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Original Article

Behavioral diversity and agonism are higher in larger groups among wild Costa Rican capuchins

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Biologists have long been interested in the causes, costs, and benefits of group living. Within species, group sizes vary and affect the behavior of group members. Yet, few studies have investigated how behavioral diversity—defined here as the number of distinct behaviors occurring in a given time period—and frequency of agonistic behaviors relate to group size. Here, we test the predictions of the Resource Distribution Hypothesis. To do so, we analyzed >65,000 behavioral scans collected over 15 yr in Sector Santa Rosa, Costa Rica, on 214 white-faced capuchins inhabiting eight social groups. We found that cross-sectional behavioral richness and diversity was higher in larger groups than in smaller groups and that individuals in larger groups exhibited significantly higher behavioral richness and diversity across the day (longitudinally). We also found that agonism frequency at the group level was higher in larger groups, suggesting increased competition. Understanding these relationships provides insight into group dynamics, patterns of interindividual competition, and potential constraints on group size.

Keywords: Cebus imitator; feeding competition; foraging behavior; group living; group size; resources distribution hypotehsis.

Introduction

Understanding the causes, costs, and benefits of group living in animals has been an enduring goal of biologists, ecologists, and ethologists (Alexander 1974; Kutsukake 2009; Hoke et al. 2019). A wide variety of mammalian species show some degree of group living (Wilson 2000; Krause and Ruxton 2002), ranging from pair-living species (eg titi monkeys [*Plecturocebus cupreus*] (Dolotovskaya et al. 2020)), to small groups that consist of multiple breeding pairs and their offspring (eg dwarf mongoose [*Helogale parvula*] (Rood 1990)) up to large, multi-level societies with dozens to hundreds of individuals at times (eg elephants [*Elephas maximus*] (Nandini et al. 2018), geladas [*Theropithecus gelada*] (Mamo and Wube 2019)). Group size not only differs among species, but also varies within species in response to environmental heterogeneity, resource availability, and predation pressure (Chapman and Rothman 2009). Further, group sizes change over time through births, deaths, and dispersals (eg feral horses [*Equus ferus*] (Marjamäki et al. 2013)), or abruptly through group fusions or fissions (eg toque macaques [*Macaca sinica*] (Dittus 1988)). Previous research suggests that group size may also directly affect the behavioral diversity of the group members (Gogarten et al. 2014; Cowl and Shultz 2017). For example, group cross-sectional behavioral diversity—defined as the number of distinct behaviors exhibited by the different members of that social group at a given moment—might increase with group size. Additionally, individuals might engage in more diverse behaviors longitudinally across the day (ie individual behavioral diversity) when they are part of larger groups.

Intriguingly, there appears to be population and/or species-specific thresholds for maximum group size, suggesting social or environmental factors that limit the maximum number of individuals that can live together in a functional grouping (Krause and Ruxton 2002). The Resource Distribution Hypothesis predicts that group size is related to resource abundance such that larger groups must range farther to encounter sufficient food to feed all members. In larger home ranges, larger groups will potentially encounter a greater variety of food types and more diverse resource patches throughout the day. More varied foods and habitats may elicit different behaviors to access the foods, or to cross habitats, potentially contributing to higher behavioral diversity in response to the different conditions. However, groups cannot range in infinitely larger spaces and group size may eventually be limited by available resources (Janson 1988; Fortin and Fortin 2009; Ward and Webster 2016).

The Resource Distribution Hypothesis also posits that group size is related to competition. Agonism, defined here as aggressive or submissive behaviors among conspecifics (eg chasing, lunging, biting, submissive expressions, avoidance, and related vocalizations etc.) is predicted to increase with group size as competition for resources increases (Sterck et al. 1997; Balasubramaniam et al. 2014). Support for this prediction has been found in wild populations (eg yellow baboons [*Papio cynocephalus*] (Markham

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et al. 2015)), in captive settings (eg bonnet macaques [*Macaca radiata*]), and under experimental conditions of food limitation (Boccia et al. 1988). In species that exhibit dominance hierarchies, the costs of increased food competition and agonism are not expected to be experienced equally by all group members. Rather, subordinate individuals are likely to be excluded from resources more often (Markham et al. 2015), and to be on the receiving end of greater frequencies of agonistic behaviors (Simons et al. 2022). Subordinate animals may need to feed on a wider diversity of foods and/or range in areas peripheral to the group, which could affect their behavioral diversity across the day.

Considering the predictions of the Resource Distribution Hypothesis, in larger groups, behavioral diversity might increase at the individual level (ie each individual exhibits an increased number of different types of behaviors over the day) or at the group level (ie the behavior of individuals differs from their group members at any given moment) as individuals cope with increased competition. An important component of behavioral diversity is foraging behavioral diversity, which reflects the specific diversity of foraging strategies that animals use to navigate an array of potentially available resources. For example, Janson (1988) found that in tufted capuchin monkeys (*Sapajus apella*), individuals in larger groups increased their foraging minutes per day. Given the hypotheses that foraging competition imposes upper limits on group size, data on foraging diversity may be particularly informative about impacts of group size on group members. Unfortunately, few empirical data on how behavioral diversity varies with group size are available, which precludes understanding the relationships among group size and behavioral diversity. Contributing new data in this area motivated the present study.

Objectives, hypotheses, and predictions

We examine the relationship between group size and multiple aspects of behavior including behavioral diversity, foraging diversity, and agonism in a population of wild, white-faced capuchin monkeys (*Cebus imitator*). We leverage longitudinally collected behavioral data from 214 known individuals in eight social groups over a span of 15 yrs. We had three objectives for this study:

(1) to investigate behavioral diversity at the group (cross-sectional) and individual (longitudinal) level, with a focus on the effect of group size. At the group level, we predict the cross-sectional behavioral diversity (ie the number of distinct behaviors observed in the social group at any moment) will be higher in larger groups. At the individual level, we predict that the longitudinal behavioral diversity (ie the number of distinct behaviors observed across the day for an individual) will be higher among individuals living in larger groups compared to individuals in smaller groups.

(2) to specifically investigate foraging diversity at the group and individual level with a focus on group size. At the group level, we predict the cross-sectional foraging diversity (ie the number of different foraging behaviors observed at any moment) will be higher in larger groups. At the individual level, we predict that the longitudinal foraging diversity (ie the number of different foraging behaviors observed across the day) of individuals living in larger groups will be higher compared to individuals inhabiting smaller groups.

(3) to investigate the relationship between agonism, dominance rank, and group size. We predict that in larger groups, the frequencies of agonism at the group and individual level will be higher, especially among the more dominant individuals.

Methods

Study species and site

White-faced capuchins (*Cebus imitator*) are a medium-sized (3-5 kg) platyrrhine monkey found throughout Panama, Costa Rica, and in small parts of Honduras and Nicaragua (Johnson and Brown 2018). They live in multi-male, multi-female groups that range in size from ~5 to 40 members (Fragaszy et al. 2004; Melin et al. 2020). Females are philopatric, while males typically leave their natal group between the ages of 4 and 6, and thereafter change social groups approximately every 3 to 5 yr (Fedigan 1993; Fedigan et al. 1996; Fedigan and Jack 2001). Following established protocols, we classified individuals into the following age classes: infant (0 to 1 yr), small immature (2 to 3), large immature (4 to 5), and adult (6 and older). While males can take several additional years to reach full body size and can be classified as having a subadult phase (6 to 9 yr; (Jack and Fedigan 2018)), they typically reach foraging competence by the age of 6, and we classify them as adults. Outside periods of male migrations, capuchin groups are generally stable (Janson et al. 2012; Campos et al. 2015). They are well known for having a flexible, omnivorous diet that is primarily frugivorous, but that also includes invertebrate and vertebrate prey (Buckley 1983; Rose 1994; Fragaszy et al. 2004; Melin et al. 2008; McKinney 2011).

Unlike species that exhibit strict ordinal, inherited dominance hierarchies characterized by unidirectional aggression and strong kin bias (eg chimpanzees [*Pan spp.*], baboons [*Papio spp.*], macaques [*Macaca spp.*], vervet monkeys [*Chlorocebus pygerythrus*] (Klass 2021)), white-faced capuchins exhibit a lower expression of kin bias and males do not form clear hierarchies, beyond an obvious alpha male (Bergstrom and Fedigan 2010; Jack and Fedigan 2018). The alpha male rank shifts when a group takeover occurs by an emigrant, or the alpha male from the group dies or disappears (Bergstrom and Fedigan 2010; Perry 2012). In females, dominance rank is inherited, such that a daughter of the highest-ranking female, for example, will outrank adult females with different mothers once she is of reproductive age. Dominance rank in females typically shifts only when groups fission or when a female dies (Bergstrom and Fedigan 2010).

We collected behavioral data on wild capuchins living in the tropical dry forest of Sector Santa Rosa, Área de Conservación Guanacaste in Costa Rica. The tropical dry forest is highly seasonal, with a hot, dry season lasting December through April, during which most of the trees are defoliated and standing water sources dry up. The rainy season spans May through November and is associated with cooler temperatures and typically daily rainfall. Periods of lower habitat-wide fruit abundance typically occur at the end of the rainy season and the start of the dry season. During this period, a population explosion of caterpillars typically occurs, and the proportion of invertebrates consumed by capuchins increases dramatically (Mosdossy et al. 2015; Hogan and Melin 2018; Orkin et al. 2019).

Study groups

Between January 25, 2007, and February 25, 2022, we collected instantaneous scan samples from 214 habituated monkeys in 8 social groups (CP, EX, RM, GN, GN2, BC, AD, and LV) ranging in size from 7 to 35 monkeys. Mean group size over the study period was 22.2 members and median group size was 23 members. Proportion of adult females per group also varied over the study period. The highest proportion of adult females (0.48) was recorded in the BC group in 2019 while the lowest proportion of adult females (0.23) was recorded in the LV group in 2010. Social group composition and size shifted temporally over the course of the 15-year data collection period (Fig. 1). The social group CP fissioned in 2013 to become AD and RM. In 2019 the social group GN fissioned into GN2 and BC.

Behavioral sampling

The number of study months varied between 5 to 12 per year between January 2007 and January 2022. In this period, we collected behavioral data on each group in rotations of 2 to 5 consecutive days, from sunrise to sunset. Each group was followed for 1 to 3 such rotations per month. Inter-observer reliability (IOR) is tested during a training period for new researchers, and they begin to collect data only once their IOR is >95% with established researchers. We conducted instantaneous scan sampling every 30 min (Martin et al. 1993). For the majority of contact hours, multiple researchers (n = 2 to 5) were present for each scan. For each scan, we recorded the instantaneous state behavior for as many individuals as we could identify within a window of up to 10 min, using an established ethogram (Supplemental Table 1A). Within foraging behaviors, we collected more specific foraging types (Supplemental Table 1B) as well as the type or species of food (when possible) that each individual was foraging on. Prior to each scan, each member of the observer team would disperse to maximize the possibility of locating each group member as quickly as possible. One observer would record each data point, and other observers would dictate the behavior of the individual primates, to minimize duplicate entries. In the rare cases where duplicate entries were recorded, the second entry was removed prior to data analysis. Typically, the behaviors of the majority of group members were recorded within the first ca. 3 min of each scan. During times when the monkeys were widely dispersed (e.g., after an intergroup encounter or during inclement weather), observers communicated via two-way radio to help ensure that data points were recorded as close together as possible, but researchers would use the full 10-min window to locate individuals. Not all monkeys in the group were always able to be found in each scan. We have taken steps to account for this in our models, as detailed below. Finally, to minimize bias in data collection, such as over-representation of more centrally located monkeys, we began sampling with different individuals each time, and moved our positioning within the group to equalize, as much as possible, the coverage and order of recording different group members.

Data analyses

In total, we collected 85, 860 individual scans from 214 individuals in 8 social groups across 635 contact days. We filtered out days for which we did not have accurate rainfall or temperature records (n = 16 d). We additionally filtered out records for individuals on days in which they had been observed for 2 or fewer scans. After these filtering steps, we proceeded with 66, 395 scans for analyses.

Diversity metrics

We used two metrics to examine behavioral diversity, leveraging methods from community ecology and studies of biodiversity, as has been done previously in studies of non-human primates and dolphins (Delfour et al. 2021; Hall et al. 2021). First, we measured richness using the R package vegan (version 2.6.4) (Dixon 2003), which captures the number of unique records in a sample. For the current study, this translates to the number of distinct behaviors observed in a scan (for group-level analyses) or in a day (for individual-level analyses). Second, we measured

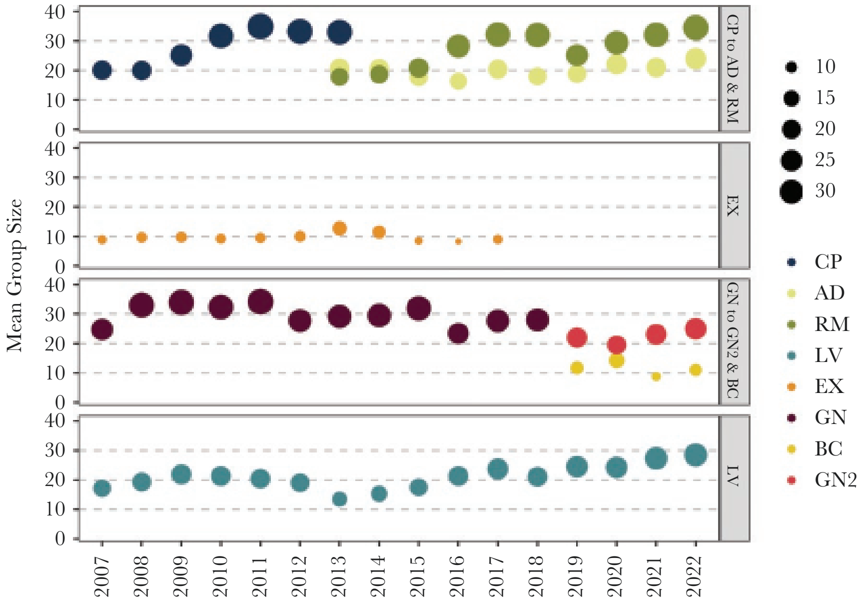

Fig. 1. Mean group size per year per social group. Each social group is censused once per month year-round. Each circle represents the mean group size per year with larger circles corresponding to larger groups. Each color corresponds to a distinct social group. Grey dashed horizontal lines demarcate size thresholds for small (15 members), and medium (25 members) social groups. CP group fissioned in 2013 into the AD group and RM group. The monthly census of EX group ceased in 2018. GN group fissioned in 2019 into GN2 group and BC group.

Shannon alpha diversity, also using the R package vegan, which captures not only observed richness, but also evenness of behavior in a defined sample. Low Shannon diversity values indicate lower diversity and that a sample that is dominated, in our study, by few behaviors. High Shannon diversity values indicate higher overall diversity, as well as more evenly distributed behaviors.

For each of the diversity metrics we conducted analyses at two distinct levels: cross-sectionally in a social group at a point in time, and longitudinally within individuals across the day. Measuring these metrics in a social group provides us with insights into the dynamics occurring at given time points among many individuals in a cohesive group, while measuring these factors within individuals provides insight into behavioral variation across the day.

Dominance rank and level

Once capuchins reach adult age, their dominance rank is assessed following methods established in Bergstrom and Fedigan (2010). In brief, long-term researchers at Sector Santa Rosa collect ad libitum dominance interactions including agonistic behaviors such as aggressive, submissive, and avoidance behaviors and vocalizations (Altmann 1974; Bergstrom and Fedigan 2010) continuously when they are with each group. The combination of rates of bi-directional aggression, intensity of kin bias, and behaviors (eg specific vocalizations, specific grooming interactions) are examined to assess dominance rank in this species annually, and/or following periods of social change (eg male emigrations, female deaths, etc.). Prior to adult age, dominance rank is not assessed as juveniles are not clearly integrated into the dominance hierarchy (Bergstrom and Fedigan 2010). Ordinal ranking differs depending on group size. To compare dominance rank across groups of different sizes, we used a variable we termed "dominance level." To calculate dominance level, we first gathered ordinal ranks from the yearly census data based on ranking methods outlined in Bergstrom and Fedigan (2010). Then, because group sizes differed, we scaled rank from 0 (lowest ranking) to 1 (highest ranking). We then created a categorical variable with three levels: low ranking, mid ranking, and high ranking. Individuals with scaled ranks from 0 to 0.32 were categorized as low ranking, while individuals with scores from 0.33 to 0.65 were categorized as mid-ranking, and individuals with scores >0.65 were categorized as high ranking. Juvenile individuals were binned into the category "unassessed."

Statistical models

We fit a series of linear mixed effects models, using the R program glmmTMB (version 1.1.10) (Brooks et al. 2017). For each model, we ran a corresponding null model and compared the AIC scores of each. Each null model was identical to the alternative model, except that each only included social group as a random effect. All but one model we fit (Group Level Foraging Shannon Diversity) outperformed its null model (Δ AIC > 2). Null model and alternative model comparisons are presented in Supplemental Tables 2–6.

To complete our first objective to assess the relationship between group size and behavioral diversity at the group and individual levels, we fit four generalized linear mixed models, with observed richness and Shannon diversity of behaviors as response variables. Our predictors of interest in all four models were group size. For the individual-level models, we also included dominance level as a fixed effect of interest. For models where behavioral richness was the response variable, and for models where number of monkeys exhibiting agonistic behaviors was the response variable, we used a Poisson distribution as these variables are count variables. For models with Shannon diversity as the response variable, we used a zero-inflated Gamma distribution, which is more appropriate for non-count data with many values that are 0. We include social group ID as a random effect to account for the effect of different groups.

In all models we controlled for variation in sampling effort to help ensure that diversity or richness did not simply reflect sampling more monkeys in larger groups. To do so, we included the proportion of the social group that was represented in each scan nested within social group. For example, if 27 out of 37 monkeys in the social group were recorded in a given scan, the proportion 0.73 was included as a random effect in the model. Because our models also included group size, this was an effective way to control for the overall sampling effort. As a further check, we also ran all models with the number of monkeys included in the scan as a random effect and the results were consistent for all analyses. For simplicity, we report the results of the former method, which also had more explanatory power (AIC).

Because environmental factors are known to influence behavior (Chapman and Fedigan 1990; Campos and Fedigan 2009; King and Cowlishaw 2009; Gestich et al. 2014), for the group-level models, we included daily maximum temperature, daily rainfall (mm), and monthly estimates of fruit biomass (kg/ha) as fixed effects to help control for their influence. Previous research has highlighted the potential importance of group demographic composition, especially with respect to adult females, in shaping behavioural diversity (King and Cowlishaw 2009; Williamson et al 2021). To help control for this potential confound, we included the proportion of adult females as a fixed effect.

For the individual level models, in addition to group size, we were interested in dominance rank. We also included daily rainfall (mm), daily maximum temperature, monthly estimate of fruit biomass (kg/ha), sex of individual, and age class of individual as controls. We included social group and proportion of monkeys recorded in each scan as random effects. We tested for autocorrelation of residuals using a Durbin-Watson test (Savin and White 1977). Autocorrelation scores were between 1.5 and 2 for the residuals from the observed richness and Shannon models for both the group-level and individual-level, indicating small but non-significant levels of positive autocorrelation.

For our second objective to assess the relationship between group size and foraging diversity at the group and individual levels, we fit similar generalized linear mixed models as detailed for objective one, with observed richness and Shannon diversity of foraging behaviors as response variables. We filtered the dataset to only include foraging behaviors (n = 36, 706 scans). Our predictor of interest for each model was group size for the group-level models, and dominance level as well as group size for the individual-level models. The control variables listed in objective one in the previous paragraph were identical to those in the models for objective two.

To address our final objective, which was to examine the relationship between agonism, dominance level, and group size, we fit a generalized linear mixed model with number of monkeys engaged in agonistic behavior as the response variable for the group-level analysis, and agonistic scans recorded across the day for individual level analysis. Our predictors of interest were group size and fruit biomass per square hectare for the group-level model. For the individual level model were additionally interested in dominance level as a predictor, as well as the potential interaction between dominance level and group size.

The control variables listed in objective one were also included in these models.

Results

Behavioral diversity at the group level

We found that group size was a positive, significant predictor of observed cross-sectional behavioral richness (Estimate = 1.16, CI = 1.12 to 1.21, $p < 0.001$) as well as Shannon diversity (Estimate = 0.88, CI = 0.86 to 0.91, $p < 0.001$) (Fig. 2). Daily maximum temperature was also positively correlated with richness and Shannon diversity (richness: Estimate = 1.02, CI = 1.0 to 1.03, p = 0.048; Shannon diversity: Estimate = 0.97, CI = 0.96 to 0.98, $p < 0.001$). Rainfall, proportion of adult females, and monthly fruit biomass were not significantly associated with richness nor Shannon diversity (**rainfall**: richness: Estimate = 0.98, CI = 0.97 to 1.00, p = 0.051; Shannon diversity: Estimate = 1.00, CI = 0.99 to 1.01, p = 0.9; **adult females**: richness: Estimate = 0.83, CI = 0.58 to 1.18, p = 0.291; Shannon diversity: Estimate = 0.98, CI = 0.75 to 1.27, p = 0.857; **fruit biomass**: richness: Estimate = 1.00, CI = 0.99 to 1.02, p = 0.853; Shannon diversity: Estimate = 0.99, CI = 0.98 to 1.00, p = 0.067) (Supplemental Table 2).

Behavioral diversity at the individual level

Group size was a significant predictor of individual behavioral richness longitudinally across the day; individuals in smaller groups exhibited lower behavioral diversity across the day compared to individuals in larger groups (Estimate = 1.02, CI = 1.01 to 0.04, $p < 0.001$). Group size was also a significant predictor of individual Shannon diversity (Estimate = 0.99, CI = 0.98 to 1.00, $p < 0.003$). The predicted values of behavioral richness and Shannon behavioral diversity at the individual level are plotted in Fig. 3. Among the variables we included as controls, age class

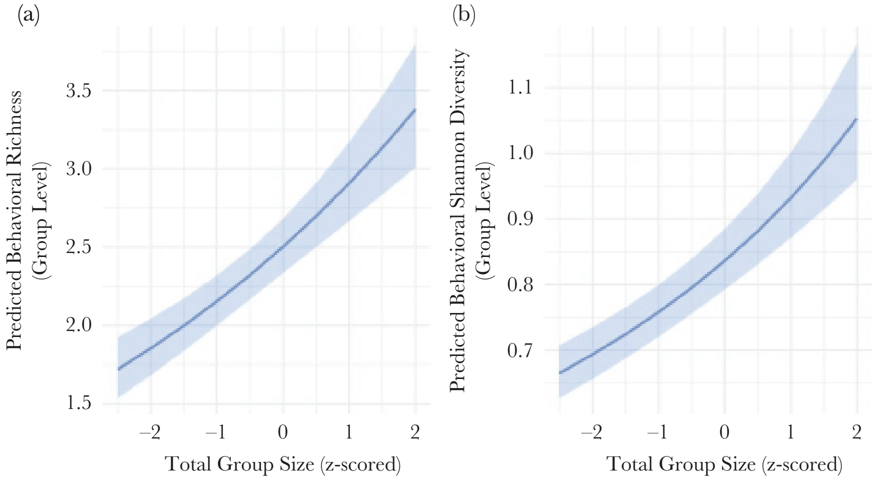

Fig. 2. Plots of two generalized linear mixed models are presented with group-level behavioral richness and group-level Shannon behavioral diversity as response variables. The predicted values of behavioral richness (y-axis) (**a**) and Shannon behavioral diversity (y-axis) (**b**) are plotted at the group level as they relate to group size (x-axis). The dark blue line is the predicted value, and the lighter blue shading represents 95% confidence intervals. Group sizes are Z-scored to improve ability to evaluate effect sizes; negative values indicate group sizes smaller than the mean group size and positive values are larger than mean group size.

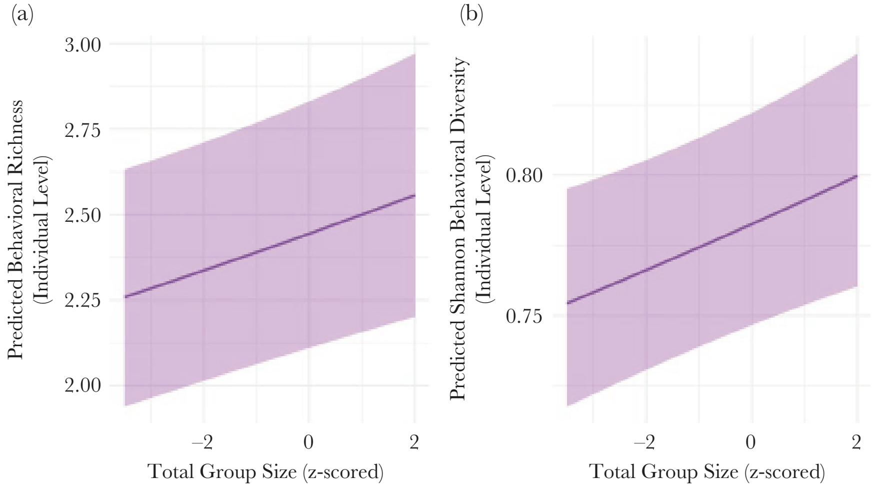

Fig. 3. Plots of two generalized linear mixed model are presented with individual behavioral richness (y-axis) (**a**) and individual Shannon behavioral diversity (y-axis) (**b**) as the response variables. We plotted the predicted values of richness and diversity as group size (x-axis) increases. The dark purple line represents the predicted values of individual-level behavioral richness and individual-level Shannon behavioral diversity, and the lighter purple shading represents 95% confidence intervals. Group sizes are Z-scored to improve ability to evaluate effect sizes; negative values indicate group sizes smaller than the mean group size and positive values are larger than mean group size.

was also significant predictor of richness and diversity; compared to infants, all older age classes were considerably more behaviorally diverse (**small immature**: richness: Estimate = 1.14, CI = 1.07 to 1.22, p < 0.001, Shannon diversity: Estimate = 0.89, CI = 0.85 to 0.93, p < 0.001; **large immature** richness: Estimate = 1.17, CI = 1.10 to 1.25, p < 0.001, Shannon diversity: Estimate = 0.87, CI = 0.83 to 0.91, p < 0.001; **adult** richness: Estimate = 1.21, CI = 1.13 to 1.29, p < 0.001, Shannon diversity: Estimate = 0.83, CI = 0.80 to 0.87, p < 0.001); (Supplemental Table 3). Sex of the individual was also a predictor of behavioral richness and diversity: males exhibited higher behavioral richness and diversity than females (**male** richness: Estimate = 0.97, CI = 0.94 to 1.00, p = 0.026, Shannon diversity: Estimate = 1.03, CI = 1.01 to 1.05, p = 0.002) (Supplemental Table 3). Rainfall was not related to behavioral richness but was positively related to Shannon diversity (**rainfall**: richness: Estimate = 0.99, CI = 0.98 to 1.01, p = 0.237, Shannon diversity: Estimate = 1.01, CI = 1.00 to 1.02, p = 0.046). Fruit biomass was not related to behavioral richness but was positively related to Shannon diversity (**fruit biomass**: richness: Estimate = 1.01, CI = 1.00 to 1.02, p = 0.180, Shannon diversity: Estimate = 0.98, CI = 0.97 to 0.99, p < 0.001). Dominance level was unrelated to behavioral diversity at the individual level (**low rank**: richness: Estimate = 0.99, CI = 0.95 to 1.02, p = 0.448; **mid rank**: richness: Estimate = 0.99,CI = 0.95 to 1.03, p = 0.564; Shannon diversity: Estimate = 1.02, CI = 0.99 to 1.05, p = 0.213; **unassessed rank**: richness: Estimate = 0.99, CI = 0.94 to 1.04, p = 0.711; Shannon diversity: Estimate = 1.02, CI = 0.99 to 1.06, p = 0.186), though low dominance individuals exhibited slightly higher Shannon diversity compared to high dominance individuals (Estimate = 1.03, CI = 1.01 to 1.06, p = 0.012). Temperature had a significant but small positive effect on behavioral diversity (richness: Estimate = 1.04, CI = 1.02 to 1.05, p < 0.001; Shannon diversity: Estimate = 0.96, CI = 0.96 to 0.97, p < 0.001) (Supplemental Table 3).

Foraging diversity at the group level

Group size was a significant predictor of cross-sectional foraging behavior richness (Estimate = 1.03, CI = 1.01 to 1.05, p = 0.010; Fig. 4a). However, the null model for Shannon foraging diversity outperformed the alternative model, suggesting Shannon foraging diversity (cross-sectional) was not impacted by group size. Daily maximum temperature was significantly positively related to foraging richness, such that richness and diversity were higher on hotter days (Estimate = 0.98, CI = 0.96 to 0.99, p = 0.004); rainfall, proportion of adult females, and available fruit biomass were not significant predictors (**rainfall**: Estimate = 1.00, CI = 0.98 to 1.01, p = 0.750; **proportion adult females**: Estimate = 0.95, CI = 0.70 to 1.30, p = 0.767; **fruit biomass**: Estimate = 1.00, CI = 1.00 to 1.00, p = 0.302) (Supplemental Table 4).

Foraging diversity at the individual level

At the individual level, group size was not significantly related to foraging richness of individuals longitudinally across the day (Estimate = 0.98, CI = 0.95 to 1.01, p = 0.167) (Supplemental Table 5). However, Shannon foraging diversity was significantly positively related to group size (Estimate = 1.03, CI = 1.01 to 1.06, p = 0.003), such that individuals in larger group exhibited a significantly higher number of distinct foraging behaviors that were distributed more evenly across the day compared to individuals in smaller groups. Ecological control variables, including temperature and rainfall were not significant predictors of foraging richness or diversity of individuals (**temperature**: richness: Estimate = 1.00, CI = 0.99 to 1.02, p = 0.633; Shannon diversity: Estimate = 1.00, CI = 0.99 to 1.01, p = 0.776; **rainfall**: richness: Estimate = 1.00, CI = 0.99 to 1.02, p = 0.635; Shannon diversity: Estimate = 0.99, CI = 0.98 to 1.00, p = 0.115) (Supplemental Table 5). Age class had a significant effect, with non-infants exhibiting higher foraging diversity than infants (**small immature**: richness: Estimate = 1.23, CI = 1.13 to 1.35, p < 0.001; Shannon diversity: Estimate = 0.84, CI = 0.78 to 0.91, p < 0.001; **large immature**: richness: Estimate = 1.23, CI = 1.12 to 1.34, p < 0.001; Shannon diversity: Estimate = 0.85, CI = 0.79 to 0.92, p < 0.001; **adult**: richness: Estimate = 1.15, CI = 1.05 to 1.26, p = 0.002; Shannon diversity: Estimate = 0.91, CI = 0.84 to 0.98, p = 0.016) (Supplemental

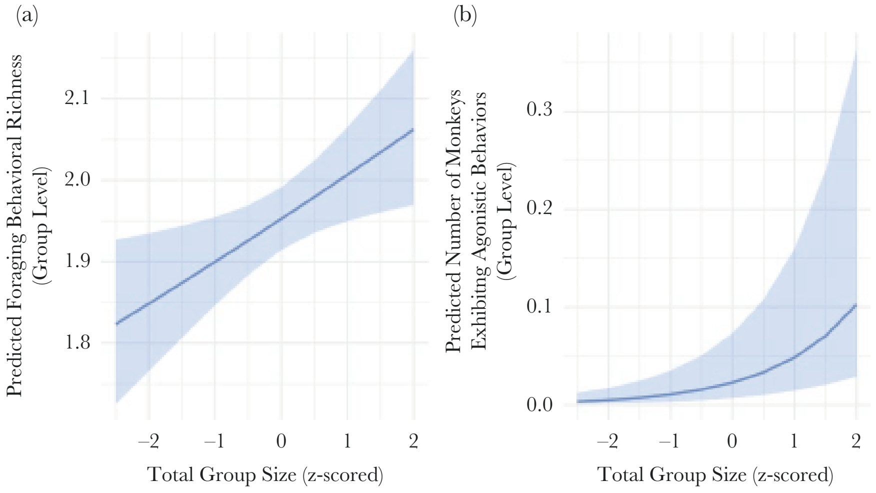

Fig. 4. Multiple generalized linear mixed models are plotted with foraging behavioral richness and Shannon foraging diversity as the response variables. We computed and plotted predicted values of foraging behavioral richness (y-axis) as a function of group size (x-axis) at the group level (**a**). We additionally fit a model with number of monkeys exhibiting agonistic behaviors as the response variable. We plotted predicted values of number of monkeys recorded in agonistic behaviors (y-axis) as a function of group size (x-axis) (**b**). In both plots, the dark blue line represents the predicted values of foraging behavioral richness, and the lighter blue represents the 95% confidence intervals. Group sizes are Z-scored to improve ability to evaluate effect sizes; negative values indicate group sizes smaller than the mean group size and positive values are larger than mean group size.

Table 5). Finally, dominance rank was significantly related to foraging diversity: mid-ranking individuals exhibited higher foraging Shannon diversity compared to high-ranking individuals (Estimate = 0.96, CI = 0.93 to 0.99, p = 0.021) (Supplemental Table 5).

Agonism and group size at the group level

Group size was a significant predictor of agonism at the group level (Estimate = 2.11, CI = 1.62 to 64, $p < 0.001$, Fig. 4b) with larger groups exhibiting higher rates of agonism compared to smaller groups. Rainfall was not significantly related to agonism (Estimate = 1.06, CI = 0.95 to 1.19, p = 0.296). Fruit biomass, temperature, and proportion of adult females in the group had a positive, significant effect on rates of agonism at the group level (**fruit biomass**: Estimate = 0.80, CI = 0.71 to 0.90, $p < 0.001$; **temperature**: Estimate = 1.21, CI = 1.10 to 1.34, $p < 0.001$; **proportion adult females**: Estimate = 383.75, CI = 51.42 to 2863.82, $p < 0.001$) (Supplemental Table 6).

Agonism, dominance rank, and group size at the individual level

At the individual level, our models suggested a positive relationship between group size and rates of agonism across the day, though the correlation was not statistically significant (Estimate = 1.12, CI = 0.95 to 1.33. p = 0.174) (Supplemental Table 6). This was true for individuals regardless of dominance rank such that high-ranking individuals exhibited similar rates of agonism in larger groups compared to high-ranking individuals in smaller groups and so on (**low rank * group size**: Estimate = 1.04, CI = 0.82 to 1.32, p = 0.758; **mid rank * group size**: Estimate = 0.96, CI = 0.76 to 1.21, p = 0.740; **high rank * group size**: Estimate = 1.19, CI = 0.97 to 1.46, p = 0.103). Age classes older than infant exhibited significantly higher rates of agonism, but no other age class effects were seen (**small immature**: Estimate = 3.93, CI = 1.49 to 10.40, p = 0.006; **large immature**: Estimate = 9.46, CI = 3.79 to 23.61, $p < 0.001$; **adult**: Estimate = 13.42, CI = 5.36 to 33.58, $p < 0.001$). (Supplemental Table 6). Sex was not a significant predictor of agonism at the individual level (Estimate = 0.86, CI = 0.73 to 1.02, p = 0.079) (Supplemental Table 6).

Discussion

Our first goal was to examine the relationships between behavioral diversity and group size. Our main findings were that cross-sectional behavioral richness and diversity at the group level were higher overall in larger groups compared to smaller groups. We also found that individuals in larger groups exhibited significantly higher behavioral richness across the day. Our second goal was to specifically look at the foraging behavioral diversity. We found that the cross-sectional richness of foraging behaviors (but not Shannon diversity) was higher in larger groups, and at the individual level, Shannon diversity of distinct foraging behaviors exhibited across the day was higher among individuals living in larger groups. Together, these findings largely support predictions of the Resource Distribution Hypothesis (RDH). Our third goal was to examine the relationships among agonism, dominance rank, and group size. We found that agonism frequency measured cross-sectionally at the group level was higher in larger groups compared to smaller groups, but surprisingly, this wasn't found at the individual level, and there was no interaction with dominance rank. Below, we discuss these findings and their significance in detail.

The diversity of behaviors expressed at any one time is higher in larger groups

We found support for our prediction that larger groups would have higher cross-sectional richness and diversity of behaviors, and specifically a larger richness of foraging behaviours, which is consistent with the hypothesis that there is pressure to diversify behaviors in a large group to decrease competition among group members. Importantly, this is controlling for variation in sampling effort, such that higher diversity or richness does not simply reflect sampling more monkeys in larger groups. Diversifying behaviors has previously been suggested to decrease intragroup competition in wild systems. In stickleback fish (*Gasterosteus aculeatus*), for example, increased population density was associated with increased competition for resources, and a corresponding diversifying of foraging behaviors was reported as a potential mitigation strategy (Svanbäck and Bolnick 2006). Similarly, banded mongooses (*Mungos mungo*) exhibit more diverse behaviors and specialized foraging niches with increased group size, which may contribute to the stability of mongoose social groups (Green et al. 2021). Although most of our results—results for three of the four predictions—are consistent with predictions of the RDH, we did not find that Shannon diversity was impacted at the group level when looking only at foraging behaviors. Further examination of the pressures leading to differences in behavioral richness (the number of distinct behaviors) versus the Shannon diversity, which factors in evenness of how the behaviors are distributed across the group, may be instructive.

At the individual level, we found that group size impacted the richness and Shannon diversity of behaviors performed by individuals across the day; individuals in larger groups were observed in a greater number of distinct behaviors. We also found similar results for Shannon diversity of foraging behaviors, specifically. This is largely consistent with the group-level results and further supports the RDH. Interestingly, mid-ranking individuals exhibited increased foraging richness and diversity compared to the highest-ranking individuals. One possible explanation is they expand the diversity of their behaviors as a way of avoiding agonistic interactions with the most dominant individuals. Previous research at this site has found evidence for within-group niche partitioning in forest strata among age and sex classes (Williamson et al. 2021), yet the authors did not assess whether niche partitioning was related to group size, and did not include dominance rank in their analyses. A logical extension of the present study would be to investigate the relationship between group size and niche partitioning in physical space or substrate use, while also considering dominance rank. Future studies may also benefit from examining whether physical separation between group members increases in larger groups to decrease direct competition, as we were not able to examine inter-individual spacing in this study.

Group size predicts agonism frequency at the group level

We found support for our prediction that higher rates of agonism are present in larger groups, controlling for the increased sampling potential in larger groups. This is consistent with other reports in primates. In a meta-analysis of 45 populations across 23 primate species, Cowl and Shultz (2017) found that group size and rates of group-level agonism (but not dyadic agonism) were positively correlated. High levels of agonisms at large group sizes can lead to destabilization of social groups. Indeed, increased competition for resources, and correspondingly heightened agonism and/or extreme behavioral diversity that impacts group cohesion, may exert an upper limit on group size (Markham et al. 2015; Ward and Webster 2016).

Our results may shed light on proximate factors leading to group fission events. At Sector Santa Rosa where the present study took place, four group fission events have been recorded in ca. 40 yr of continuous observation (two cases are presented in Fig. 1, and another case took place in group RM several months after the data collection for this study ceased). In each case, the permanent fission of one group into two smaller groups occurred at group sizes of >35 monkeys. This raises the possibility of a rough upper limit of group size in our population, above which the costs exceed the benefits, at least for a subset of the individuals in the group. These upper levels of group size are represented in the largest groups we studied here, which showed the highest rates of agonism. Future extensions of this research might usefully include a comparison of rates of agonism and behavioral diversity directly before and after fission events. Examining fissions that occur at different group sizes and in a variety of ecological contexts across the white-faced capuchin distribution would further contextualize our results. Similarly, longitudinal studies of a wide diversity of group-living mammals will further expose the many fascinating dynamics of group-living.

Though we found that agonism frequency overall was higher in larger groups, our prediction that individuals in larger groups would exhibit higher rates of agonism across the day was not supported. Furthermore, patterns of agonism were consistent across dominance levels, such that individuals were engaged in agonistic behaviors at similar frequencies, regardless of their dominance rank. These results suggest that high-ranking individuals did not drive the overall increase in agonism that accompanied groups of larger size. This is perhaps surprising, and invites future, more detailed investigations of how group size impacts individuals at different levels of the dominance hierarchy. Additionally, given that many socially living mammals have evolved behaviors (eg reconciliation, post-conflict affiliation) to stabilize social relationships after aggressive interactions (Cowl and Shultz 2017), investigating rates of reconciliatory behaviors in different group sizes would be interesting and relevant.

Limitations, conclusions, and future directions

Like many studies of wild social mammals, our study has limitations. One limitation of our ethogram was the level of detail regarding agonism: future research may benefit from more nuanced records of agonistic interactions, including contexts leading up to the agonistic behaviors. A further limitation of our methods was our approach to recording behavioral scans, which may have introduced bias in two ways: first, despite our efforts to move around the group, consistently peripheral monkeys may be underrepresented in our data; second, individuals who were recorded near the end of the scan interval are less likely to have been exhibiting the same behavior as they were at the start of the scan record, decreasing the likelihood of capturing simultaneous behaviors. Though we attempted to mitigate this bias in our data collection (see Methods), it nevertheless may exist. Finally, we were not able to control for impacts of intergroup encounters, which some research suggests may affect behavioral diversity (Wilson et al. 2012).

Despite these limitations, we present clear evidence that group size affects multiple aspects of behavior in a wild population of socially living primates. Increased richness and diversity of behaviors was seen cross-sectionally at the group level and across the day at the level of individual monkeys when social groups had more members. Group size also clearly predicted rates of agonism in this population at the group level. Taken together, the results from this study suggest that diversifying behaviors is one way in which this species may be mitigating the costs of intragroup competition. Future studies on this species could include physical proximity to other groups and temporal proximity to intergroup encounters as potentially important predictors of behavioral diversity. More broadly, incorporation of behavioral diversity into future studies of social dynamics or examining behavioral diversity and group fissions in existing long-term datasets, represents an important line of questioning in pursuit of understanding the causes, costs, and benefits of group living.

Supplementary material

Supplementary material is available at *Behavioral Ecology* online.

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Author contributions

Shasta Webb (Conceptualization [equal], Data curation [equal], Formal analysis [lead], Writing—original draft [lead], Writing—review & editing [equal]), Silvia Carboni (Writing—original draft [equal], Writing—review & editing [equal]), Allegra N. DePasquale (Data curation [equal]), Rachel E. Williamson (Data curation [equal]), Saúl Cheves Hernandez (Data curation [equal]), Ronald Lopez (Data curation [equal]), and Amanda Melin (Conceptualization [equal], Data curation [equal], Supervision [equal], Writing—original draft [equal], Writing—review & editing [equal])

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Conflicts of interest

None declared.

Data availability

Analyses reported in this article can be reproduced using the data provided by Webb et al. (2025).

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