associations.

Potential categorization systems represent different ways that available information can be summarized or *compressed* by individuals. Compression is a form of information reduction which can remove redundancies and noise in observations [14, 19, 20]. When compression results in a simplified representation, especially if continuous characteristics are grouped into discrete categories, this is often referred to as *coarse-graining*. In the context of mixed-species groupings, individuals may not focus on which particular species is present, but rather on categorical information. For example, evaluating color may be important in areas with predation risks, where individuals may preferentially associate with groups that match its main color and avoid groups where it would be an unusual minority color and could be subject to higher predation risks. All of these decisions are based on keying in to different types of information and provide different insights into which information the individuals themselves value or are able to evaluate in making decisions.

These coarse-graining methods may help animals better process the often complex information available to them to more easily or efficiently use parts of the information. Individuals may have evolved information-reduction processes like coarse-graining to collapse rich observational information into more manageable categories in order to more quickly and effectively make decisions [20]. Thinking carefully about coarse-graining is critical to taking an animal's perspective on the kinds of information it is able to perceive, process, and use [19].

Temporary species aggregations with high turnover provide a unique situation in which to test how and why individuals of one species associate with individuals of other species, and especially to investigate the categories of information these decisions may be based upon. Here, we use a suite of statistical and network methods to better understand how individuals make decisions about associating with other species. We use data from parrots that form temporary mixed-species aggregations to eat clay on exposed river banks in Peru. Individual parrots make decisions about

when to visit the clay wall, where to land on the wall, and when to depart. In this system, clay consumption is thought to provide necessary nutrients such as sodium, which are otherwise rare in the tropical environment [5]. Individuals interact frequently with other species at the clay, often by responding to alarm calls and aggressing against other species. Due to these interactions, individuals likely make grouping decisions to balance three factors: to access needed resources, to decrease predation risk, and to avoid species which may be aggressive towards them.

We analyzed data on clay lick use for 12 species of parrots. These species vary in several characteristics, most obviously in size, shape, and color. Species vary in size from very small parakeets (Dusky-headed parakeet, *Aratinga weddellii*, 108g) up to the largest macaws (Red-and-green macaw, *Ara chloropterus*, 1250g). Variability in size likely affects heterospecific interactions (for example, aggression from larger species towards smaller species) but could also affect predation risk. Species also vary in shape from species with long tails and narrow wings (e.g. parakeets and macaws) to species with short tails and blunt wings (e.g. large parrots). These differences in body configuration affect how each species flies and their agility, which could be important for flying in mixed groups or for predator avoidance. Additionally, species also vary in plumage coloration, with back colors of green, blue, or red, and facial colors of white, grey-green, yellow, orange, and blue. These variations in plumage color could be important for predation avoidance; previous research has suggested this may be important in grouping dynamics, but has not specifically tested for this pattern [7]. Overall, this variability in characteristics provides a range of information that species could potentially use to make decisions about which other species to associate with on the wall.

We use grouping patterns and dynamic decision-making about which groups to join or leave to infer the likely types of information species may be using to make these decisions. The balance of costs and benefits may be different for each species and may vary based on the composition of species in the group. The perceptual and discrimination abilities may also differ across species. To test how each species makes grouping decisions, we divide information into different levels to determine which best explains the association patterns for each species of parrot as they make decisions about which ephemeral aggregations to join in order to consume clay. Our coarse-graining methods allowed us to categorize individuals in different ways to test which species are "interchangeable" with one another at the species level, then see if a coarser categorization could better explain co-occurrence patterns. To do this, we (1) quantify mixed-species co-occurrence patterns, (2) quantify dynamic joining decisions, and (3) use both co-occurrence and joining patterns to identify the categorization systems most likely used by each species to make decisions about how to associate with other species. Our results show that using these two perspectives, static co-occurrences and dynamic joining, provides very different insight into the ways species interact with each other. Overall, a better understanding of the information that individuals are using to make their decisions would help better predict multi-species grouping behaviors, potentially help understand how and why these groupings might change, and could provide novel insight into the cognition underlying this decision-making process.

Methods

Data sources and processing

We used observations of parrots visiting the Colpa Colorado clay lick in southeastern Peru ($13°08'$S, $69°37'$W), which is part of a long-term monitoring project. The clay lick is a 500 meter long and

25-30 meter tall cliff eroded out of the western bank of the upper Tambopata River. The soils of the clay lick have high levels of sodium and cation exchange capacity [6, 15, 23]. This clay lick is used by over 29 species of birds including 18 species of parrots [4].

We used eleven years of data collected from 2002 to 2012. Observations at the clay lick take place year-round. Starting when the first birds visit the clay lick at dawn, observers at the clay lick conduct scans every 5 minutes. In each scan, they record the number of individuals of each species present on each area of the cliff. Because previous studies have shown that clay lick visitation varies at different times of year for different species [5], we used data from a single season for our analyses. We chose the early wet season (October to December), which is a season of high activity at the clay lick [5]. We also focused on the early morning observation periods, which is when the most species visit the clay (see Supplemental Figure S1). We filtered the data to include only scans before 09:00.

We focused our analyses on the 12 species that were frequent visitors to the clay lick (see Table S1): Blue-headed parrot (BH, *Pionus menstruus*), Blue-and-yellow macaw (BY, *Ara ara-rauna*), Chestnut-fronted macaw (CF, *Ara severus*), Dusky-headed parakeet (DH, *Aratinga wed-dellii*), Mealy parrot (ME, *Amazona farinosa*), Orange-cheeked parrot (OC, *Pyrilia barrabandi*), Red-bellied macaw (RB, *Orthopsittaca manilata*), Red-and-green macaw (RG, *Ara chloropterus*), White-bellied parrot (WB, *Pionites leucogaster*), White-eyed parakeet (WE, *Psittacara leucoph-thalmus*), and Yellow-crowned parrot (YC, *Amazona ochrocephala*). We included only scans in which there was at least one individual of one of these 12 parrot species present. To facilitate data collection, the clay lick is divided into standardized zones. To facilitate comparisons across years, we used scans from 12 zones: 1A, 1B, 1C, 2A, 2B, 2C, 3A, 3B, 3B1, 3B2, and 3C. We excluded any scan with a nonstandardized location code and any scans missing a date and time.

Prior to starting any analyses, we split the available data into two parts: one for exploration and one for validation. This allowed us to use half the data for exploratory analyses and to generate hypotheses, which can then later be tested using the other half of the data. This process allowed us to focus on exploratory analyses but preserved our ability to then use these results for hypothesis testing in a way that avoids 'HARKing' (*Hypothesizing After the Results are Known*). We partitioned the data into two halves by whether the dates of the observations occurred on odd or even days and randomly chose to use the even-numbered days for exploration (preserving the odd-numbered days for validation). The post-processed data set contained a total of 7357 scans in the exploration set. All data processing and analyses were conducted in the R programming environment [24].

Summarizing the extent to which species mix

To describe the basics of our mixed species aggregations, we first quantified the extent to which species were found within mixed groups using two summary measures. First, we determined the total number of species present during each 5-min scan and report the frequency at which we observed different numbers of species together. We analyzed this for two spatial scales: across the entire wall and within each zone on the wall. Second, we quantified the species diversity of groups observed during each 5-min scan on the same two scales using Shannon entropy in the R package *vegan* [10, 22].

Quantifying species-level associations using co-occurrence patterns

We analyzed the overall structure of inter-species associations on the clay lick. For our purposes, individuals of one species are scored as co-occurring with individuals of another species if they are observed on the same zone during the same 5-minute observation scan. For each pair of species, we counted the number of scans in which at least one individual from both species was located on the same zone at the same time. This approach uses only presence or absence of inter-species co-occurrences rather than the total number of individuals of each species involved. We used these data to build association networks, where the nodes in the network represent species and the edges represent their co-occurrence patterns. All network processing and plotting was done with the package *igraph* [9].

We constructed a species-level social network with two types of edges: one representing affiliative edges and another representing avoidant edges. Affiliative edges occur when the observed number of co-occurrences between two species was higher than expected by chance and avoidant edges occur when observed co-occurrences were lower than expected by chance. We used two statistical methods to find statistically significant affiliative or avoidant associations: an uncontrolled binomial test and a controlled linear mixed effects regression. Each of these methods provides a unique and complimentary perspective on the co-occurrence patterns at the clay lick.

First, we used an uncontrolled binomial method to find the probabilities of co-occurrences among all species pairs. Edges were ruled as statistically significant by conducting a two-tailed binomial test where k is the observed number of co-occurrences between two species, N is the total number of observations, and θ is the independent probability of observing the two species in the same observation, given each species' baseline probability of appearing in the dataset. Where the binomial test yielded a significant result between two species, an edge was ruled in between them, and the type of the edge (affiliative or avoidant) was determined by the tail in which k fell. We conducted 66 pairwise comparisons (to evaluate 66 undirected edges without self-loops) and significance levels were corrected for multiple comparisons using the Bonferroni method [3], a highly conservative method for reducing false positives [18], yielding a significance threshold of $p < 0.05/66 = 0.000\overline{75}$.

Second, we conducted a linear mixed effects regression (lmer) using the R package *lme4* [2] to control for other factors, such as preferences for foraging on certain zones or at certain times of the day, which could be driving co-occurrences (e.g., see Figures S1, S2,and S3). This method allowed us to obtain a clearer picture of the co-occurrence patterns that are driven purely by the presence of other species. We conducted a lmer analysis for each species, with that species' presence or absence on the clay lick entered as the dependent variable. Independent variables were the presence/absence of each of the remaining 11 species and the ID of the zone in the current observation, with additive effects. Random effects were entered for time of day (ex: 06:00) and date (ex: 21-10-2010). The significance of each species as a predictor was assessed by comparing a reduced model (omitting the species in question) to the full model (including the species as a predictor) using an ANOVA. Where the full model performed significantly better than the reduced model, an edge between the two species was ruled in. The type of edge was determined by the sign of the estimate, with positive estimates denoting affiliative edges (meaning the dependent variable species was more likely to be present when the predictor species was present) and negative estimates denoting avoidant edges (meaning the dependent variable species was less

likely to be present when the predictor species was present). This analysis is capable of detecting asymmetrical relationships between species (for example, species B might predict the presence of species A, but not vice-a-versa). We conducted a total of 132 comparisons (to evaluate 132 directed edges without self-loops) and the significance threshold was corrected accordingly to $p < 0.05/132 = 0.000\overline{378}$.

Quantifying dynamic joining and leaving patterns

While co-occurrence patterns can inform us about which species are more often together or apart, we also addressed attraction and avoidance more directly by analyzing dynamic decision-making on a scan by scan basis. We compared whether species were present or absent in one scan, to whether they were present or absent in the next scan, 5 minutes later. We defined several event types from this dynamic perspective. A species may be attracted to a group containing individuals from another species and *join* them (species A is absent at time 1 but present at time 2 when species B is present at both times 1 and 2). Alternatively, species may be repulsed from a group containing individuals of another species and *leave* (species A present at time 1 but absent at time 2 when species B is present at both times 1 and 2). Two species might also *co-stay* (both present at both times 1 and 2), *co-join* (neither present at time 1 but both present at time 2), or *co-leave* (both present at time 1, neither present at time 2).

First, we assessed at how often each species was involved in each event type. Next, we focused on the join and leave events and determined how often a given focal species actively joined or left a group, versus how often that focal species was passively joined or left by others. We quantified the skew in active/passive joining events as the number of active joins divided by the total number of join events (active+passive) that the species was involved in. We tested this skew in joining and leaving patterns against the baseline presence of the species to identify outlier species that fell above or below the 95% confidence interval. We used this as evidence to identify species which joined more, were joined more, left more, or were left more than expected, given their baseline presence.

We then investigated symmetries and asymmetries in actions taken between pairs of species. We constructed five networks, one per action type, showing the ranked preference of each species partners for the given action type. Taking join events for example, we drew three directed edges from each focal species to the species that it joined the most, the second-most, and the third-most. From this representation, we observe which pairs of species reciprocate actions (i.e. both join each other as their first choice partner) an which do not. We also observe which species are the most and least popular recipients of certain action types.

Identifying potential categorization schemes

Although species-level information is a convenient way for us to summarize co-occurrence and joining patterns, that information may not be what the parrots are using to make these decisions. They may instead be using less detailed information, like joining flocks based on more general categories like color or general body shape. This process is known as "coarse-graining" [14, 19, 20], where more detailed information (like species categories) are lumped together into larger and less specific categories (like color or shape that could combine multiple species into the same category).

We tested whether the observed co-occurrence patterns and joining patterns are best explained by grouping parrots under seven different categorization systems. (1) Grouping by species. (2) Grouping by clade, to account for similarities in general body shape, which may affect how species move and their agility in avoiding predators. (3) Grouping by size, determined by the average body mass of the species, to account for the possibility of size-based aggression. (4) Grouping by whether parrots are large macaws or not, because the large macaws are much larger than all the other parrots and could potentially be highly aggressive to smaller species. (5) Grouping by majority back body color, which is the most obvious color when birds are perched on the wall and could be used both by other parrots to make joining decisions as well as potentially by predators. (6) Grouping by rear head color, which could make species distinctive in flocks and could be used by both other parrots and predators. (7) Grouping by distinctive face color, which may be used as a social signal when parrots are nearby each other on the wall. Table 1 shows how we grouped species under each of the seven categorization systems.

For each species, we constructed a set of seven nested linear mixed effects models, where each model encoded one categorization system, using the co-occurrence data and the dynamic joining data. For the co-occurrence data, the dependent variable was the species presence/absence on the clay lick during a scan. For the joining data, the dependent variable was whether or not the species had just joined the clay lick (meaning the species was present in a scan at time t but not in a scan at time $t-1$). We controlled for zone preferences and effects from the time and date of observations by including zone in the model as a predictor and time and date as random effects. The remaining predictors corresponded to each categorization system. The grouping procedure worked by creating a new variable, such as "small parrot", assigning a 1 to each observation if any of the 11 predictor species of the type "small parrot" were present, and assigning a 0 otherwise. For the co-occurrence data, a predictor species was coded as present if it appeared in scan t. For the joining data, a predictor species was coded as being present for the join event if it was present at a scan in time t and a scan in time $t-1$.

We compared these seven models using an ANOVA and identified the model with the lowest AIC as the best-fit model [1]. In general, models with fewer parameters have lower AIC and models that describe the data better have lower AIC [8], so this procedure allowed us to identify cases when lower-complexity category systems described the data equally as well as higher-complexity category systems.

We also report the results of each best-fit model to understand how the species relate to one another (in terms of avoidance or attraction) within the inferred categorization schemas. Negative estimates on co-occurrence or joins per category type indicate avoidance and positive estimates indicate affiliation. We threshold these relationships and report all category predictors with t values between -2 and 2 as being neutral relationships.

Results

Summarizing the extent to which species mix

High degrees of interspecies mixing was observed within zones of the clay lick (Figure 1) and across the entire clay lick as a whole (Fig. S4). When analyzing the clay lick as a whole, 79% of scans (3815 observations) recorded individuals from more than one species present on the entire
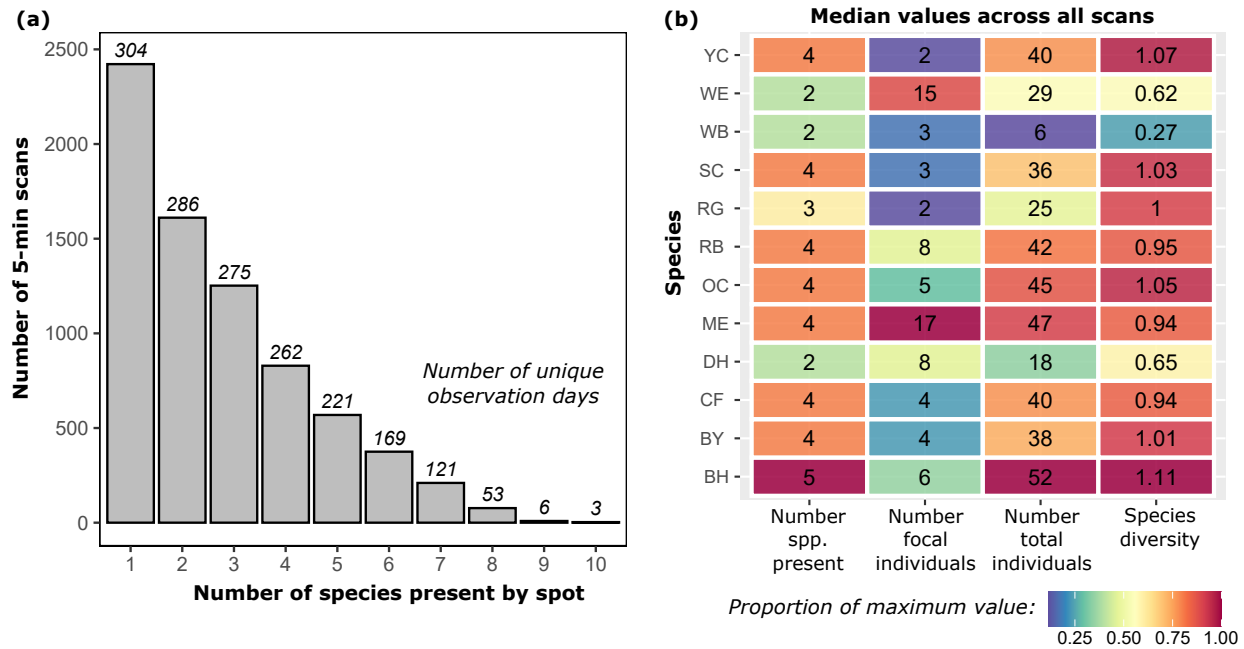
Figure 1: Summaries of the extent of mixed species groupings by zone. Panel (a) shows the number of scans with groups comprised of different numbers of species (with the number of unique sampling days annotated in italic). Panel (b) summarizes how often each species participated in mixed species groupings. For each focal species, values indicate: (1) the median number of species present in a zone during a single scan when each focal species was present, (2) the median number of focal individuals present during each scan at each zone, (3) the median total number of individuals present during each scan at each zone (across both the focal species and all other species), and (4) the median species diversity in groupings during each scan at each zone that each focal species was present in. Colors in cells indicate each value's proportion to the maximum value per measure for each column, with red highlighting the maximum values for each column.

wall at the same time, with a median of 3 species present on the entire wall at the same time. We recorded a maximum of 11 of the 12 potential species on the entire wall at the same time during a single scan. When analyzing the clay lick by zone, a finer spatial co-occurrence scale, 67% of scans (4935 observations) recorded individuals from more than one species present at the same zone at the same time, with a median of 2 species present at the same time. We recorded a maximum of 10 of the 12 potential species on the same zone during a single scan. As shown in Figure 1b, Blue-headed parrots were observed with the highest median number of species, the largest median total number of individuals, and in the highest species diversity of groupings, although generally with small numbers of conspecifics. In contrast, White-bellied parrots were observed with fewer other species and were present in groupings with the lowest species diversity compared to the other parrots.
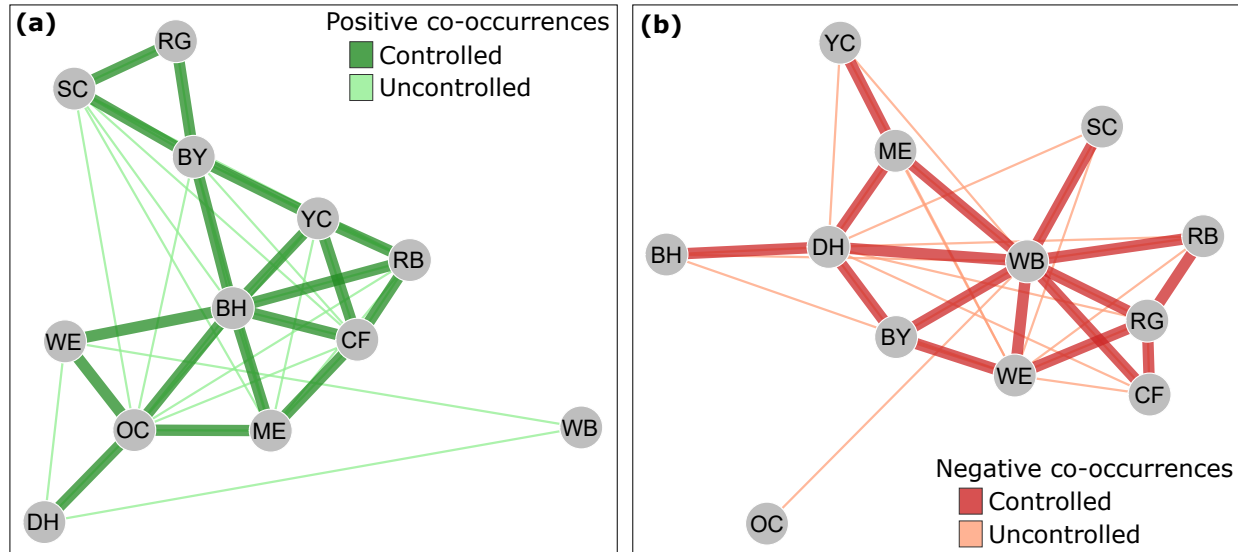
Figure 2: Networks of significant species co-occurrences at the clay lick: (a) positive co-occurrences, where species co-occur above levels expected by chance, and (b) negative co-occurrences, where species co-occur below levels expected by chance. Networks show the raw probability of seeing each pair of species together on the clay lick, beyond chance co-occurrence, uncontrolled for the effects of foraging preferences for zone, time, and day (thinner edges) as well as co-occurrences controlled for these effects with the lmer (thicker edges). Only edges with p-values more extreme than Bonferroni-corrected alpha levels are shown as statistically significant associations.

Co-occurrence patterns

We found that some species occurred together on the same zone of the clay lick more often than expected by chance (Fig. 2a), while others occurred together less than expected by chance (Fig. 2b). Blue-headed parrots had the highest number of controlled positive co-occurrences with other species while White-bellied parrots had the lowest, with no positive co-occurrences with any species (when controlled with lmer approach). White-bellied parrots also had the highest number of controlled negative co-occurrences with other species, while Orange-cheeked parrots had no negative co-occurrence associations to other species (when controlled).

We found that these positive and negative negative co-occurrence associations could be partially explained by size differences between pairs of species. Species with larger size differences tended to have more negative associations while species that were more similar in size had more positive associations (Fig. **??**). The mean difference in body size was 224 grams for positive ties and 590 grams for negative ties and a Mann Whitney U test found that the these two groups differed significantly ($U = 216, n_1 = 18, n_2 = 16, p = 0.006$, one-tailed).

Dynamics of attraction and avoidance

About 90% of the observation scans occurred in runs of 5 minute intervals and could be used to investigate fine-grained joining, staying, and leaving actions. Overall, we found a large amount of

variability across species in the patterns of actions they take on the clay lick. Figure 3a shows the number of times that each focal species actively joined a mixed-species group (left) and the number of times it was passively joined by other species (right).The skew between these two numbers provides information about the sociality of each species and can even vary greatly between species with a similar number of total join events. For example, in Figure 3a, Orange-cheeked parrots and Red-bellied macaws were involved in a comparable number of join events (1878 and 2008, respectively) but exhibited skews in opposite directions: the Orange-cheeked parrot joined others more than it was joined by them while the Red-bellied macaw was joined by others more than it joined them. Figure 3b shows the number of times that each focal species left a mixed-species group (left) and it number of times that other species left it (right). The raw number of co-stay, co-join, and co-leave events per species are shown in Figure **??**.

It is possible that species who were involved in more join events were more social than those involved in fewer join events. However, these numbers were highly correlated with each species' baseline frequency of visiting the clay lick ($r = 0.79$) because species who spend a lot of time on the clay lick will simply be joined and do more joining than species who visit the clay lick less. Figures 3c and d show join and leave ratios as a function of species' baseline frequency of visiting the clay lick. In both cases, a regression yielded a significantly negative relationship between ratio and baseline frequency for join events ($\beta = -0.623, SE = 0.123, t = -5.053, p < 0.001$) and leave events ($\beta = -0.497, SE = 0.113, t = -4.384, p = 0.001$).

Because these raw joining and leaving events could be affected by species prevalence, we compared these raw patterns against the baseline presence of the species and identified several outlier species who joined or left mixed groupings at rates above or below expectations. Outliers were identified as the species that fall outside of the 95% confidence interval, shown as the grey envelope around the regression line, in Figures 3c and d. In Figure 3c, Scarlet macaws, Orange-cheeked parrots, and Blue-headed parrots all showed evidence for attraction to heterospecifics as they joined groups at higher than expected rates. In constrast, Dusky-headed parakeets, White-eyed parakeets, and Red-bellied macaws were all joined by others at higher than expected rates, indicating that these focal species were more likely to attract others. In Figure 3d, White-bellied parrots and Chestnut-fronted macaws left mixed groupings more often than expected, indicating potential avoidance of other species, whereas Orange-cheeked parrots, White-eyed parakeets, Blue-headed parrots, and Mealy parrots were more likely to be left by others, indicating that these species were avoided.

Beyond simply varying in their overall joining and leaving patterns, focal species may vary in the particular species they join and leave. Figure 4 shows each species' top three preferred partners for the five different action types. For example, White-eyed parakeets were most often observed joining White-bellied parrots, second most often observed joining Mealy parrots, and third most often observed joining Chestnut-fronted macaws (Fig. 4a). Sometimes these choices are reciprocated: the Chestnut-fronted macaw and Red-bellied macaw both choose each other as their top partner to join on the clay lick. However, these preferences were often unreciprocated: the Red-and-green macaws were most likely to co-stay with Blue-and-yellow macaws, but Blue-and-yellow macaws were most likely to co-stay with Mealy parrots.

The preference networks in Figure 4 also helped us understand the relative popularity of different species for different action types. For example, more species chose the Red-bellied macaw as

their preferred partner, followed by the Chestnut-fronted macaw and the Mealy parrot. These patterns were supported by a separate analysis, which showed that Red-bellied macaws and Chestnut-fronted macaws were typically the first species to land on the clay lick in the morning, and therefore might have been prime partners to join for that reason (see Figure S3). Mealy parrots also exhibited the longest average run lengths on the clay lick (being present for an average of 4.6 consecutive scans) and this may have made them a common species to both join and leave.

Inferring categorization systems from co-occurrence and joining patterns

When we used static co-occurrence patterns to infer the categorization system for each species, we found that 7 of the 12 parrot species had co-occurrence patterns best described by using all 12 species as categories (Fig. 5). The remaining five species had co-occurrence patterns that could best be described using fewer categories. Red-and-green macaws and Scarlet macaws used back color (three categories: green, red, or blue) and had a preference for red and blue-backed species and avoided green-backed species. White-bellied parrots and White-eyed parakeets used just two categories: whether the species was a large macaw or not, and avoided both of these categories, with stronger avoidance of large macaws than non-large macaws. Blue-and-yellow macaws were best-fit with a large macaw category system and preferred large macaws while avoiding others. However, because Blue-and-yellow macaws were the sole blue-backed species, we could not differentiate between their use of large macaws or back color as there were the same number of choices in the two categorization systems (under back color categorization, they preferred red-backed species and avoided green-backed species). None of the other categorization systems (see Table 1) we investigated were best fits for explaining co-occurrence patterns in any of our species. We found no significant linear association between species mass and the complexity of the categorical system they used (R-squared=0.1314; p-value=0.1337).

We found a different pattern when we used dynamic joining decisions to infer the categorization system for each species. We identified many more of our potential categorization systems as best-fit models and found a higher diversity of categorization systems potentially used by our species. With the dynamic data, the species categorization system was the best-fit for only 3 focal species (Blue-headed parrot, Dusky-headed parakeet, Orange-cheeked parrot). Size was used by 3 species, 2 species used clade, 2 species used large macaw, 1 species used head color, and 1 species used back color (Fig. 6). We found no significant linear association between species mass and the complexity of the categorical system they used (R-squared=0.1209; p-value=0.144).

Across focal species, some species significantly joined or avoided joining other species at different rates, indicating general attraction to or repulsion from other species. For example, White-bellied parrots and White-eyed parakeets had the highest number of preferred species they joined (8 other species each, 73% of total species) while Dusky-headed parakeets, Red-and-green macaws, and Yellow-crowned parrots were the most selective and had the lowest number of preferred species they joined (2 species each, preferring just 18% of potential species). Chestnut-fronted macaws significantly avoided the highest number of species (8 species, 73%); Blue-headed parrots also avoided many other species (7 species avoided, 64%). Dusky-headed parakeets, Red-and-green macaws, Scarlet macaws, White-bellied parrots, and White-eyed parakeets did not significantly avoid any of the other species.

Of potential associates, Chestnut-fronted macaws were the most popular, with significantly pre-

11

ferred associations from 9 other species (82% of species). Red-bellied macaws and Yellow-crowned parrots were also preferred by many other species (8 significant preferences each). In contrast, Orange-cheeked parrots, Red-and-green macaws, and Scarlet macaws were only preferred by 2 other species each (18% of species). Chestnut-fronted macaws, Red-bellied macaws, and Yellow-crowned parrots were not significantly avoided by any other species. Orange-cheeked parrots and White-bellied parrots were the least popular associates and were avoided by the most other species (4 each, 36% of species). While White-bellied parrots and White-eyed parakeets preferred to associate with the most other species (8, 73%), this preference was asymmetric and only 3 and 4 other species preferred to associate with them, respectively.

Using joining decisions also allowed us to better differentiate asymmetric relationships. For example, White-bellied parrots used a large macaw categorizing system in both the co-occurrence and joining datasets, but the direction of preferences to categories changed: in the co-occurrence data, they avoided both large macaws and non large macaws, but in the joining data, they prefer non large macaws while still avoiding large macaws.

Discussion

In this paper, we describe the mixed species aggregations of 12 species of parrots as they form groups to ingest clay from a riverbank in Peru. We found evidence that species co-occurrences and joining decisions were non-randomly structured and identified significant associations both above and below expected rates, providing multiple lines of evidence of species preferences and avoidance in these mixed groups. We then used both co-occurrence and joining data to identify the best-fit categorization systems for each species, which represent the simplest kinds of information that each species could use to make observed association decisions.

We found evidence in our dataset that different parrot species used different categorization systems to structure their co-occurrence and joining patterns. However, we also found very different results when we compared category systems inferred from static co-occurrence data compared to the more dynamic joining data.

Using the static co-occurrence data, we found that just over half the species used the most information-rich coarse-graining method we investigated, dividing up potential associates at the species level (12 categories). However, 5 of the 12 species showed evidence suggesting use of a simpler categorization system, which coarse-grained multiple species into a two or three-category system.

While co-occurrence measures can tell us which species co-occur more or less often than expected, dynamic joining and leaving patterns provide additional insight into how these species groupings come to be. Using the dynamic joining data, we were able to further refine our inference of category systems likely used by each species. This joining data focuses on which species are present on a zone when the focal species joins the group, and likely represents more active decision-making than the more static co-occurrence data. Co-occurrence is the product of two species' decisions, and all the higher-order interactions that put two species on the wall together, while joining decisions are centered more on the decision-making of each focal species. For example, a species is unlikely to join a group containing a species it is actively avoiding. With the joining decisions data, we identified a much more varied set of category systems used by our focal

species. Species categorization was still used by 3 species (12 categories) but most species used simpler categorization systems: 2 species used clade (5 categories), 3 used size (3 categories), 1 used back color (3 categories), 1 used rear head color (3 categories), and 2 used large macaws (2 categories). Face color (5 categories) was not used by any of the species. As with the co-occurrence categories, we did not observe a significant effect of species size on the complexity of the categorization system used to make joining decisions.

The overall patterns of preference and avoidance also differed between the static co-occurrence patterns and the dynamic joining decisions. For example, White-bellied parrots had no preferred association with other species , but showed a significant preference for 8 species when we analyzed their joining decisions. This species also had the highest number of negative associations when we used the controlled co-occurrence patterns (8 negative associations), but we found no evidence that it actively avoided any other species when we considered joining decisions (and it was only avoided by 4 other species). Orange-cheeked parrots also showed strong differences between the statically and dynamically-derived associations: it was positively associated with many more species when we considered the joining data (7 species) than when we considered the co-occurrence data (4 species). Even more striking, Orange-cheeks had no negative co-occurrence associations (when controlled with lmer) but was significantly avoided by 4 species when we considered the dynamic joining data.

The methods we used to categorize association types can also lead to reversals in the directionality or type of associations. For example, in our analyses, we found that joining and leaving decisions often could not be condensed down to a simple species-level attraction or repulsion: species that joined another significantly more often than expected may also leave each other more often than expected. A more nuanced approach to identifying how and why species interact with other species could help us better understand the costs and benefits of these associations and how changes in conditions may alter the cost-benefit ratios.

Our results also show that careful consideration of not just association types, but also the ways in which species may categorize each other, is likely to provide additional insight into mixed species groupings. However, it is important to note that our approach to identifying the simplest and best fit categorization systems cannot definitively determine how each species categorizes each other. Our methods can identify the likely categorization system based on the actions of each species. A better understanding of how each focal species may group other species into categories would provide insight into the sets of species that may be considered functionally interchangeable associates. Hypotheses about why these species may be functionally interchangeable could then focus on social, ecological, and cognitive factors. For example, categorization system results could be paired with classic cognitive testing to determine whether a species treats others as interchangeable because perceptually it cannot tell the difference between individuals of different species. Similarly, testing for patterns during different times of year, when the ecological factors such as food availability may be different, could provide insight into whether categorization systems are robust to changes or flexible and responsive. Finally, focusing on behavioral interactions between species or sets of species could provide insights into the social costs or benefits of associating with other species.

Association patterns in mixed species flocks can be complex and multifaceted. The types of attraction and repulsion or attraction and avoidance patterns each species uses can also differ

across species. Our methods allowed us to parse preferences in several ways, using multiple measures to quantify patterns in mixed-species flocks. These methods allowed us to better weight the types of connections between species, from the perspective of each species involved. This more nuanced approach to asking why some species aggregate will help better test hypotheses about the costs and benefits of these mixed species aggregations.

Acknowledgements

Author contributions

V.F. helped conceptualize the project, conducted all analyses, and helped write and edit the manuscript. E.P. helped brainstorm analyses and designed some of the network analyses. D.J.B. developed the data collection protocols, supervised field efforts, and commented on the manuscript. E.A.H. helped conceptualize the project, helped with analyses and visualization of the results, and helped write and edit the manuscript.

Ethics

This work was conducted with permission from the Instituto Nacional de Recursos Naturales (INRENA, Peru), the Servicio Nacional de Areas Protegidas (SERNANP, Peru), and the Institutional Animal Care and Use Committees of Duke University (2000–2006) and Texas AM University (2006–2016).

Data accessibility

All data and code will be made available on GitHub on publication of the paper.

Table 1: Description of categories. Columns show how species were grouped using different categorization schemes. Number in parentheses in column headings shows the number of categories for each categorization scheme.

Species (12)	Clade (5)	Size (3)	Large macaw (2)	Back color (3)	Rear head color (3)	Face color (5)
BH	Small parrot	Small	No	Green	Blue	Blue
BY	Large macaw	Large	Yes	Blue	Blue	White-faced
CF	Small macaw	Medium	No	Green	Green	White-faced
DH	Parakeet	Small	No	Green	Green	Green-grey
ME	Large parrot	Medium	No	Green	Green	Green-grey
OC	Small parrot	Small	No	Green	Black	Yellow-flash
RB	Small macaw	Medium	No	Green	Green	White-faced
RG	Large macaw	Large	Yes	Red	Red	White-faced
SC	Large macaw	Large	Yes	Red	Red	White-faced
WB	Small parrot	Small	No	Green	Orange	Orange
WE	Parakeet	Small	No	Green	Green	Green-grey
YC	Large parrot	Medium	No	Green	Green	Yellow-flash

Figure 3: Summary of general attraction and avoidance patterns per species: (a) joining patterns show the number of times each species joined groups with another species compared to the number of times another species joined each focal species and (b) leaving patterns show the number of times each species left a mixed species group compared to the number of times other species left each focal species. White diamonds indicate the skew in these numbers, which are partially explained by the baseline presence of each species on the clay lick in (c) and (d). Ratios equal to 0.5 mean there is no skew, ratios over 0.5 mean the focal species joined other more, and ratios under 0.5 mean the focal species was joined by others more. The line shows the result of a linear regression analysis and the grey envelope shows the 95% confidence interval. Species that fall outside of the 95% confidence interval have joining and leaving patterns that are not entirely explained by their baseline presence on the clay lick: species with ratios above the confidence interval join or leave other species on the wall more than expected based on their baseline presence while species with ratios below the confidence interval are joined or left by other species on the wall more often than expected.
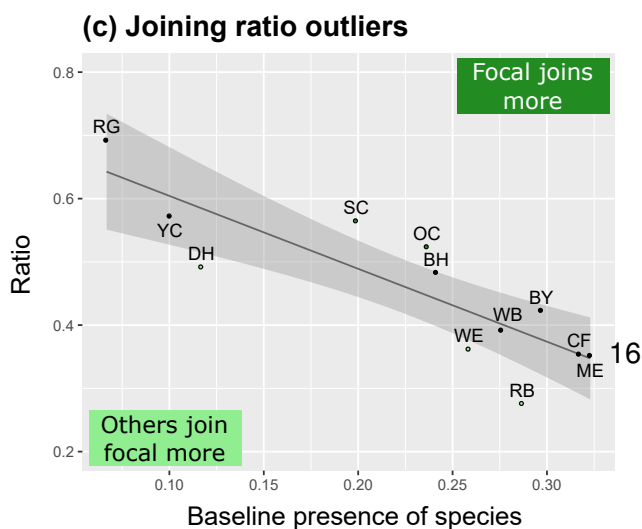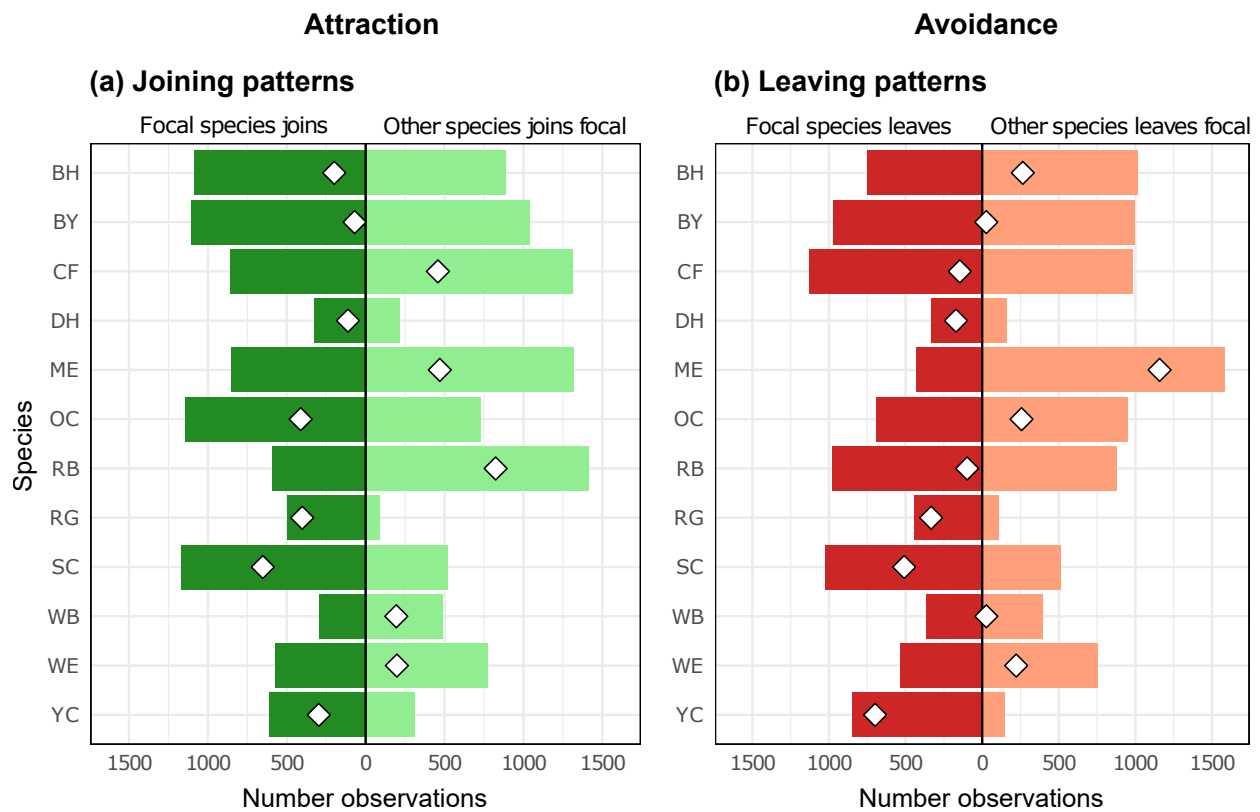

16
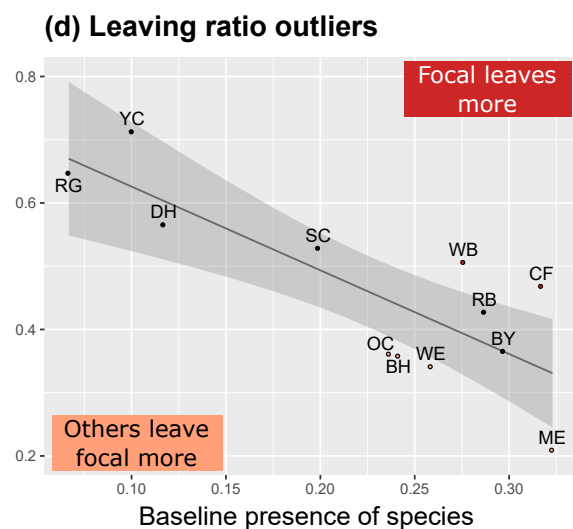
Figure 4: Event type networks showing each species' top preferences of partner species' for each of the main action types: (a) join, (b) leave, (c) co-stay, (d) co-join, and (e) co-leave. Edges show each species preferred partner for the event type: red edges show each species' top choice in partner to perform the action, orange edges show the second choice, and yellow edges show the third choice. In panels a-b, second and third choices are not plotted if these events occurred less than half as many times as the first choice. In panels c-e, only first choices were plotted.

17
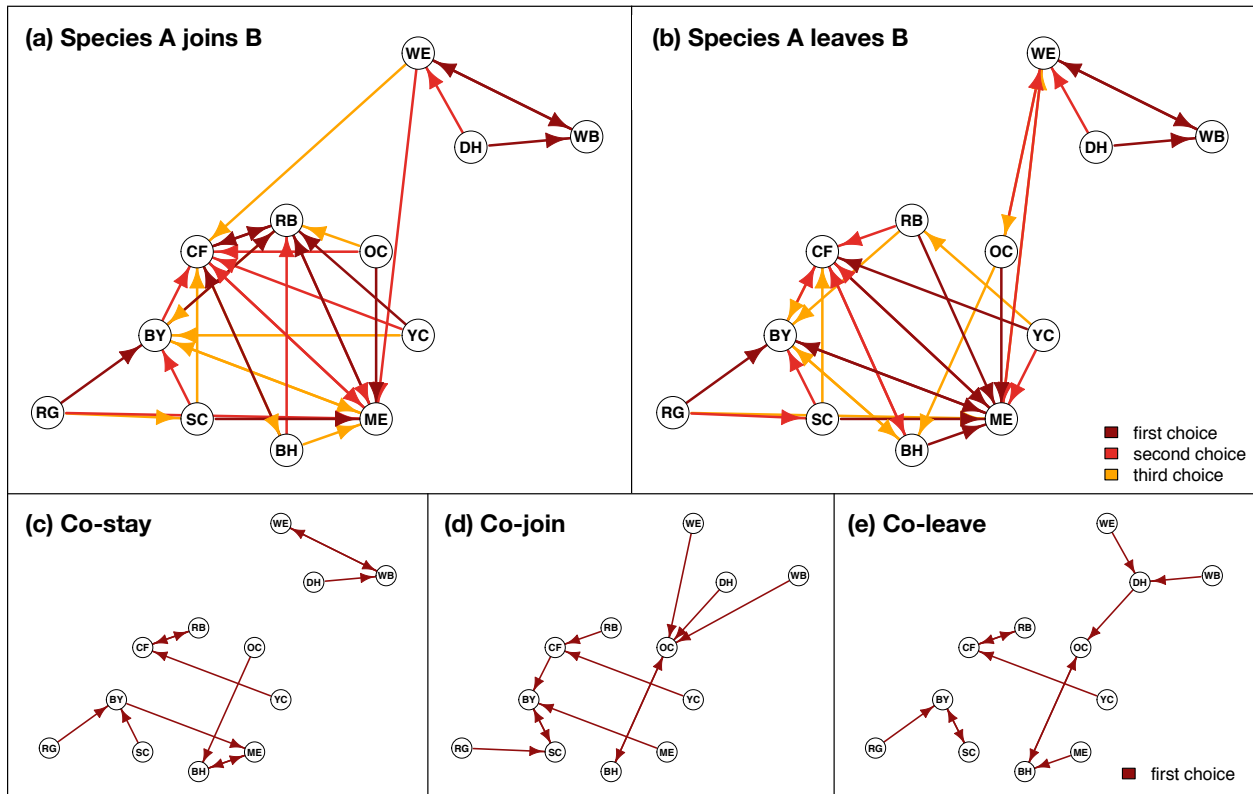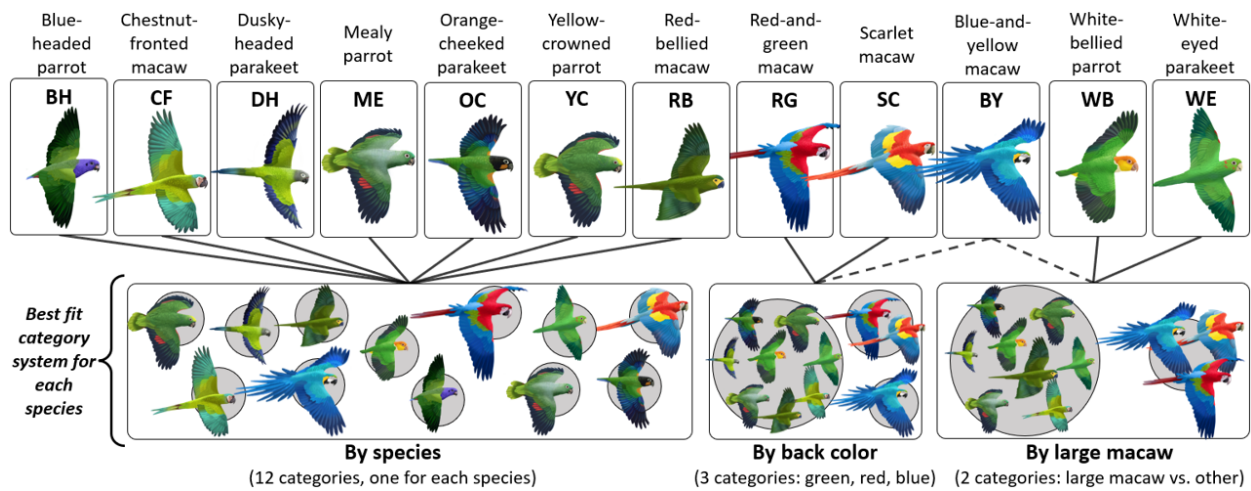
Figure 5: Best fit categorization methods by species for static co-occurrence patterns. Each species is connected to the model which best described their co-occurrence patterns with the least amount of complexity. Blue-and-yellow macaws are connected with dashed lines to both back color and large macaws categories as these could not be differentiated due to category membership similarity (it is the only blue-colored species in the back color category). Species artwork by V. Darby Moore.
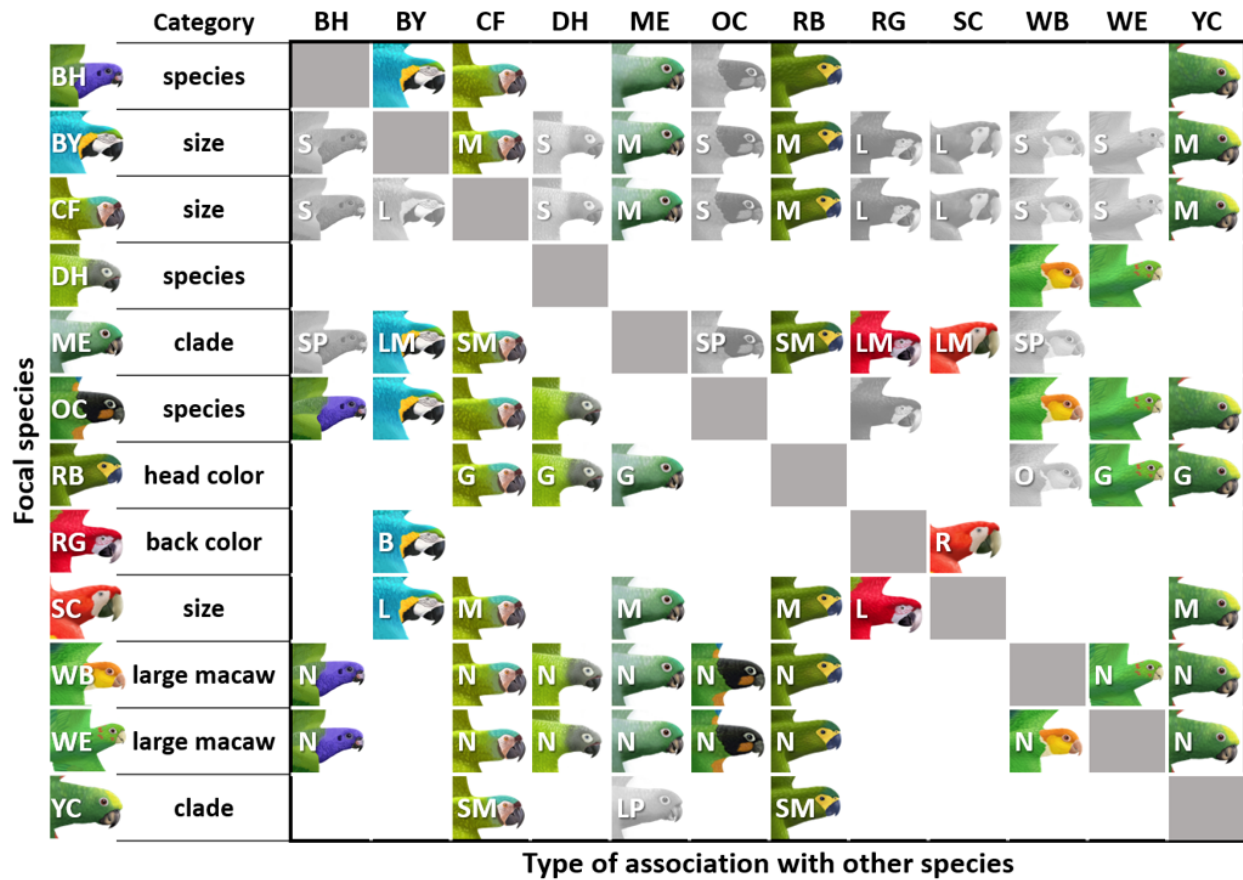
Figure 6: Best fit categorization methods by species for dynamic joining decisions. Each focal species is labeled in the first column, followed by the best-fit categorizing system inferred from that species' joining patterns. Across the table, species the focal significantly prefers are shown in color, while species they significantly avoid are shown in greyscale. Empty cells are species with which the focal did not have a significantly positive or negative association. For species with best-fit models that coarse-grained species into categories, the category labels appear for each preferred or avoided species (for size: S=small, M=medium, L=large; for clade: SP=small parrot, SM=small macaw, LP=large parrot; for head color: G=green, B=blue, K=black, R=red, O=orange; for large macaw: Y=is a large macaw, N=is not a large macaw); see Table 1 for species assignments to categories. Species artwork by V. Darby Moore.

References

[1] Akaike, H. 1998 Information theory and an extension of the maximum likelihood principle. In *Selected papers of hirotugu akaike*, pp. 199–213. Springer.

[2] Bates, D., Mächler, M., Bolker, B. & Walker, S. 2015 Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**(1), 1–48. (doi:10.18637/jss.v067.i01)

[3] Bonferroni, C. 1936 Teoria statistica delle classi e calcolo delle probabilita. *Pubblicazioni del R Istituto Superiore di Scienze Economiche e Commericiali di Firenze*, **8**, 3–62.

[4] Brightsmith, D. J. 2004 Effects of weather on parrot geophagy in Tambopata, Peru. *https://doi.org/10.1676/03-087B*, **116**(2), 134–145. (doi:10.1676/03-087B)

[5] Brightsmith, D. J., Hobson, E. A. & Martinez, G. 2018 Food availability and breeding season as predictors of geophagy in Amazonian parrots. *Ibis*, **160**(1), 112–129. (doi:10.1111/IBI.12515)

[6] Brightsmith, D. J., Taylor, J. & Phillips, T. D. 2008 The Roles of Soil Characteristics and Toxin Adsorption in Avian Geophagy. *Biotropica*, **40**(6), 766–774. (doi:10.1111/J.1744-7429.2008.00429.X)

[7] Brightsmith, D. J. & Villalobos, E. M. 2011 Parrot Behavior at a Peruvian Clay Lick. *The Wilson Journal of Ornithology*, **123**(3), 595–602. (doi:10.1676/09-109.1)

[8] Burnham, K. P. & Anderson, D. R. 2004 Multimodel inference: understanding aic and bic in model selection. *Sociological methods & research*, **33**(2), 261–304.

[9] Csardi, G. & Nepusz, T. 2006 The igraph software package for complex network research. *InterJournal*, **Complex Systems**, 1695.

[10] Dixon, P. 2003 VEGAN, a package of R functions for community ecology. *Journal of Vegetation Science*, **14**(6), 927–930. (doi:10.1111/J.1654-1103.2003.TB02228.X)

[11] Dunning, J. B. 1993 *CRC handbook of avian body masses, first edition*. CRC Press, first edition edn. (doi:10.1201/9781420064452)

[12] Farine, D. R., Aplin, L. M., Sheldon, B. C. & Hoppitt, W. 2015 Interspecific social networks promote information transmission in wild songbirds. *Proceedings of the Royal Society B: Biological Sciences*, **282**(1803). (doi:10.1098/RSPB.2014.2804)

[13] Farine, D. R., Garroway, C. J. & Sheldon, B. C. 2012 Social network analysis of mixed-species flocks: exploring the structure and evolution of interspecific social behaviour. *Animal Behaviour*, **84**(5), 1271–1277. (doi:10.1016/J.ANBEHAV.2012.08.008)

[14] Flack, J. C. 2017 Coarse-graining as a downward causation mechanism. *Philosophical transactions. Series A, Mathematical, physical, and engineering sciences*, **375**(2109), 20160 338. (doi:10.1098/rsta.2016.0338)

[15] Gilardi, J. D., Duffey, S. S., Munn, C. A. & Tell, L. A. 1999 Biochemical Functions of Geophagy in Parrots: Detoxification of Dietary Toxins and Cytoprotective Effects. *Journal of Chemical Ecology 1999 25:4*, **25**(4), 897–922. (doi:10.1023/A:1020857120217)

[16] Goodale, E., Beauchamp, G. & Ruxton, G. D. 2017 *Mixed-species groups of animals: behavior, community structure, and conservation*. Academic Press.

[17] Goodale, E., Sridhar, H., Sieving, K. E., Bangal, P., Colorado Z., G. J., Farine, D. R., Heymann, E. W., Jones, H. H., Krams, I. *et al.* 2020 Mixed company: a framework for understanding the composition and organization of mixed-species animal groups. *Biological Reviews*, **95**(4), 889–910. (doi:10.1111/BRV.12591)

[18] Haynes, W. 2013 *Bonferroni correction*, pp. 154–154. New York, NY: Springer New York. (doi:10.1007/978-1-4419-9863-7_1213)

[19] Hobson, E. A., Ferdinand, V., Kolchinsky, A. & Garland, J. 2019 Rethinking animal social complexity measures with the help of complex systems concepts. *Animal Behaviour*, **155**, 287–296. (doi:10.1016/J.ANBEHAV.2019.05.016)

[20] Marzen, S. E. & DeDeo, S. 2017 The evolution of lossy compression. *Journal of the Royal Society, Interface*, **14**(130), 20170 166. (doi:10.1098/rsif.2017.0166)

[21] Morse, D. H. 1977 Feeding Behavior and Predator Avoidance in Heterospecific Groups. *BioScience*, **27**(5), 332–339. (doi:10.2307/1297632)

[22] Oksanen, J., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'hara, R., Simpson, G., Solymos, P., Stevens, M. *et al.* 2013 Package 'vegan': Community ecology package.

[23] Powell, L. L., Powell, T. U., Powell, G. V. N. & Brightsmith, D. J. 2009 Parrots Take It with a Grain of Salt: Available Sodium Content May Drive Collpa (Clay Lick) Selection in Southeastern Peru on JSTOR. *Biotropica*, **41**(3), 279–282.

[24] R Core Team 2018 *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Supplemental Information

Table S1: List of the 12 parrot species used in the analyses. For size comparison, mean species mass is shown in grams, rounded to nearest whole number [11].

| Code	Species	Scientific name	Mass (g)
BH	Blue-headed parrot	*Pionus menstruus*	247
BY	Blue-and-yellow macaw	*Ara ararauna*	1125
CF	Chestnut-fronted macaw	*Ara severus*	430
DH	Dusky-headed parakeet	*Aratinga weddellii*	108
ME	Mealy parrot	*Amazona farinosa*	610
OC	Orange-cheeked parrot	*Pyrilia barrabandi*	178
RB	Red-bellied macaw	*Orthopsittaca manilata*	370
RG	Red-and-green macaw	*Ara chloropterus*	1250
SC	Scarlet macaw	*Ara macao*	1015
WB	White-bellied parrot	*Pionites leucogaster*	155
WE	White-eyed parakeet	*Psittacara leucophthalmus*	157
YC	Yellow-crowned parrot	*Amazona ochrocephala*	510

SI1. Overview of clay lick use

We considered the clay lick use, co-occurrence, and group leaving/joining decisions in 12 parrots species (Table S1). We first investigated patterns of clay lick use timing (Fig. S1) and how clay lick use varied by spot (Fig. S2). We also investigated which species were the first to land on the clay lick each morning. At the start of each day, parrots do not land on the clay lick immediately; they enter the area and gather in nearby trees or make several circling passes by the clay lick before landing on it. The first scan of the day begins when the first individual(s) land. Figure S3 shows the number of times each species was present on the first scan of the day and the subset of those scans in which the species was the only one present in the first scan. For example, the Red-bellied macaw was present in the first scan on 193 days, often with other species, but in 101 of those scans it was the only species present (indicating that it was the very first species to land on the clay lick that day). There are a total of 307 days in the dataset. Finally, we looked at the overall patterns of mixed-species groupings at the scale of the whole wall (Fig. S4, in contrast to the finer-scale analyses by spot presented in Fig. 1). We also tested whether these co-occurrences were associated with mass differences between pairs of species (Fig. S5).

SI2. Networks of attraction and avoidance by zone

The previous section showed that species-specific foraging preferences differ markedly across the zones of the clay lick, resulting in different combinations of species on each zone. Although our main analysis focused on inferring a single social structure while controlling for differences in zone preferences (Figure 2), it is possible that species could be interacting with one another differently on different zones. In this section, we tested whether the detected affiliative and avoidant relationships were indeed general patterns by examining the robustness of these networks across the three most popular zones on the clay lick (1A, 2C, 3C, see Fig. S6). We repeated the linear mixed effects regression analysis per each of these zones (removing zone as a predictor, but

Figure S1: Clay lick usage by time of day, aggregated over all species (left) and broken down by species (right). Clay lick usage differed by time of day and by zone. Figure S1 shows clay lick usage rates from 04:58 (the earliest recorded time of first usage) to 09:00. Usage is reported as the raw number of individuals recorded across all observation scans per minute. For example, at 06:00 a total of 4879 individuals were recorded across 121 scans. Clay lick timing was similar across most species except for the three large macaws (BY, RG, SC) who tended to return again in the late morning.
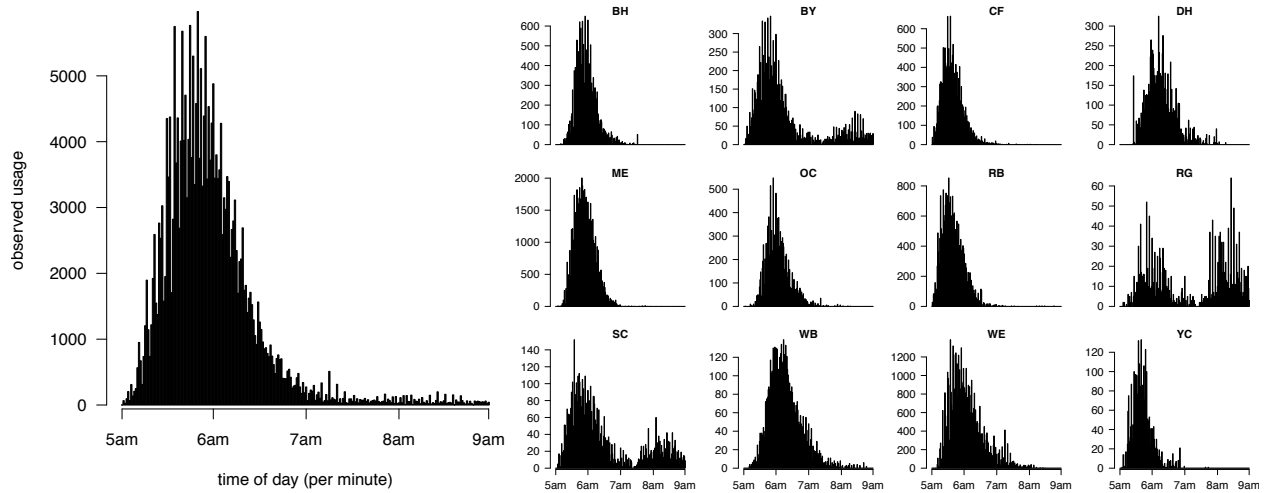
leaving time and day as random effects) to construct a network of significant ties (as done for Figure 2). We compare the resulting networks and look for evidence of zone-dependent affiliations by identifying any flips in tie type between two species (from avoidant to affiliative, or vice-a-versa) across zones. We also found the number of times each species was involved in co-stay, co-join, and co-leave events (Fig. S7).

Figure S2: Usage of each zone on the clay lick showing each species' usage of the 11 zones on the clay lick. Each bar shows the number of observations in the dataset where at least one individual of the species was present on the zone. For example, the dataset contains 1013 observations where BH is present on 2C. The three most popular zones were 1A, 2C, and 3C, and accounted for 22%, 44%, and 18% of all visitations, respectively. Visual inspection shows that the species cluster into two usage regimes, with the 9 species on the left patterning together (showing peak usage centered on 2C) and the 3 species on the right patterning together (showing peak usage centered on 1A).
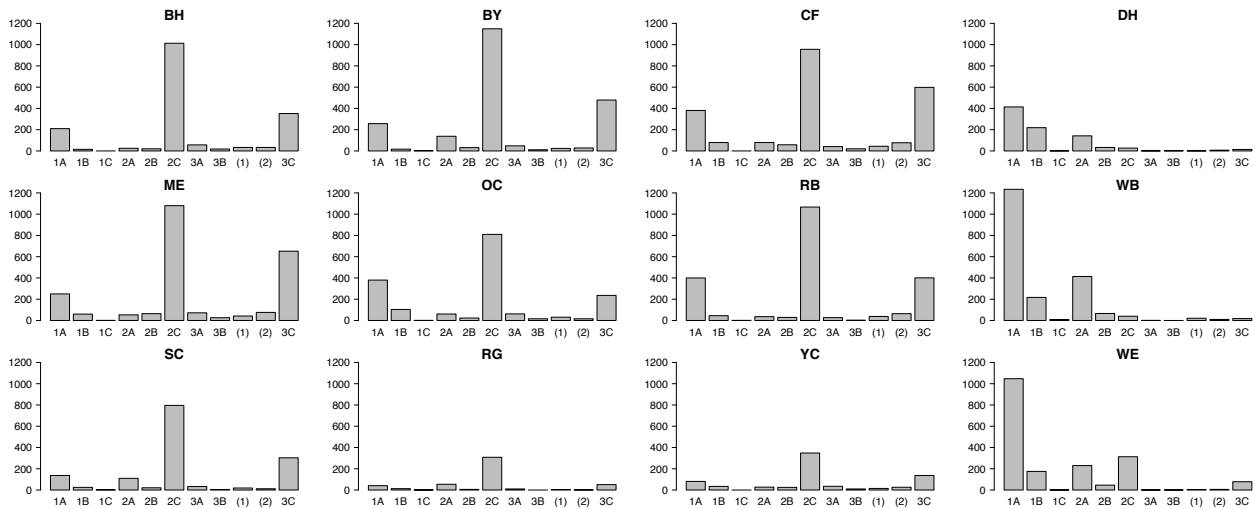
Figure S3: The first species to land on the clay lick each day showing the number of times each species was present on the first scan of the day (bar height) and the subset of those scans in which the species was the only one present in the first scan (in dark grey).
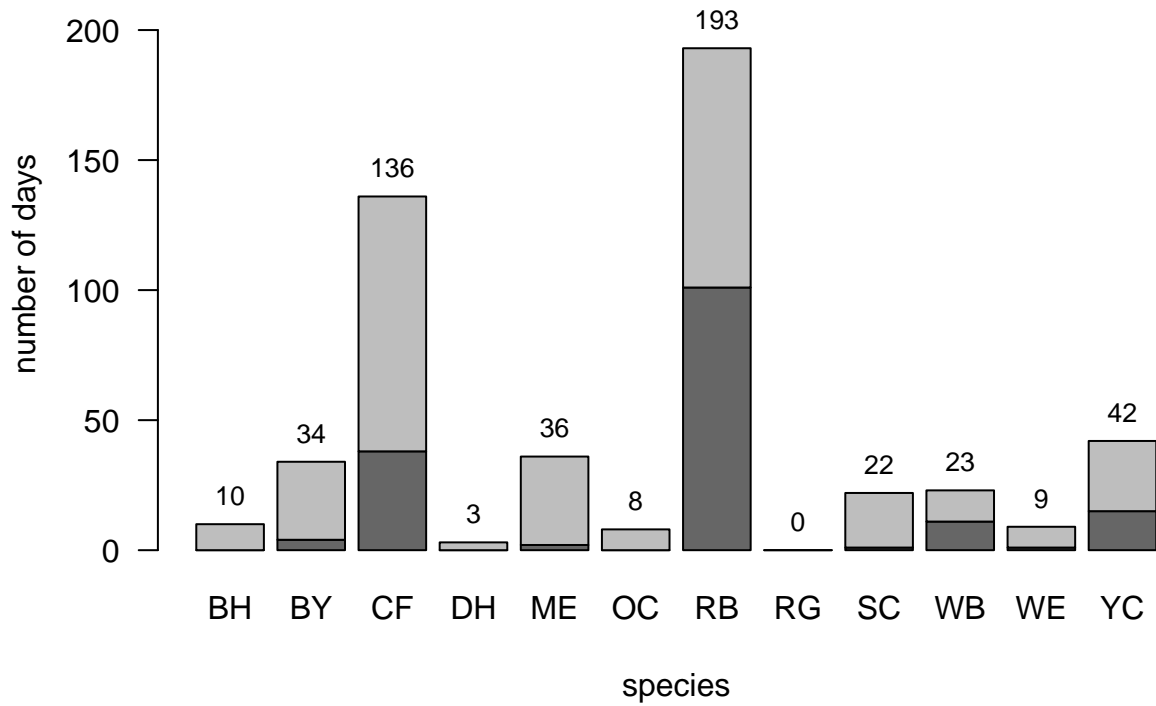
Figure S4: Summaries of the extent of mixed species groupings across the entire wall. Panel (a) shows the number of scans with groups comprised of different numbers of species with the number of unique sampling days annotated in italic. Panel (b) summarizes how often each species participated in mixed species groupings. For each focal species, values indicate: (1) the median number of species present anywhere on the wall during a single scan when each focal species was present, (2) the median number of focal individuals present during each scan anywhere on the wall, (3) the median total number of individuals present during each scan anywhere on the wall (across both the focal species and all other species), and (4) the median species diversity in groupings during each scan anywhere on the wall during scans that the focal species was present. Colors in cells indicate each value's proportion to the maximum value per measure for each column, with red indicating maximum values for each column.
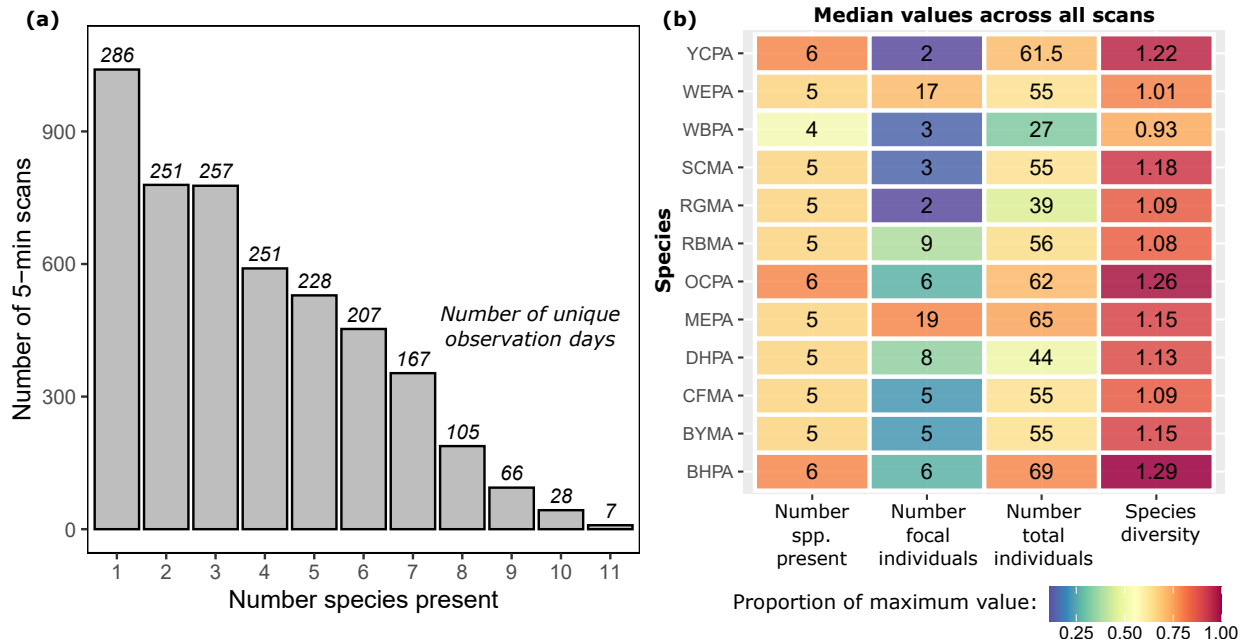
Figure S5: Body mass differences can explain part of the variation in association types. Negative associations are more likely to occur between species with a larger difference in body mass and positive associations are more likely to occur between species with similar body mass. Bars show the difference in body mass between all possible pairs of species and are ordered from largest to smallest. Red bars show associations that were significantly negative in the main controlled network (Fig. 2) and blue bars show significantly positive associations. Species names and mean body mass are shown in Table S1.
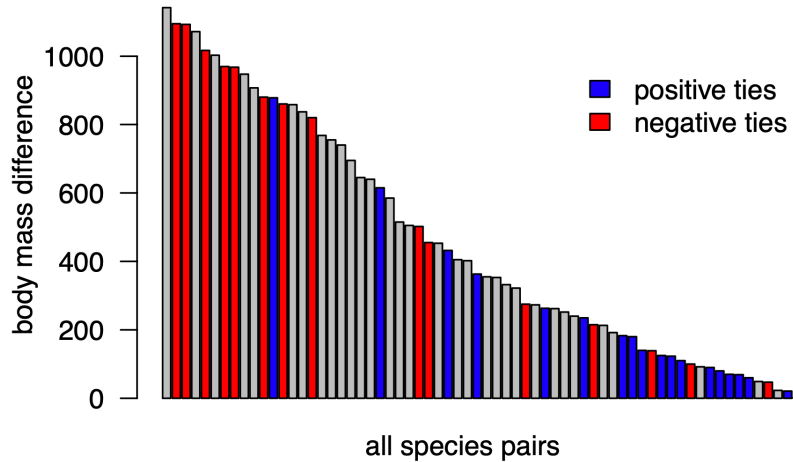

Figure S6: Within-zone interactions. The panels show the resulting networks extracted from zones 1A (left), 2C (middle), and 3C (right). We do not find any evidence of affiliation flips among ties across zones and the general structure of the network appears to be stable. However, we do find one tie flip compared to the main network (Figure 2): the Dusky-headed parakeet and the White-bellied parrot show a significantly avoidant tie on the main network, but show a significantly affiliative tie on zones 2C and 3C. One interpretation of this result might be that when these species are in the minority, as they are on 2C and 3C, they show more affiliation among themselves compared to when they are located on their preferred zone, 1A, and in the majority.
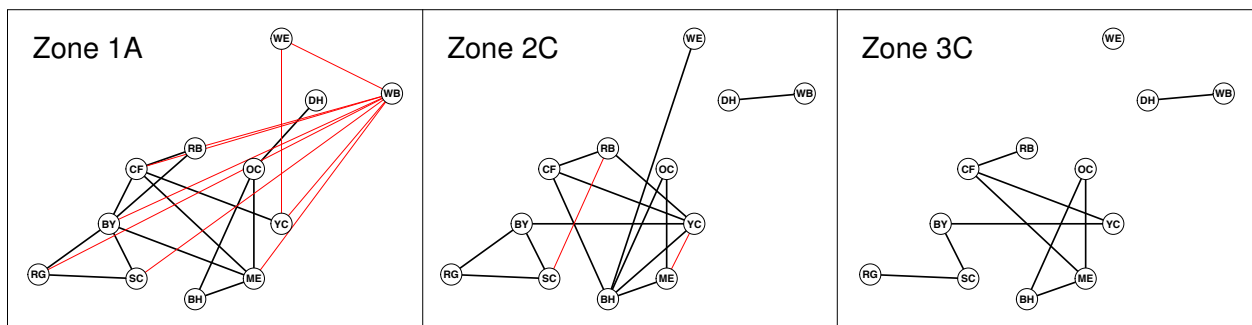

27

Figure S7: These plots show the relative frequencies of the different event types as well as the overall sociality of each species. For example, DH, RG, and WB are the least involved in coordinated events with others.