

## RESEARCH ARTICLE

# Foraging networks and social tolerance in a cooperatively breeding primate (*Callithrix jacchus*)

María Fernanda De la Fuente<sup>1</sup>  | Cédric Sueur<sup>2</sup>  | Paul A. Garber<sup>3</sup>  |  
Júlio César Bicca-Marques<sup>4</sup>  | Antonio Souto<sup>5</sup>  | Nicola Schiel<sup>1</sup> 

<sup>1</sup>Departamento de Biologia, Universidade Federal Rural de Pernambuco, Recife, Brazil

<sup>2</sup>Institut Pluridisciplinaire Hubert Curien (IPHC), Université de Strasbourg, CNRS, Strasbourg, France

<sup>3</sup>Department of Anthropology, Program in Ecology, Evolution, and Conservation Biology, University of Illinois, Urbana, IL, USA

<sup>4</sup>Escola de Ciências da Saúde e da Vida, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil

<sup>5</sup>Departamento de Zoologia, Universidade Federal de Pernambuco, Recife, Brazil

## Correspondence

María Fernanda De la Fuente  
Email: ferni211@yahoo.com.ar

## Funding information

Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Number: 88881.064998/2014-01; Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: APQ 403126/2016-9, PQ 303306/2013-0 and PQ 304475/2018-1

Handling Editor: Eric Vander Wal

## Abstract

1. Within-group competition over food resources can be a major cost of social living. In the wild, foragers are confronted with social (e.g. hierarchical rank) and ecological (e.g. food availability and distribution) challenges that affect their foraging decisions and feeding success. Exhibiting prosocial behaviours, such as tolerance at feeding sites, can benefit group members by developing affiliative social relationships, enhancing access to resources and maximizing fitness.
2. We examined social tolerance at feeding sites in *Callithrix jacchus*, a cooperatively breeding primate species. We investigated the set of social (rank, age and sex) and ecological (food availability) factors that influence the structure and dynamics of within-group foraging association networks.
3. We designed and conducted an experimental field study of four wild groups of common marmosets in which we controlled food distribution (concentrated or scattered) and productivity (high, medium or low food rewards). Then, we used social network analyses to assess the number and strength of foraging associations among group members, their effects on individual food consumption, and whether recent experiences with conspecifics during foraging affected subsequent associations.
4. Overall, common marmoset foraging association networks were cohesive, as group members jointly occupied feeding sites. The number and strength of associations varied depending on the ecological context. Associations were stronger during conditions in which food was concentrated at a single site. Individuals obtained greater access to food resources when sharing a feeding site with conspecifics, but once a food item was obtained, the forager moved to a nearby tree and consumed it away from others. Additionally, the strength of previous foraging associations and subsequent levels of social tolerance at feeding sites were positively related, a relationship compatible with the ability of memorizing associations over time and recalling the information in future decision-making.
5. In sum, marmosets adjusted their partner choices and the strength of foraging associations in response to food availability. They exhibited increased social tolerance at feeding sites during conditions in which opportunities for contest competition were expected to be greatest. These cooperative breeding primates

appear to mutually benefit by maintaining cohesive and strong affiliative relationships, and by increasing opportunities for coordinated behaviour and offspring survival.

#### KEYWORDS

associations, common marmoset, field experiment, group cohesion, social network

## 1 | INTRODUCTION

Social living animals face a trade-off between the advantages and disadvantages of being part of a group. Enhanced predator detection and territorial defense might benefit most or all group members, while competition over resources (i.e. food and/or mates) might increase levels of intragroup aggression (Sterck et al., 1997; Sussman & Garber, 2011). Optimal foraging theory predicts that animals should behave to maximize their fitness when searching for food by adopting strategies that decrease time/energy costs of finding food and increase energy intake (Chaves & Alves, 2010; Pyke et al., 1977). However, this model does not consider the influence of social factors during foraging, in which individuals interact affecting each other's decision-making and payoffs (Giraldeau & Dubois, 2008). Other theoretical frameworks, such as the social foraging theory, analyse the costs and benefits of cooperation and competition in animals, predicting that the foraging strategies of group-living individuals are influenced by the identity and actions of other group members (Giraldeau & Caraco, 2000). In addition to ecological factors, such as food productivity and distribution, foraging strategies and success are affected by social factors, such as dominance status, kinship and cooperative interactions (Keynan et al., 2015; Li et al., 2021). According to socioecological models (originally developed for primate species, but also applied to other species: elephants, Archie et al., 2006; feral cats, Bonanni et al., 2007; hyenas, Smith et al., 2007; rooks, Scheid et al., 2008), social foragers potentially face two types of intragroup feeding competition (Isbell, 1991; van Schaik & van Noordwijk, 1988; Sterck et al., 1997). Scramble competition occurs when the first individual to find a resource consumes it prior to the arrival of other group members, obtaining a 'finder's advantage' (greatest when resources are limited) without aggressive interference. In contest competition, a single or a small set of dominant individuals can monopolize, aggressively or not, resources concentrated in small- or medium-sized food patches. Behavioural strategies that allow individuals to accomplish a balance between the costs and benefits of social living, such as participating in collective or cooperative actions, forming coalitions and maintaining or ascending to a position of high rank, can shape the relationships (i.e. interactions and associations) between group members (Sueur et al., 2018).

By forming and developing affiliative social relationships, individuals can enhance their access to resources and maximize fitness

(Schülke et al., 2010; Stanton & Mann, 2012). In this context, social tolerance can be described as the probability that conspecifics remain in close proximity to each other in the presence of valuable resources (e.g. foraging contexts and during mating) while displaying low levels or no conspicuous aggression (Cronin & Sánchez, 2012). The benefits of within-group tolerance and prosocial behaviours include lower rates of agonistic interactions, reduced risk of injury, improved access to and sharing of resources, enhanced predator vigilance, cooperative range defense and the transmission of social and ecological information by closely observing and following conspecifics (Miller et al., 2014; Pasquaretta et al., 2014).

Wild foragers are commonly confronted with a range of ecological and social challenges associated with spatial and temporal changes in food availability, as well as with different types of social relationships among group members (i.e. individual's dominance rank), that affect foraging decisions and the degree to which individuals are tolerant or intolerant of conspecifics (Marshall et al., 2015). It can be expected that at larger, more productive and/or dispersed feeding sites (e.g. trees producing a large food crop or several nearby small food patches), the benefits of investing time and energy in monopolizing resources are low, and group members are expected to be more tolerant of conspecifics and co-feed. In contrast, at defensible and highly depletable feeding sites (e.g. trees with a small food reward), higher-ranking foragers are expected to be less tolerant and actively exclude conspecifics to obtain priority access to resources and increase food intake (i.e. contest competition; Sterck et al., 1997).

Maintaining close spatial proximity to group mates who are likely to exhibit an increased predisposition to share resources is a strategy employed by some social foragers (King et al., 2011). Group members may exhibit foraging partner preferences based on dominance rank, age, sex and/or kinship. In some species, individuals who share a similar rank establish stronger bonds (e.g. rhesus monkeys: de Waal, 1991; brown capuchin monkeys: Parr et al., 1997; Sorraia horses: Heitor et al., 2006; spotted hyenas: Smith et al., 2007) and associate or more commonly share access to feeding and drinking sites. Stronger associations result in greater mutual social and resource-related benefits than those shared by individuals of more distant rank positions (Smith et al., 2007; de Waal, 1991). In species in which adults are more tolerant of immature group members, who may be less efficient and less competitive foragers than adults, young individuals benefit by obtaining food-related information and developing foraging skills through

social influence (e.g. primates: Schiel & Huber, 2006; birds: Holzhaider et al., 2010; meerkats: Thornton & Clutton-Brock, 2011). Evaluating how group members affiliate, track and adjust their associations under changing conditions of food availability offers critical insight into our understanding of the evolution of sociality.

We conducted a field experiment designed to examine foraging associations in a species of cooperatively breeding New World primate, the common marmoset *Callithrix jacchus*. Callitrichines are distinguished among primates by their unique system of cooperative infant caregiving, in which a group generally contains a single breeding female, who can produce up to two sets of twin infants per year. The breeding female is assisted by helpers, principally several resident adult males, to successfully rear her offspring (Digby et al., 2011; Koenig, 1995). Common marmosets live in groups of 3 to 16 individuals composed of multiple adult males and females, juveniles and infants (Digby et al., 2011; Garber et al., 2019), and are characterized by a pyramidal-like hierarchy with the breeding female at the top, followed by all other group members (with decreasing social rank based on age; De la Fuente et al., 2019). Offspring may stay in their natal group past puberty and become helpers, but also individuals can disperse and migrate between groups. Common marmosets exploit a wide range of food items including plant exudates, fruit, invertebrate and vertebrate prey (Schiel & Souto, 2017). In the wild, they forage as a cohesive group, whose members are attracted to the others' food discoveries and, in general, are tolerant of co-sharing feeding sites (Schiel & Huber, 2006). Even though intragroup agonistic interactions are uncommon, they can occur in feeding contexts and increase after changes in group composition (rates of  $\sim 0.08$  to  $0.25$  per hour, Lazaro-Perea et al., 2000).

In a previous study examining foraging strategies in common marmosets presented with controlled experimental conditions characterized by changes in food productivity and distribution (De la Fuente et al., 2019), we found that, except for the breeding female who had the highest feeding success, all other group members, including adults and juveniles experienced relatively equal feeding success. Overall, group members shared experimental food platforms (feeding sites) to obtain resources during almost half (48%) of foraging visits. Here, we investigate how social and ecological factors influence the structure and dynamics of within-group foraging associations and social tolerance at feeding sites. We test predictions of four hypotheses (Table 1).

## 2 | MATERIALS AND METHODS

### 2.1 | Study site and study groups

We studied four groups of common marmosets living in the semi-arid Caatinga scrublands at the Baracuhy Biological Field Station ( $7^{\circ}31'42''\text{S}$ ,  $36^{\circ}17'50''\text{W}$ ) in the state of Paraíba, northeast of Brazil (see De la Fuente et al., 2019 for details on the study site). We studied each group, named ALG, COQ, PRI and VAC, for a period of 4 months. The size of the groups ranged from five to eight individuals

(including infants) at the beginning of the study. A single VAC and PRI individual left its group during the last experimental condition. ALG decreased in size from seven to four individuals due to the emigration of two adult males followed by the immigration of a new adult male in the third experimental condition, and the emigration of two adult females in the fourth experimental condition (Table S1). We adjusted our analyses accounting for these group changes by removing individuals who disappeared from a given experimental condition (see Figure 1). Group members were habituated to the presence of human observers prior to the study. We trapped and marked adults with coloured beaded collars and shaved different tail segments of juveniles for individual identification (Garber et al., 2019).

### 2.2 | Rank assessment

We assessed social rank using the frequency of all agonistic interactions that occurred between dyads during experimental conditions. We calculated the normalized David's score (NDS; de Vries et al., 2006) for each group member as it provides a measure of an individual's success taking into account the power of its opponent and allows us to construct a ranking order based on the winner and loser of agonistic interactions; that is, the higher the frequency of interactions won, the higher the rank. We recorded the identity of individuals involved in the interaction, the type of agonistic interactions (i.e. low intensity, no physical contact such as vocalizations and piloerection; and high intensity, all interactions that had a risk of physical injury such as fights, attacks and chases), and the winner and loser of the interaction (i.e. the winner caused the loser to perform a submissive posture/vocalization or to fled from the interaction). The single breeding female of COQ, PRI and VAC were the highest ranking individuals, followed by adult males, other adult females and juveniles. We assessed rank twice in the ALG group because of changes in adult composition. In this group, adult males occupied the highest ranks, followed by adult females, and juveniles (Table S1).

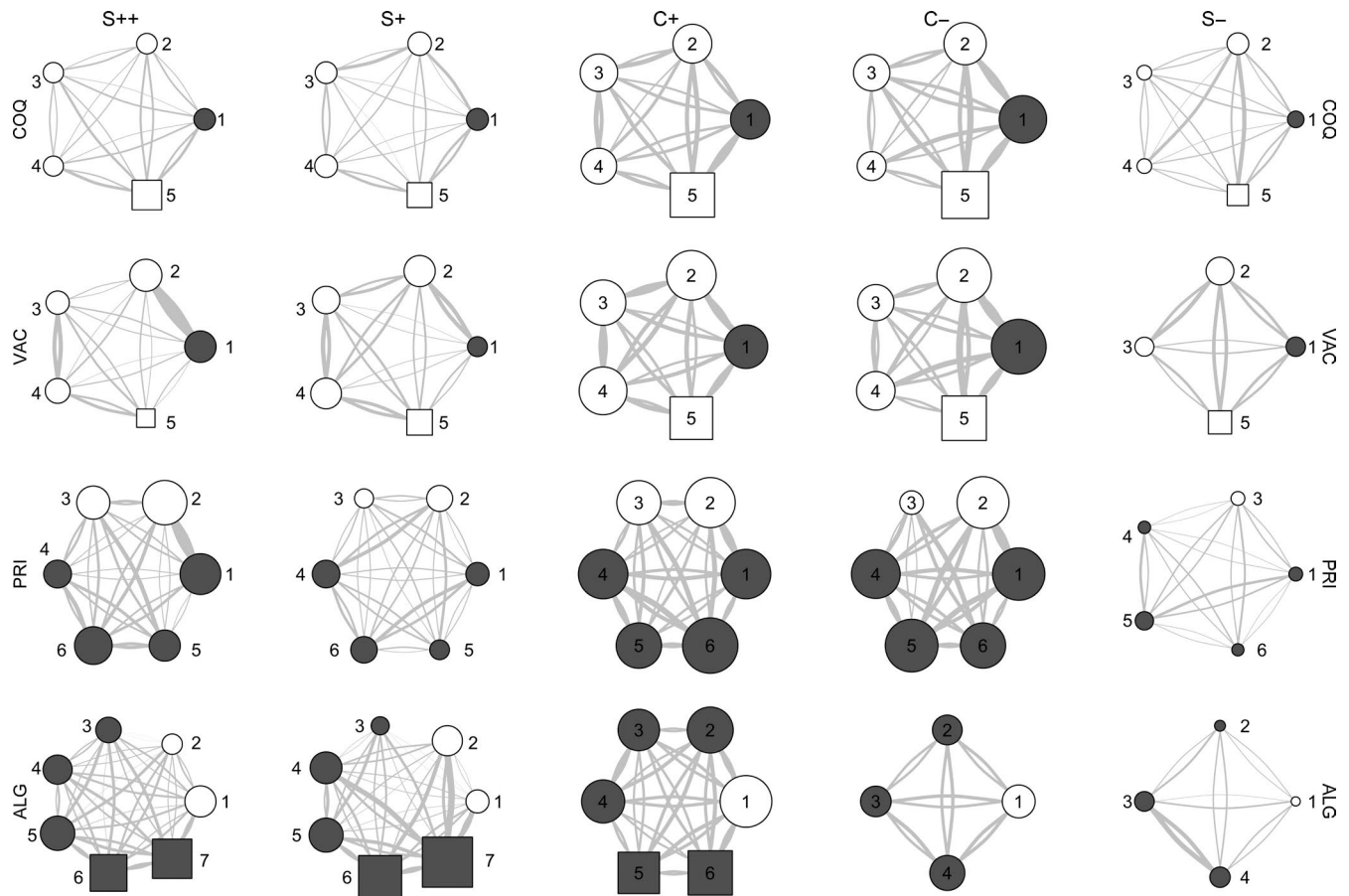
### 2.3 | Field experiments

We established an experimental feeding station by placing four wooden feeding platforms (50 cm  $\times$  50 cm) in a square arrangement (2.5 m apart from each other) in each study group's home range (see Figure S5). A marmoset on one platform could see all other platforms and its visitors. We fixed a clear plastic container with accessible or inaccessible food rewards (controlled number of 3 g banana pieces, see Table S2 for details on the amount of food offered per group) on each platform. Accessible containers had two openings (5 cm  $\times$  3 cm) enabling two or more group members to feed on and share a platform. Inaccessible containers had small holes to allow for olfactory cues, but the marmosets could not access the food reward.

We conducted five experimental conditions in which food was concentrated (C) on a single feeding platform or scattered (S) among

**TABLE 1** Hypotheses (H) and predictors tested to investigate social tolerance at feeding sites in wild groups of common marmosets (see Figures S1–S4 for graphical representations)

<b>H1. Ecological and social factors influence individual levels of social tolerance</b>		
Predictors	a. Food availability (distribution and productivity)	Given marmosets' social system, we expect that group members will associate at feeding sites under all food conditions (De la Fuente et al., 2019). However, individuals will share feeding sites (i) with less group members and (ii) for smaller proportions of time when food is concentrated and/or insufficient to satiate all foragers (i.e. increased opportunity for feeding competition, Sterck et al., 1997) than when food is scattered and/or sufficient to satiate all foragers
	b. Individual's age	Given that immature individuals are less efficient foragers (Schiel & Huber, 2006) and can pose lower levels of competition, we expect that juveniles will share a feeding site (i) with a greater number of group members (other juveniles and adults) and (ii) for greater proportions of time than adults will among them
	c. Individual's sex/rank class	Given that the breeding females are the highest ranking and the most aggressive individuals of our study groups (De la Fuente et al., 2019), we expect that they will be less tolerant to get access to resources, resulting in sharing feeding sites (i) with less group members and (ii) for smaller proportions of time than other group members
<b>H2. Common marmosets have dyadic foraging partner preferences</b>		
Predictors	a. Food availability	If group members have foraging partner preferences (King et al., 2011), we expect that dyadic associations will be stable under all food conditions. Nevertheless, the proportion of time that a dyad of preferred partners shares a feeding site will depend on the productivity and distribution of food rewards. Dyads will spend greater proportions of time sharing feeding sites when there is plenty of food scattered than when food is concentrated and/or quickly depletable
	b. Rank distance	If dyads with closer ranks establish stronger bonds (Heitor et al., 2006; Parr et al., 1997; Smith et al., 2007; de Waal, 1991), we expect that such dyads will share feeding sites for greater proportions of time than other dyads
	c. Dyad age composition	Given that immature individuals pose lower levels of competition (Schiel & Huber, 2006), we expect that dyads composed of an adult and a juvenile will spend greater proportions of time sharing a feeding site than dyads composed of two adults
	d. Dyad sex composition	Given the callitrichine social system (Ferrari, 2009; Yamamoto et al., 2009), we expect that (i) breeding females will associate for greater proportions of time with adult males than with other adult females, and that (ii) adult males will associate for greater proportions of time with each other
<b>H3. Social tolerance influences individual food consumption</b>		
Predictors	a. Number of group members with whom an individual shares a site	If remaining in close proximity with more group members during foraging can increase individual's access to resources (de Waal, 1991), we expect that sharing feeding sites with more group members will increase individual food consumption
	b. Proportion of time sharing a site	Given that the longer an individual spends in a feeding site, the greater the amount of resources that it can get, we expect that sharing a platform for greater proportions of time will increase an individual's food consumption
	c. Avoidance events performed	Given that the avoidance of sharing a feeding site can cause smaller proportions of time spent on it, we expect that the frequency of avoidance events performed by an individual will be inversely related to its food consumption
	d. Agonistic events received	If receiving agonistic interactions reduces access to resources (Michels, 1998), we expect that the frequency of agonistic events received by an individual will be inversely related to its food consumption
<b>H4. Recent foraging experiences influence social tolerance at the (A) individual and (B) dyad levels</b>		
Predictors	a. Previous foraging associations	If group members recall their recent foraging interactions (Hattori et al., 2012), we expect that the proportion of time that individuals and dyads spend sharing a feeding site during the most recent session of foraging will show a positive relationship with the proportion of time that they will spend sharing a site in the next session
	b. Previous avoidance events	We expect that the frequency of avoidance events performed by an individual/dyad in the most recent foraging session will be negatively related to the proportion of time that it will spend sharing a feeding site in the next session
	c. Previous agonistic events	We expect that the frequency of agonistic events experienced by an individual/dyad in the most recent foraging session will be negatively related to the proportion of time that it will spend sharing a feeding site in the next session
	d. Previous food consumption	Given that satiation may influence individual's motivation to sharing a feeding site to access resources, we expect that the amount of food that it has ingested during the most recent foraging session will be negatively related to the proportion of time that it spends sharing a feeding site in the next session



**FIGURE 1** Foraging association networks of study groups (COQ, VAC, PRI and ALG) in each experimental condition (S++, S+, C+, C- and S-). For each network: circles = adults, squares = juveniles, white = males, grey = females. Each individual (node) is identified by its rank position number. The links (edges) between individuals are dyadic associations. The size of nodes represents node strength and the thickness of links represents dyads' association strengths, relative to each dyad member, in which thicker ties show stronger associations. We created graphs using R package IGRAPH (Csárdi & Nepusz, 2006)

three of the four feeding platforms. The amount of food provided at the feeding station could be high (++) , medium (+) or low (-; Table 2). We calculated the amount of food offered to each study group based on its mean daily consumption during a 1-week feeding trial ran prior to the beginning of the experiments. We adjusted proportionately the amount of food whenever the size or composition of a group changed. Each experimental condition lasted 10 successive days with a pause of 11 days between conditions. Based on the marmosets' daily activity (De la Fuente et al., 2014), we conducted three experimental sessions per day, at 6:00 a.m., 10:30 a.m. and 3:00 p.m., resulting in a maximum of 30 sessions per condition (three sessions per day  $\times$  10 days). Each session began when the marmosets arrived at a distance of 5 m from the feeding station and lasted until the group moved away the same distance and no individual returned to it in the next 10 min. Sessions lasted from ~5 to ~30 min (mean  $\sim 12 \pm SD \sim 7$  min). Food distribution and productivity remained constant throughout each condition. We designed the experiments to simulate conditions of food availability similar to those encountered in the wild and to observe how marmosets interact and associate when foraging under these conditions.

## 2.4 | Data collection

We carried out the experiments with groups COQ and ALG from July to October 2015 and with groups PRI and VAC from April to July 2016. Four trained observers collected the behavioural data. In addition, we videotaped all sessions using two Canon Powershot SX50 HS (Canon Inc.) cameras placed 1.5 m from each feeding station. We simultaneously videoed and recorded the behaviours of all group members during the experiments using the 'all occurrences' sampling method (Altmann, 1974, see ethogram of the common marmoset in Schiel & Souto, 2017). During each session, we recorded all individual platform visits, individual time spent on a platform (in seconds), food consumption (i.e. the total number of 3-g banana pieces consumed by each group member), the identity of individuals sharing a platform (individuals on the same platform at the same time, see below), social interactions on a platform (e.g. aggression and avoidance events), the amount of time and the number of group members with which each individual shared a platform during a session.

## 2.5 | Social network measures

Social networks are composed of nodes (actors) and edges (connections between nodes). We constructed foraging association networks in which nodes represent group members and edges represent their foraging associations on a feeding platform. Foraging associations (number and strength, see below) on a feeding platform represent our measures of social tolerance at feeding sites, given that when individuals shared a platform they remained in close proximity to each other in the presence of a valuable resource (banana pieces) while displaying relatively low rates of aggression (number of high intensity agonistic events/number of shared platform visits, Table S3; Figure S6). We considered that two individuals shared a platform when they spent  $\geq 3$  s together on the platform. In 62% of shared platform visits lasting from 3 to 10 s, one or both individuals of a dyad obtained a food reward while being in close spatial proximity (i.e. up to 50 cm apart; see Figure S7). Due to small group size and the fact that we reliably identified all individuals throughout the experiment, we used individual-based measures (node degree and node strength) and a dyad-based measure (dyad association strength; Sueur et al., 2011) per session to examine social tolerance of common marmosets at feeding sites. By calculating these measures per session we can assess how patterns of association change in response to the experimental conditions and over time. We defined these measures as follows:

**Node degree:** the number of group members with which the focal individual was observed sharing one or several platforms during a session (number of associations). Node degree can vary from 0 (if

the individual did not share a platform with any other group member) to the group size minus 1 (as a marmoset can share a platform with all other group members, but itself). **Node strength:** the sum of all weights (proportion of time sharing a platform with other individuals, see below) of the focal individual's associations with other group member(s) during a session. Given that the total amount of time spent on a platform during a session (i.e. time alone + time together with group mates) varied among individuals, we calculated this measure as the proportion of time the focal individual shared a platform with any other group member during a session relative to the total amount of time the focal individual spent on a platform during that session. Node strength can range from 0, when the focal individual did not share a platform during a session, to 1, when it spent all the time with other individual(s) on a platform during a session. We used node degree and node strength as measures of individual levels of social tolerance (see Table 3). The highest their values, the highest is an individual's social tolerance.

**Dyad association strength:** the proportion of time that a dyad shared a platform relative to the total amount of time that each member of the dyad spent on a platform during a session. Given that each individual can spend different amounts of time on platforms during a session, we considered two values per dyad, relative to each individual's total time spent on the platforms. Dyad association strength can range from  $>0$  (since we only accounted for dyads that shared a platform, this value could not be zero) to 1, when the focal dyad spent their entire time during a session sharing platforms with each other. We used dyad association strength as a measure of dyad levels of social tolerance (see Table 3). The highest the value, the highest is a dyad's social tolerance.

**TABLE 2** Description of the experimental conditions with different food distribution (S: scattered, C: concentrated) and productivity (++: high, +: medium, -: low). \*We used condition S++ to simulate a situation in which food competition is not expected regarding its distribution and productivity

Experimental conditions	Description	Food amount in a platform
*S++	High food productivity (twice the average amount consumed by the group in the feeding trial) scattered in three of the four feeding platforms	Each platform had sufficient food to satiate two of three group members
S+	Medium food productivity (the average amount consumed by the group in the feeding trial) scattered in three of the four feeding platforms	Each platform had enough food to satiate one of three group members
C+	Medium food productivity concentrated in one of the four feeding platforms	The platform had sufficient food to satiate almost all group members
C-	Low food productivity (half the average amount consumed by the group in the feeding trial) concentrated in one of the four feeding platforms	The platform had enough food to satiate about one of two group members
S-	Low food productivity scattered in three of the four feeding platforms	Each platform did not have sufficient food to satiate a single group member

We also calculated the frequency of avoidance events and the frequency of agonistic events that occurred on a platform during a session. Avoidance behaviour is considered a strategy to prevent conflicts in which an individual adjusts its spatial position with respect to the potential aggressor/competitor to reduce the likelihood of an agonistic encounter and/or food stealing event (Aureli & de Waal, 2000). An avoidance event occurred when an individual left a feeding platform upon the arrival of another group member on the same platform and in the absence of any detectable agonistic behaviour. We considered as an avoidance event, whenever a marmoset spent  $\leq 2$  s on a platform with another group member. This was the amount of time that we assumed that it took to leave the platform after anticipating a potential conspecific's approach. Agonistic events (i.e. agonistic interactions) occurred when an individual directed an aggressive behaviour towards another individual on a feeding platform. Aggression could be of low (no physical contact) or high (physical contact or injury risk) intensity (see Section 2.2).

## 2.6 | Testing the randomness of associations

Data on associations are often captured via the 'Gambit of the Group', which assumes that all individuals within a group, observed in a given location and at a certain point in time, are associated (Farine, 2017). We conducted field experiments in which we stimulated group members to visit the platforms to get valuable food resources (banana pieces). We observed active tolerance at feeding platforms directly instead of passive associations or proximities, thereby not qualifying as the 'Gambit of the Group'. Therefore, we conducted pre-network permutations of the raw foraging association data to assess whether associations occurred randomly or not. We used the ANTS R package (Sosa et al., 2020) to perform multiple network analyses (i.e. a network per group per condition). Overall, 81% of the observed foraging associations among dyads did not occur randomly, as they were higher or lower than those expected under the permutation process (one side  $p \leq 0.05$ ; see Tables S4–S7). Some dyads preferred to associate with each other at feeding sites under different experimental conditions, while others did not. The observed network edges were nearly always preferred or avoided.

## 2.7 | Data analysis

Permutations in social network analyses may not control for non-independence and lead to strong rates of false positives and false negatives, making them inappropriate for testing hypotheses via regression analyses (Hart et al., 2021; Puga-Gonzalez et al., 2021; Weiss et al., 2021). Following these authors' recommendations we used MCMCglmm [Generalized Linear Mixed Models (GLMMs) with a Markov Chain Monte Carlo (MCMC) approach] to properly account for these confounds. Adopting this approach yields both correct  $p$ -values and effect size estimates, leading to more reliable

statistical inferences. We conducted all statistical analyses using the R software version 3.5.1 (R Core Team, 2018). Before constructing the models, we evaluated the multicollinearity between the predictor factors by calculating the variance inflation factor (VIF, R package CAR, Fox & Weisberg, 2011). Except for one case (see below), there was no correlation between any pair of predictors (all VIF < 2; Hair et al., 2010). We fitted all GLMM models using the R package LME4 (Bates et al., 2015).

### 2.7.1 | Model fitting

We adjusted GLMMs with Gaussian error distribution to fit our models, and used error distributions according to the response variable whenever data were not normally distributed. We used Poisson distribution for count data and Binomial distribution for proportional data (Crawley, 2007). To evaluate model's validity, we carried out GLMM diagnostics with respect to over-dispersion, the distribution of residuals (see residual distribution plots on Figure S8), and variance structure. Whenever necessary, we allowed heterogeneous variance among levels of nominal values (following Zuur et al., 2009).

We constructed two GLMMs to assess if ecological (food availability) and social (individual's age, sex and rank) factors influence individual levels of social tolerance (node degree and node strength; H1, see Table 1). The first model had node degree as the response variable, and the second had node strength as the response variable. Based on the distinct behaviour of the breeding female (De la Fuente et al., 2019), we included her as a separate class from other females in our analyses. By doing this, the sex and rank of individuals were collinear (VIF > 2, Hair et al., 2010), what may cause nonsignificant parameter estimates if they are included together in the models. Therefore, we used sex/rank class of individuals (breeding females—BF, females—F and males—M), age (adults—A and juveniles—J; we did not include data collected on subadults in our analyses because they were present during only two of the five experimental conditions in the ALG group, see Table S1), and experimental conditions as predictors for both H1 models. We included group identity and session as random effects. We did not include individual's ID as a random effect in the models because its high collinearity with the predictors age and sex/rank class (VIF > 10) would influence the assessment of its effect. We adjusted the node degree model with a Poisson error distribution and the node strength model with a Binomial error distribution.

We constructed a GLMM to investigate if common marmosets have dyadic foraging partner preferences under different ecological conditions (food availability) and social compositions (dyad's rank, age, sex composition; H2, see Table 1). The model had dyad association strength (our measure of dyad levels of social tolerance) as the response variable. The predictor variables were experimental condition, dyad rank distance (i.e. the difference between rank positions of two individuals: can range from 1 in dyads with adjacent rank positions to 6 in the dyad with the most distant rank

**TABLE 3** Final selected models after multi-model inferences, including each model's response variables, predictor variables, random effects, marginal and conditional  $R^2$ 

Hyp	Final models			$R^2$ GLMM	
	Response variables	Predictor variables	Random effects	Mar	Con
H1	Node degree	Age + Sex * Exp_con	Groups ID + Daily sessions	0.15	0.16
	Node strength	Age * Exp_con + Sex * Exp_con	Groups ID + Daily sessions	0.16	0.21
H2	Dyad association strength	Rank_dist * Exp_con + Age_comp * Exp_con + Sex_comp * Exp_con	Groups ID + Daily sessions	0.11	0.15
H3	Food consumption	Node_stren + Node_deg + Avoid_events	Individual ID + Exp_con	0.09	0.49
H4	(A) Node strength	Prev_node_stren + Prev_food_cons + Prev_avoid_ev + Prev_agr_ev	Individual ID + Exp_con	0.11	0.14
	(B) Dyad association strength	Prev_dyad_assoc_stren + Prev_avoid_ev + Prev_agr_ev	Dyad ID + Exp_con	0.16	0.36

Note: Hyp (H): hypotheses; Mar: marginal  $R^2$  (describes the proportion of variance explained by the fixed factors), Con: conditional  $R^2$  (describes the proportion of variance explained by both the fixed and random factors); Exp\_con: experimental condition; Rank\_dist: dyad rank distance; Age\_comp: dyad age composition; Sex\_comp: dyad sex composition; Node\_stren: node strength; Node\_deg: node degree; Avoid\_events: avoidance events; Prev\_node\_stren: Previous node strength; Prev\_food\_cons: Previous food consumption; Prev\_avoid\_ev: Previous avoidance events; Prev\_agr\_ev: Previous agonistic events; Prev\_dyad\_assoc\_stren: previous dyad association strength. ID: identity.

positions in the group with seven individuals), dyad sex composition (BF-M, BF-F, F-F, F-M and M-M), and dyad age composition (A-A and A-J; we did not include the J-J level in our analyses because there was more than one juvenile only in the ALG group during three experimental conditions). We included group identity and session as random effects, and adjusted the model using a Binomial error distribution.

We run a GLMM to test if individual levels of social tolerance (node degree and node strength), avoidance events performed and agonistic events received influenced food consumption (i.e. the number of 3-g banana pieces consumed by each group member; H3, see Table 1). We included node degree, node strength, the frequency of avoidance events performed and the frequency of agonistic events received as predictors. We used individual identity and experimental condition as random effects. We adjusted the model with a Gaussian error distribution.

We constructed two GLMMs to examine if the most recent foraging experiences (i.e. the experiences in the previous experimental session: foraging associations, avoidance and agonistic events, and food consumption) influenced subsequent levels of social tolerance at the level of individuals (node strength; H4A) and dyads (dyad association strength; H4B, see Table 1). In the first model (H4A), we used node strength in a session ( $n$ ) as the response variable, and node strength, frequency of avoidance events performed, frequency of agonistic events received and food amount consumed by an individual in the previous session ( $n - 1$ ) as predictors. We included individual identity and experimental condition as random effects. In the second model (H4B), we used dyad association strength in a session ( $n$ ) as the response variable, and dyad association strength, frequency of avoidance events and frequency of agonistic events among dyads in the previous session ( $n - 1$ ) as predictors. We included dyad identity and experimental condition as random effects. We adjusted both models using a Binomial error distribution.

## 2.7.2 | Model selection

We conducted multi-model inferences for each GLMM to compare and order models according to their Akaike information criterion after correction for small sample sizes (AICc) and normalized Akaike weights (AICw; Burnham & Anderson, 2004). We conducted model selection using the R package MuMIn (Bartoń, 2018). Model selection tests all possible models with the independent variables and ranks them according to their AIC. The best model has the lowest AIC, whose variables explain a greater variance than those in other models (including the null model). This method is better than testing a full model (where some variables decrease the explanation of the variance) or using a step-model selection, which does not allow testing all possible models (Burnham & Anderson, 2002). We considered models with a  $\Delta AIC < 2$  as candidate models (following Burnham & Anderson, 2002) and included all predictor variables present in these candidate models to construct our final models (see model inference in Tables S8–S13). We present the final selected models in Table 3.

We applied the MCMC approach to our final selected models using the R package MCMCGLMM (Bayesian method, Hadfield, 2010) to identify the predictors of the final models that significantly influenced the response variables. We ran MCMCglmm models for a minimum of 230,000 iterations after a burn-in of 30,000 (first 30,000 iterations omitted to avoid autocorrelation problems) and a thinning interval of 200 (one from every 200 iterations used in the Markov chain to estimate the posterior distribution of the parameters) to reduce autocorrelation by determining an effective sample of 1,000 for all estimated parameters. We fitted models with uninformative priors ( $V = 1$ ,  $nu = 0.002$ ), so that all information came from the data. We based these parameters by checking the stability of the models. We visually assessed all models for approximate convergence of the MCMC chain (chain stability), autocorrelation and posterior distribution (see plots on the Figures S9–S14). We set the significance



level at 0.05 and present the 95% credible intervals according to the Bayesian method that we used.

This research adhered to the Brazilian laws governing wild animal research (SISBio n° 46770-1), was approved by the Ethics Committee for Animal Use of the Federal Rural University of Pernambuco (CEUA n° 144/2014) and fulfilled the ethical requirements of the University of Illinois for Animal Research (IACUC n° 14263).

### 3 | RESULTS

On average, each group member participated in  $25 \pm 5$  sessions (mean  $\pm$  SD) out of a maximum of 30 sessions per experimental condition (Figure 1). At least two common marmosets shared feeding platforms in  $81 \pm 15\%$  of these sessions. Dyads shared platforms in 5,407 visits (we did not include in the analyses those sessions in which individuals participated, but there was no sharing of a platform). Individuals shared platforms with one to six group members [depending on the maximum number of individuals in each group; most frequently observed (mode): two individuals]. Time spent sharing a platform varied among individuals from 3 to 606 s (mean  $\pm$  SD:  $75 \pm 73$  s; with most visits lasting from 3 to 10 s).

We recorded 955 avoidance events (rate of 17 events per 100 shared platform visits) and 1,449 agonistic events (rate of 26 events per 100 shared platform visits) during shared visits. Of the cases of agonism, 65% were of low intensity (no physical contact) and 66% occurred during experimental conditions C+ and C-, when low and medium amounts of food were concentrated on a single platform (for details, see Table S3).

#### 3.1 | Ecological and social factors influence individual levels of social tolerance (H1)

Experimental condition (i.e. food availability) and individual age class influenced node degree, but individual sex/rank class did not (final model output in Table S14). The number of individuals with whom marmosets shared a platform during a session was greatest under conditions in which all food available was concentrated on a single platform, regardless of the amount of food (mode: C+: 4 individuals and C-: 3 individuals), and lowest under conditions in which food was distributed on three platforms (modes: S++, S+, and S-: 1 individual), not supporting H1a. In addition, juveniles shared a platform during a session with a greater number of group members than did adults (overall mode: juveniles: three individuals; adults: two individuals), supporting H1b.

Experimental condition, sex/rank class, and their interaction affected node strength, but age class did not (final model output in Table S15). Overall, the proportion of time that individuals shared a platform with others during a session was highest under both conditions in which food (low and medium amount) was concentrated on a single platform (mean  $\pm$  SD: C+:  $0.58 \pm 0.33$  and C-:  $0.59 \pm 0.33$ ), followed by the condition in which a high amount of food was

scattered across three platforms (mean  $\pm$  SD: S++:  $0.37 \pm 0.32$ ), and lowest when medium and low amounts of food were scattered (S+:  $0.27 \pm 0.26$ , and S-:  $0.16 \pm 0.15$ ), not supporting H1a again. As revealed by the interaction effect (Figure 2), node strength varied according to individual sex/rank class among experimental conditions (Table S15). Breeding females exhibited higher node strength than other females in S++, C+ and C-, and higher node strength than males in S++, not supporting H1c. The node strength of males was higher than that of females in C-.

#### 3.2 | Common marmosets have dyadic foraging partner preferences (H2)

Experimental condition, dyad's rank distance, sex composition, age composition and the interactions between experimental condition and both rank distance and sex composition influenced dyad association strength (final model output in Table S16). The proportion of time a dyad shared a feeding platform during a session was lowest when a low amount of food was scattered across three platforms (mean  $\pm$  SD: S-:  $0.12 \pm 0.11$ ), followed by the other food scattered experimental conditions (mean  $\pm$  SD: S++:  $22 \pm 0.20$ ; S+:  $18 \pm 0.17$ ), and it was highest for the concentrated food conditions (mean  $\pm$  SD: C+:  $0.31 \pm 0.23$ , C-:  $0.34 \pm 0.27$ ), not supporting H2a.

Overall, rank distance was negatively related to dyad association strength (i.e. dyads with closer rank positions spent more time together on a feeding platform than dyads composed of individuals of distant ranks; Table S16), as expected in H2b. However, the relationship was evident only when medium and high amounts of food were scattered across three platforms (S++ and S+). On the contrary, we found that dyads with more distant rank positions had higher association strengths during both concentrated conditions (C+ and C-) and the scattered low amount of food (S-), partially rejecting H2b (Figure 3a). The strength of adult-adult dyad association was consistently lower than that of adult-juvenile dyads during all experimental conditions (no interaction; Table S16), supporting H2c. Regarding sex composition, the overall dyad association strength was highest for breeding female-male dyads (Table S16), but association strengths varied between experimental conditions (Figure 3b), partially supporting H2d. Dyadic associations between a breeding female and a male were stronger than all other dyads when a low amount of food was concentrated on a single platform (C-) and when high amounts of food were scattered (S++). Dyads composed of a breeding female and a male, or two males had stronger associations than other dyads when a medium amount of food was concentrated on a single platform (C+).

#### 3.3 | Social tolerance influences individual food consumption (H3)

Node degree and amount of food consumed by individual marmosets were positively related. However, food consumption was negatively

related to node strength and positively related to the frequency of avoidance events performed (final model output in Table S17). The frequency of agonistic events received was not selected as a predictor for food consumption during model inference (see Table S11). Only H3a was supported.

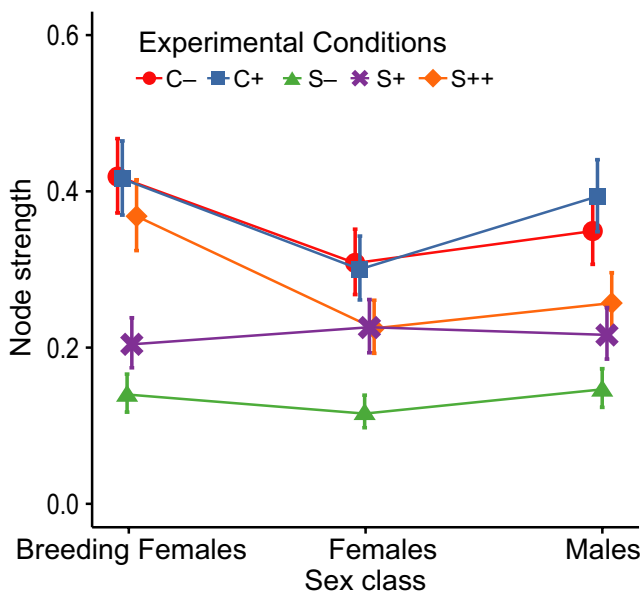
### 3.4 | Recent foraging experiences influence social tolerance at the (A) individual and (B) dyad levels (H4)

At the individual level, only node strength during the previous session positively affected node strength in the next session (final model output in Table S18). Avoidance events directed to another individual, agonistic events received and individual food consumption during the previous session did not affect node strength in the

next session. Similarly, only dyad association strength in the previous session positively affected dyad association strength in the next session (Table S18). The frequency of avoidance and agonistic events among dyads during previous sessions did not affect dyad association strength in subsequent session. Only H4a was supported for both individuals and dyads.

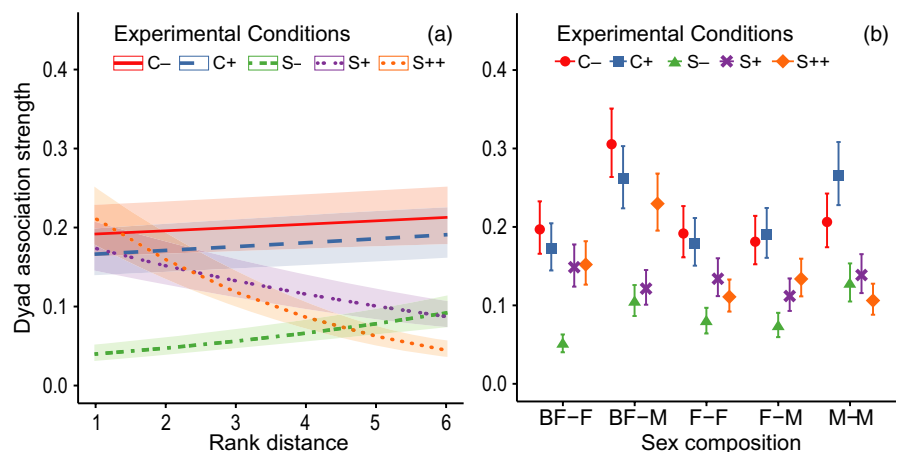
## 4 | DISCUSSION

We used social network analysis to investigate how social (rank, sex and age) and ecological factors (food distribution and productivity) influence within-group social tolerance at experimentally controlled feeding sites in four groups of free-living *Callithrix jacchus* in northeastern Brazil. Overall, both social and ecological factors influenced social tolerance during foraging and depending on the ecological context (food availability), group members associated or co-fed at feeding sites with different group members and in different intensities. Contrary to what was expected based on Sterck et al.'s (1997) socioecological theoretical framework, common marmoset associations were stronger (i.e. they associated with more group members and for a greater proportion of time) when food was concentrated at a single feeding site than when food was scattered, regardless of whether that feeding site had low or medium amounts of food rewards. Breeding females were characterized by stronger foraging associations with certain group members when food was concentrated, suggesting that despite their high social rank, they did not monopolize feeding sites. These findings contradict expectations of increased contest competition at defensible resources (Isbell, 1991; van Schaik & van Noordwijk, 1988; Sterck et al., 1997) as reported in some non-primate (e.g. spotted hyaena: Holekamp et al., 1996; ruddy turnstones: Vahl et al., 2005) and primate species (vervet monkeys: Whitten, 1983; capuchin monkeys: Janson, 1985; Japanese macaques: Hanya, 2009) characterized by linear dominance hierarchies and in which several females breed. It appears that the demands of a cooperative breeding system, in which several group members engage in infant caregiving, results in the formation of strong social alliances among group members. In some cooperatively breeding species, helpers have been shown to be close kin (Green et al., 2016).



**FIGURE 2** Model estimates for node strength (proportion of time individuals spent sharing a platform with other(s) during a session) and standard error for sex/rank class during each experimental condition (food distribution: scattered (S) or concentrated (C); productivity: high (++), medium (+) or low (-))

**FIGURE 3** Model estimates of dyad association strength (proportion of time a dyad spent sharing a platform during a session) and standard error for dyads with different rank distance during each experimental condition (a), and for dyads with different sex class composition (BF: breeding female, F: female, M: male) during each experimental condition (b)



In other cooperatively breeding species, helpers are unrelated to breeders, but may engage in infant caregiving to gain experience that increases future reproductive success (nulliparous females) or as a strategy (resident males) to increase mating opportunities with the breeding female (Bicca-Marques, 2003; Roberts, 2005; Sussman & Garber, 2011). Social tolerance in contexts such as foraging may represent a beneficial behavioural strategy to both dominant and subordinate group members to enhance group stability, promote cooperative bonds and food sharing, increase the care and protection of infants, and enhance future reproductive success. In contrast, not being tolerant or tolerated may have social and fitness costs resulting in from losing future reciprocal benefits.

Cooperative infant rearing is rare among mammals (e.g. meerkats: Kutsukake & Clutton-Brock, 2006a; African wild dogs: Courchamp & Macdonald, 2001), although common in a variety of bird species (Cockburn, 2006), in which subordinate non-breeding group members (helpers), of one sex or both sexes, assist breeding individuals in the care of offspring and are essential for their survival (Clutton-Brock, 2006). Breeding individuals profit by forming strong affiliative bonds and being tolerant of conspecifics whose efforts contribute to the group's reproductive success. In some species of cooperatively breeding birds and mammals, dominant individuals more frequently preen/groom subordinates than subordinates preen/groom them (jungle babblers: Gaston, 1977; Arabian babblers: Zahavi, 1990; dwarf mongoose: Rasa, 1987), including common marmosets (Lazaro-Perea et al., 2004). In feeding experiments, the dominant individual of a cooperatively breeding wild canid (grey wolves: *Canis lupus*) tolerated and allowed subordinate pack members to access the food, whereas in an independently breeding domestic species (dogs: *Canis lupus familiaris*) the most dominant individual exhibited more despotic behaviour and monopolized the food source (Dale et al., 2017). Captive groups of cooperative breeding primates were generally more tolerant and prosocial in an experimental feeding context than independently breeding species (Burkart et al., 2014).

Foraging dyads composed of the breeding female and a male, or two males, were characterized by the highest association strength under the most competitive conditions (concentrated food). Breeding female and male dyads also associated for longer times in the least competitive condition (scattered high amount of food). Callitrichine females produce dizygotic twin offspring during most births (Ferrari & Digby, 1996), each of which can be sired by a different male (Garber et al., 2016), and dizygotic twins might show chimerism (Sweeney et al., 2012). In the absence of genetic data to assess relatedness in the study groups, we could not assess the role of kinship and paternity. However, adult males are the main helpers in callitrichine groups and their numbers are positively correlated with infant survivorship (Garber, 1997; Koenig, 1995). The recorded patterns of sex-related foraging partner preferences across different food availability contexts are consistent with the tolerant social relationships among breeders and helpers in cooperative species (Aureli & Schaffner, 2006; Massen et al., 2020). These partner preferences might also reflect reproductive competition among females. For example, in a within-group reproductive conflict context, the

pregnant dominant female meerkat *Suricata suricatta* is usually tolerant of male helpers, but is aggressive to older or unrelated subordinate females who might potentially reproduce and/or kill her offspring (Kutsukake & Clutton-Brock, 2006b). Although groups of common marmosets often contain multiple females, in general only a single female breeds (Digby et al., 2011). The breeding females in our groups were more tolerant of male co-feeders than of female co-feeders.

In all experimental conditions juveniles associated with a greater number of group members during a feeding session (node degree) than did adults, and dyads composed of an adult and a juvenile presented stronger associations than those composed of two adults. Additionally, under the more competitive conditions of concentrated food, and when low amounts of food were scattered, dyads of more distantly ranked individuals associated for longer periods of time (in our groups breeding female-juvenile and male-juvenile dyads). Similarly, dyads of grey wolves with greater rank distances (young individuals occupying lower ranks) were more likely to peacefully share a food source than those composed of individuals with more similar ranks (Dale et al., 2017). These results may reflect the fact that juveniles are less efficient foragers than adults and are considered less effective feeding competitors (Fragaszy & Boinski, 1995). It is also likely that proximity with older group members during feeding activities (usually their parents; Weiss, 2006) facilitates social learning in young individuals by enabling them to closely observe more experienced, model foragers (Thornton & Clutton-Brock, 2011). In most species of birds and mammals, the development of foraging skills, such as locating feeding sites and food items (Clark, 2010; Midford et al., 2000), and handling/feeding techniques occur in early life via social learning (Boogert et al., 2008; Slagsvold & Wiebe, 2011). In cooperative breeders, multiple adult group members (breeding and non-breeding caretakers) are tolerant of immatures during foraging as they share or exchange food with them or tolerate scrounging (Clutton-Brock, 2006; Jaeggi & Gurven, 2013; Midford et al., 2000). Callitrichine breeding females (through gestation and lactation) and adult male helpers (through carrying and food providing) invest more time and energy in offspring caregiving than other group members (Bicca-Marques, 2003; Garber, 1997), which might explain the stronger associations and tolerance with juveniles in the more competitive situations of our experimental design.

In contrast, under less competitive conditions (scattered high and medium amounts of food) dyads composed of individuals of closer rank associated for longer periods. Closer ranks might represent a higher potential of competition as they are usually occupied by individuals of similar age/size that might have similar feeding needs (Archie et al., 2006; Dale et al., 2017). However, the low benefits of investing time and energy in monopolizing more productive or dispersed food sources select for higher tolerance (Sterck et al., 1997). These findings are compatible with an ability of adjusting foraging partner choices and regulating the intensity of associations based on the ecological context. Given that the number and strength of social bonds that an individual maintains with other group members (i.e. the structure of the social network) influence group stability,

coordination and cohesion, species that live in small groups have the opportunity for all group members to build strong social relationships (Sueur et al., 2011). For example, female chacma baboons that live in smaller groups have more stable relationships with their preferred partners than females living in larger groups (Silk et al., 2012). In meerkats, social networks based on foraging, grooming and dominance interactions became less dense as group size increased, suggesting that individuals were limited in their number of partners (Madden et al., 2009). The ability of callitrichines to establish and maintain a cohesive group with strong associations and prosocial relationships among all or most group members is hypothesized to increase opportunities for mutual social and resource-related benefits, such as cooperative behaviours and offspring survival (Garber, 1997).

Common marmosets consumed more food per capita when they associated with a greater number of group members (node degree), spent less time in association (node strength) and avoided co-feeders more frequently. That is, marmosets obtained greater access to food by jointly occupying a feeding platform and moving off it to a nearby tree for ingestion of the food reward alone. The strategy of eating 1 to 2 m away from others increased feeding success by avoiding food sharing with and/or food theft by infants and juveniles (Jaeggi & Gurven, 2013). In a similar experimental field study, all or most members of saddleback tamarin *Leontocebus weddelli* groups, in which adult females were socially equal or dominant to adult males, commonly jointly fed from the pulp of an entire banana that was too large to remove from the feeding platform (Bicca-Marques & Garber, 2005). In contrast, groups of emperor tamarins *Saguinus imperator*, in which an adult male was the most dominant individual, were less tolerant of conspecifics on feeding platforms under the same circumstances. Although the authors did not quantify the amount of food ingested by each tamarin, the differences between saddlebacks and emperors are compatible with both food availability and species' intrinsic social characteristics (e.g. dominance structure), and the identity and behaviour of conspecifics playing important roles in within-group social relationships, foraging strategies and resource acquisition, as predicted by theoretical models (Giraldeau & Caraco, 2000).

Finally, the proportion of time that common marmosets spent sharing a feeding site with a partner during a previous foraging session influenced the proportion of time that those individuals shared a site in their next session. It appears that the strength of past foraging associations can directly influence future levels of social tolerance at feeding sites and that individuals may be able to track their foraging relationships with other group members over time as reported for capuchin monkeys (Hattori et al., 2012). Such pattern is compatible with some form of social memory—or the ability of individuals to track and recall previous social interactions with group members resulting in stable foraging associations over time—that might be analogous to the less cognitively demanding concept of 'attitudinal reciprocity', in which individuals respond to a positive past attitude of their partner in a similar way (de Waal, 2000). Captive ravens can remember an experience

and prefer to exchange reciprocally with experimenters who have cooperated in the past than with those who did not (Müller et al., 2017). An alternative explanation is that stable relationships between preferred partners are maintained and reinforced at different times and through different prosocial activities (e.g. grooming, food sharing and cooperative behaviours; Cronin, 2012; Kutsukake & Clutton-Brock, 2010; Lalot et al., 2021). Given that our data are limited to three periods of the day (foraging sessions), and that we lack information on the interactions and behaviours that have occurred among group members between experimental sessions, we need to be careful in interpreting this result. Research on the relationship between tolerance at feeding sites and other forms of affiliative behaviour prior to and after foraging events can help us identify other 'currencies' that shape marmoset social networks, such as grooming, mating and infant caregiving in cooperative breeders.

In conclusion, using an experimental approach, we quantitatively evaluated foraging association patterns and dynamics in free-ranging common marmoset groups under different controlled conditions of food productivity and distribution. The foraging association networks of common marmosets were overall cohesive and mediated by the interaction of socioecological factors, corroborating that social tolerance in cooperatively breeding societies appears to be shaped by a balance between within-group competition over resources and within-group cooperative/prosocial behaviours needed to enhance individual survival and group fitness. The cooperative infant caregiving system requires that all or most individuals establish and maintain strong social relationships and engage in spatially and temporally coordinated behaviours in order to protect, transport and provision the young (Clutton-Brock, 2006). These relationships may have evolved through mutualistic benefits shared by all group members. Breeding individuals need helpers to successfully rear their offspring and enhance their reproductive success. Therefore, tolerating conspecifics at feeding sites may promote group cohesion and serve as an incentive for adults to remain in the group as caregivers. In turn, non-breeding individuals can benefit from the joint or coordinated activities of conspecifics, such as predator vigilance and territory defense, and by accumulating experience in infant care that will be useful if they become breeders (Garber et al., 2016; Hodge et al., 2008; Snowdon & Cronin, 2007).

Given the complexity and variety of animal societies, evaluating the patterns, quality, and dynamics of social relationships, under multiple contexts and in species with different social systems, can offer a comparative perspective on the diversity and evolution of social behaviour. Studies comparing social relationships and strategies among cooperatively breeding birds, primates and other mammals may shed light into taxonomic differences in the costs and benefits of competition and cooperation in the evolution of social group living.

#### ACKNOWLEDGEMENTS

We are grateful to Dr Geraldo Baracuhy for allowing us to conduct this study at the Baracuhy Biological Field Station. We also thank

Filipa Abreu, Júlia Vasconcelos, Yara Lima and Chrissie McKenney for their help in the field, and Christini Caselli for suggestions on the early version of this manuscript. P.A.G. wishes to thank Chrissie, Sara, Jenni, and Dax for their continued love and support. J.C.B.-M. thanks CNPq for research fellowships (PQ 303306/2013-0 and 304475/2018-1). This study was supported by grants from CAPES (PVE n° 88881.064998/2014-01), CNPq (APQ 403126/2016-9) and a PhD grant from CAPES awarded to M.F.D.I.F. C.S. is a junior member of IUF (Academic Institute of France).

## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHORS' CONTRIBUTIONS

P.A.G. and J.C.B.-M. conceived the idea; P.A.G., J.C.B.-M., N.S., A.S. and M.F.D.I.F. co-designed the field methods; M.F.D.I.F. collected field data; M.F.D.I.F. and C.S. performed data analyses; M.F.D.I.F. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.7pvmcvdtn> (De la Fuente et al., 2021).

## ORCID

María Fernanda De la Fuente  <https://orcid.org/0000-0002-4137-2404>

Cédric Sueur  <https://orcid.org/0000-0001-8206-2739>

Paul A. Garber  <https://orcid.org/0000-0003-0053-8356>

Júlio César Bicca-Marques  <https://orcid.org/0000-0002-5400-845X>

Antonio Souto  <https://orcid.org/0000-0003-1692-1958>

Nicola Schiel  <https://orcid.org/0000-0002-2454-0912>

## REFERENCES

- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49(3/4), 227–267. <https://doi.org/10.1163/156853974X00534>
- Archie, E. A., Morrison, T. A., Foley, C. A., Moss, C. J., & Alberts, S. C. (2006). Dominance rank relationships among wild female African elephants, *Loxodonta africana*. *Animal Behaviour*, 71, 117–127. <https://doi.org/10.1016/j.anbehav.2005.03.023>
- Aureli, F., & de Waal, F. B. M. (2000). *Natural conflict resolution*. University of California Press, pp. 409.
- Aureli, F., & Schaffner, C. (2006). Causes, consequences and mechanisms of reconciliation: The role of cooperation. In P. M. Kappeler & C. P. van Schaik (Eds.), *Cooperation in primates and humans* (pp. 121–136). Springer.
- Bartoń, K. (2018). *MuMIn: Multi-model inference*. R package version 1.40.4. Retrieved from <https://CRAN.R-project.org/package=MuumIn>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bicca-Marques, J. C. (2003). Sexual selection and the evolution of foraging behavior in male and female tamarins and marmosets. In C. B. Jones (Ed.), *Sexual selection and reproductive competition in primates: New perspectives and directions* (pp. 455–475). American Society of Primatologists.
- Bicca-Marques, J. C., & Garber, P. A. (2005). Use of social and ecological information in tamarin foraging decisions. *International Journal of Primatology*, 26(6), 1321–1344. <https://doi.org/10.1007/s10764-005-8855-9>
- Bonanni, R., Cafazzo, S., Fantini, C., Pontier, D., & Natoli, E. (2007). Feeding order in an urban feral domestic cat colony: Relationship to dominance rank, sex and age. *Animal Behaviour*, 74, 1369–1379. <https://doi.org/10.1016/j.anbehav.2007.02.029>
- Boogert, N. J., Reader, S. M., Hoppitt, W., & Laland, K. N. (2008). The origin and spread of innovations in starlings. *Animal Behaviour*, 75(4), 1509–1518. <https://doi.org/10.1016/j.anbehav.2007.09.033>
- Burkart, J. M., Allon, O., Amici, F., Fichtel, C., Finkenwirth, C., Heschl, A., Huber, J., Isler, K., Kosonen, Z. K., Martins, E., Meulman, E. J., Richiger, R., Rueth, K., Spillmann, B., Wiesendanger, S., & van Schaik, C. P. (2014). The evolutionary origin of human hyper-cooperation. *Nature Communications*, 5, 4747. <https://doi.org/10.1038/ncomms5747>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multi-model inference: A practical information-theoretic approach* (2nd ed.). Springer-Verlag.
- Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference understanding AIC and BIC in model selection. *Sociological Methods & Research*, 33(2), 261–304. <https://doi.org/10.1177/0049124104268644>
- Chaves, F. G., & Alves, M. A. (2010). Teoria do forrageamento ótimo: Premissas e críticas em estudos com aves. *Oecologia Australis*, 14(2), 369–380. <https://doi.org/10.4257/oeco.2010.1402.03>
- Clark, J. A. (2010). White-tailed ptarmigan food calls enhance chick diet choice: Learning nutritional wisdom? *Animal Behaviour*, 79(1), 25–30. <https://doi.org/10.1016/j.anbehav.2009.09.021>
- Clutton-Brock, T. H. (2006). Cooperative breeding in mammals. In P. M. Kappeler & C. P. van Schaik (Eds.), *Cooperation in primates and humans. Mechanisms and Evolution* (pp. 173–190). Springer.
- Cockburn, A. (2006). Prevalence of different models of paternal care in birds. *Proceedings of the Royal Society B: Biological Sciences*, 273(1592), 1375–1383. <https://doi.org/10.1098/rspb.2005.3458>
- Courchamp, F., & Macdonald, D. W. (2001). Crucial importance of pack size in the African wild dog *Lycaon pictus*. *Animal Conservation*, 4(2), 169–174. <https://doi.org/10.1017/S1367943001001196>
- Crawley, M. J. (2007). *The R book*. John Wiley & Sons LTD.
- Cronin, K. A. (2012). Prosocial behavior in animals: The influence of social relationships communication and rewards. *Animal Behaviour*, 84(5), 1085–1093. <https://doi.org/10.1016/j.anbehav.2012.08.009>
- Cronin, K. A., & Sánchez, A. (2012). Social dynamics and cooperation: The case of nonhuman primates and its implications for human behavior. *Advances in Complex Systems*, 15(1). <https://doi.org/10.1142/S021952591250066X>
- Csárdi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal, Complex Systems*, 1695. Retrieved from <http://igraph.org>
- Dale, R., Range, F., Stott, L., Kotrschal, K., & Marshall-Pescini, S. (2017). The influence of social relationship on food tolerance in wolves and dogs. *Behavioral Ecology and Sociobiology*, 71, 107. <https://doi.org/10.1007/s00265-017-2339-8>
- De la Fuente, M. F., Schiel, N., Bicca-Marques, J. C., Caselli, C. B., Souto, A., & Garber, P. A. (2019). Balancing contest competition, scramble competition, and social tolerance at feeding sites in wild common marmosets (*Callithrix jacchus*). *American Journal of Primatology*, 81(4), e22964. <https://doi.org/10.1002/ajp.22964>
- De la Fuente, M. F., Souto, A., Sampaio, M. B., & Schiel, N. (2014). Behavioral adjustments by a small neotropical primate (*Callithrix jacchus*) in a semiarid Caatinga environment. *The Scientific World Journal*, 1–8. <https://doi.org/10.1155/2014/326524>
- De la Fuente, M. F., Sueur, C., Garber, P. A., Bicca-Marques, J. C., Souto, A., & Schiel, N. (2021). Data from: Foraging networks and social tolerance in a cooperatively breeding primate (*Callithrix jacchus*). *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.7pvmcvdtn>

- de Vries, H., Stevens, J. M. G., & Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour*, 71(3), 585–592. <https://doi.org/10.1016/j.anbehav.2005.05.015>
- de Waal, F. B. M. (1991). Rank distance as a central feature of rhesus monkey social organization: A sociometric analysis. *Animal Behaviour*, 41(3), 383–395. [https://doi.org/10.1016/S0003-3472\(05\)80839-5](https://doi.org/10.1016/S0003-3472(05)80839-5)
- de Waal, F. B. M. (2000). Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behavior*, 60(2), 253–261. <https://doi.org/10.1006/anbe.2000.1471>
- Digby, L. J., Ferrari, S. F., & Saltzman, W. (2011). The role of competition in cooperatively breeding species. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.), *Primates in perspective* (pp. 91–107). Oxford University Press.
- Farine, D. R. (2017). A guide to null models for animal social network analysis. *Methods in Ecology and Evolution*, 8(10), 1309–1320. <https://doi.org/10.1111/2041-210X.12772>
- Ferrari, S. F. (2009). Social hierarchy and dispersal in free-ranging buffy-headed marmosets (*Callithrix flaviceps*). In S. M. Ford, L. M. Porter, & L. C. Davis (Eds.), *The smallest anthropoids: The marmoset/callimico radiation* (pp. 155–165). Springer.
- Ferrari, S. F., & Digby, L. J. (1996). Wild *Callithrix* groups: Stable extended families? *American Journal of Primatology*, 38(1), 19–27. [https://doi.org/10.1002/\(SICI\)1098-2345\(1996\)38:1<19::AID-AJP3>3.0.CO;2-W](https://doi.org/10.1002/(SICI)1098-2345(1996)38:1<19::AID-AJP3>3.0.CO;2-W)
- Fox, J., & Weisberg, S. (2011). *An R companion to applied regression* (2nd ed.). Sage Publications. Retrieved from <http://socserv.socsci.mcmaster.ca/~jfox/Books/Companion>
- Fragaszy, D. M., & Boinski, S. (1995). Patterns of individual diet choice and efficiency of foraging in wedge-capped capuchin monkeys (*Cebus olivaceus*). *Journal of Comparative Psychology*, 109(4), 339–348. <https://doi.org/10.1037/0735-7036.109.4.339>
- Garber, P. A. (1997). One for all and breeding for one: Cooperation and competition as a tamarin reproductive strategy. *Evolutionary Anthropology*, 5(6), 187–199. [https://doi.org/10.1002/\(SICI\)1520-6505\(1997\)5:6<187::AID-EVAN1>3.0.CO;2-A](https://doi.org/10.1002/(SICI)1520-6505(1997)5:6<187::AID-EVAN1>3.0.CO;2-A)
- Garber, P. A., Caselli, C. B., McKenney, A. C., Abreu, F., De la Fuente, M. F., Araújo, A., Arruda, M. F., Souto, A., Schiel, N., & Bicca-Marques, J. C. (2019). Trait variation and trait stability in common marmosets (*Callithrix jacchus*) inhabiting ecologically distinct habitat in northeastern Brazil. *American Journal of Primatology*, 81(7), e23018. <https://doi.org/10.1002/ajp.23018>
- Garber, P. A., Porter, L. M., Spross, J., & Fiore, A. D. (2016). Tamarins: Insights into monogamous and non-monogamous single female social and breeding systems. *American Journal of Primatology*, 78(3), 298–314. <https://doi.org/10.1002/ajp.22370>
- Gaston, A. J. (1977). Social behaviour within groups of jungle babblers (*Turdoides striatus*). *Animal Behaviour*, 25(4), 828–848. [https://doi.org/10.1016/0003-3472\(77\)90036-7](https://doi.org/10.1016/0003-3472(77)90036-7)
- Giraldeau, L. A., & Caraco, T. (2000). *Social foraging theory*. Princeton University Press.
- Giraldeau, L. A., & Dubois, F. (2008). Social foraging and the study of exploitative behavior. *Advances in the Study of Behavior*, 38, 59–104.
- Green, J. P., Freckleton, R. P., & Hatchwell, B. J. (2016). Variation in helper effort among cooperatively breeding bird species is consistent with Hamilton's rule. *Nature Communications*, 7, 12663. <https://doi.org/10.1038/ncomms12663>
- Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, 33(2), 1–22. <https://doi.org/10.18637/jss.v033.i02>
- Hair, J., Black, W. C., Babin, B. J., & Anderson, R. E. (2010). *Multivariate data analysis* (7th ed.). Pearson Education International.
- Hanya, G. (2009). Effects of food type and number of feeding sites in a tree on aggression during feeding in wild *Macaca fuscata*. *International Journal of Primatology*, 30, 569–581. <https://doi.org/10.1007/s10764-009-9361-2>
- Hart, J. D. A., Weiss, M. N., Brent, L. J. N., & Franks, D. W. (2021). Common Permutation Methods in Animal Social Network Analyses so not Control for non-independence. *bioRxiv*, 1–21. <https://doi.org/10.1101/2021.06.04.447124>
- Hattori, Y., Leimgruber, K., Fujita, K., & de Waal, F. B. M. (2012). Food-related tolerance in capuchin monkeys (*Cebus apella*) varies with knowledge of the partner's previous food-consumption. *Behaviour*, 149, 171–185. <https://doi.org/10.1163/156853912X634124>
- Heitor, F., Oom, M. M., & Vicente, L. (2006). Social relationships in a herd of Sorria horses. Part II. Factors affecting affiliative relationships and sexual behaviours. *Behavioral Processes*, 73(3), 231–239. <https://doi.org/10.1016/j.beproc.2006.05.005>
- Hodge, S. J., Manica, A., Flower, T. P., & Clutton-Brock, T. H. (2008). Determinants of reproductive success in dominant female meerkats. *Journal of Animal Ecology*, 77, 92–102. <https://doi.org/10.1111/j.1365-2656.2007.01318.x>
- Holekamp, K. E., Smale, L., & Szykman, M. (1996). Rank and reproduction in the female spotted hyaena. *Journal of Reproduction and Fertility*, 108(2), 229–237. <https://doi.org/10.1530/jrf.0.1080229>
- Holzhaider, J. C., Hunt, G. R., & Gray, R. D. (2010). Social learning in New Caledonian crows. *Learning & Behavior*, 38(3), 206–219. <https://doi.org/10.3758/LB.38.3.206>
- Ishell, L. A. (1991). Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, 2(2), 143–155. <https://doi.org/10.1093/beheco/2.2.143>
- Jaeggi, A. V., & Gurven, M. (2013). Natural cooperators: Food sharing in humans and other primates. *Evolutionary Anthropology*, 22(4), 186–195. <https://doi.org/10.1002/evan.21364>
- Janson, C. (1985). Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology*, 18(2), 125–138. <https://doi.org/10.1007/BF00299041>
- Keynan, O., Ridley, A. R., & Lotem, A. (2015). Social foraging strategies and acquisition of novel foraging skills in cooperatively breeding Arabian babblers. *Behavioral Ecology*, 26(1), 207–214. <https://doi.org/10.1093/beheco/aru181>
- King, A. J., Clark, F. E., & Cowlishaw, G. (2011). The dining etiquette of desert baboons: The roles of social bonds, kinship, and dominance in co-feeding networks. *American Journal of Primatology*, 73(8), 768–774. <https://doi.org/10.1002/ajp.20918>
- Koenig, A. (1995). Group size, composition, and reproductive success in wild common marmosets (*Callithrix jacchus*). *American Journal of Primatology*, 35(4), 311–317. <https://doi.org/10.1002/ajp.1350350407>
- Kutsukake, N., & Clutton-Brock, T. H. (2006a). Social functions of allogrooming in cooperatively breeding meerkats. *Animal Behaviour*, 72(5), 1059–1068. <https://doi.org/10.1016/j.anbehav.2006.02.016>
- Kutsukake, N., & Clutton-Brock, T. H. (2006b). Aggression and submission reflect reproductive conflict between females in cooperatively breeding meerkats. *Behavioral Ecology and Sociobiology*, 59, 541–548. <https://doi.org/10.1007/s00265-005-0079-7>
- Kutsukake, N., & Clutton-Brock, T. H. (2010). Grooming and the value of social relationships in cooperatively breeding meerkats. *Animal Behaviour*, 79(2), 271–279. <https://doi.org/10.1016/j.anbehav.2009.10.014>
- Lalot, M., Delfour, F., Mercera, B., & Bovet, D. (2021). Prosociality and reciprocity in bottlenose dolphins (*Tursiops truncatus*). *Animal Cognition*. <https://doi.org/10.1007/s10071-021-01499-z>
- Lazaro-Perea, C., Arruda, M. F., & Snowdon, C. T. (2004). Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. *Animal Behaviour*, 67(4), 627–636. <https://doi.org/10.1016/j.anbehav.2003.06.004>
- Lazaro-Perea, C., Castro, C. S. S., Harrison, R., Araujo, A., Arruda, M. F., & Snowdon, C. T. (2000). Behavioral and demographic changes

- following the loss of the breeding female in cooperatively breeding marmosets. *Behavioral Ecology and Sociobiology*, 48(2), 137–146. <https://doi.org/10.1007/s002650000215>
- Li, M. F., Arseneau-Robar, T. J. M., Smeltzer, E. A., & Teichroeb, J. A. (2021). Be early or be tolerated: Vervet monkey, *Chlorocebus pygerythrus*, foraging strategies in a dispersed resource. *Animal Behaviour*, 176, 1–15. <https://doi.org/10.1016/j.anbehav.2021.03.010>
- Madden, J. R., Drewe, J. A., Pearce, G. P., & Clutton-Brock, T. H. (2009). The social network structure of a wild meerkat population: 2. Intragroup Interactions. *Behavioral Ecology and Sociobiology*, 64(1), 81–95. <https://doi.org/10.1007/s00265-009-0820-8>
- Marshall, H. H., Carter, A. J., Ashford, A., Rowcliffe, J. M., & Cowlshaw, G. (2015). Social effects on foraging behavior and success depend on local environmental conditions. *Ecology and Evolution*, 5(2), 475–492. <https://doi.org/10.1002/ece3.1377>
- Massen, J. J. M., Haley, S. M., & Bugnyar, T. (2020). Azure-winged magpies' decisions to share food are contingent on the presence or absence of food for the recipient. *Scientific Reports*, 10, 16147. <https://doi.org/10.1038/s41598-020-73256-0>
- Michels, A. M. (1998). Sex differences in food acquisition and aggression in captive common marmosets (*Callithrix jacchus*). *Primates*, 39(4), 549–556. <https://doi.org/10.1007/bf02557576>
- Midford, P. E., Hailman, J. P., & Woolfenden, G. E. (2000). Social learning of a novel foraging patch in families of free-living Florida scrub-jays. *Animal Behaviour*, 59(6), 1199–1207. <https://doi.org/10.1006/anbe.1999.1419>
- Miller, R., Schiestl, M., Whiten, A., Schwab, C., & Bugnyar, T. (2014). Tolerance and social facilitation in the foraging behaviour of free-ranging crows (*Corvus corone corone*; *C. c. cornix*). *Ethology*, 120(12), 1248–1255. <https://doi.org/10.1111/eth.12298>
- Müller, J. J. A., Massen, J. J. M., Bugnyar, T., & Osvald, M. (2017). Ravens remember the nature of a single reciprocal interaction sequence over 2 days and even after a month. *Animal Behaviour*, 128, 69–78. <https://doi.org/10.1016/j.anbehav.2017.04.004>
- Parr, L. A., Matheson, M. D., Bernstein, I. S., & de Waal, F. B. M. (1997). Grooming down the hierarchy: Allogrooming in captive brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*, 54(2), 361–367. <https://doi.org/10.1006/anbe.1996.0419>
- Pasquaretta, C., Levé, M., Claidière, N., van de Waal, E., Whiten, A., MacIntosh, A. J. J., Pelé, M., Bergstrom, M. L., Borgeaud, C., Brosnan, S. F., Crofoot, M. C., Fedigan, L. M., Fichtel, C., Hopper, L. M., Mareno, M. C., Petit, O., Schnoell, A. V., di Sorrentino, E. P., Thierry, B., ... Sueur, C. (2014). Social networks in primates: Smart and tolerant species have more efficient networks. *Scientific Reports*, 4, 7600. <https://doi.org/10.1038/srep07600>
- Puga-Gonzalez, I., Sueur, C., & Sosa, S. (2021). Null models for animal social network analysis and data collected via focal sampling: Pre- or network permutation? *Methods in Ecology and Evolution*, 12, 22–32. <https://doi.org/10.1111/2041-210X.13400>
- Pyke, G. H., Pulliam, H. R., & Charnov, E. L. (1977). Optimal foraging: A selective review of theory and tests. *The Quarterly Review of Biology*, 52, 138–154. <https://doi.org/10.1086/409852>
- R Core Team. (2018). *R: A language and environment for statistical computing*. R foundation for statistical computing. Retrieved from <https://www.R-project.org/>
- Rasa, O. A. E. (1987). The dwarf mongoose: A study of behavior and social structure in relation to ecology in a small, social carnivore. *Advances in the Study of Behavior*, 17, 121–161. [https://doi.org/10.1016/S0065-3454\(08\)60178-3](https://doi.org/10.1016/S0065-3454(08)60178-3)
- Roberts, G. (2005). Cooperation through interdependence. *Animal Behaviour*, 70(4), 901–908. <https://doi.org/10.1016/j.anbehav.2005.02.006>
- Scheid, C., Schmidt, J., & Noë, R. (2008). Distinct patterns of food offering and co-feeding in rooks. *Animal Behaviour*, 76, 1701–1707. <https://doi.org/10.1016/j.anbehav.2008.07.023>
- Schiel, N., & Huber, L. (2006). Social influences on the development of foraging behavior in free-living common marmosets (*Callithrix jacchus*). *American Journal of Primatology*, 68(12), 1150–1160. <https://doi.org/10.1002/ajp.20284>
- Schiel, N., & Souto, A. (2017). The common marmoset: An overview of its natural history, ecology and behavior. *Developmental Neurobiology*, 77(3), 244–262. <https://doi.org/10.1002/dneu.22458>
- Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology*, 20(24), 2207–2210. <https://doi.org/10.1016/j.cub.2010.10.058>
- Silk, J. B., Alberts, S. C., Altmann, J., Cheney, D. L., & Seyfarth, R. M. (2012). Stability of partner choice among female baboons. *Animal Behaviour*, 83(6), 1511–1518. <https://doi.org/10.1016/j.anbehav.2012.03.028>
- Slagsvold, T., & Wiebe, K. L. (2011). Social learning in birds and its role in shaping a foraging niche. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 969–977. <https://doi.org/10.1098/rstb.2010.0343>
- Smith, J. E., Memenis, S. K., & Holekamp, K. E. (2007). Rank-related partner choice in the fission-fusion society of the spotted hyena (*Crocuta crocuta*). *Behavioral Ecology and Sociobiology*, 61(5), 753–765. <https://doi.org/10.1007/s00265-006-0305-y>
- Snowdon, C. T., & Cronin, K. A. (2007). Cooperative breeders do cooperate. *Behavioral Processes*, 76(2), 138–141. <https://doi.org/10.1016/j.beproc.2007.01.016>
- Sosa, S., Puga-Gonzalez, I., Hu, F., Pansanel, J., Xie, X., & Sueur, C. (2020). A multilevel statistical toolkit to study animal social networks: Animal Network Toolkit (ANT) R package. *Scientific Reports*, 10, 12507. <https://doi.org/10.1038/s41598-020-69265-8>
- Stanton, M. A., & Mann, J. (2012). Early social networks predict survival in wild bottlenose dolphins. *PLoS One*, 7(10), e47508. <https://doi.org/10.1371/journal.pone.0047508>
- Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, 41, 291–309. <https://doi.org/10.1007/s0026500050>
- Sueur, C., Deneubourg, J.-L., Petit, O., & Couzin, I. D. (2011). Group size, grooming and fission in primates: A modeling approach based on group structure. *Journal of Theoretical Biology*, 273(1), 156–166. <https://doi.org/10.1016/j.jtbi.2010.12.035>
- Sueur, C., Jacobs, A., Amblard, F., Petit, O., & King, A. (2011). How can social network analysis improve the study of primate behavior? *American Journal of Primatology*, 73(8), 703–719. <https://doi.org/10.1002/ajp.20915>
- Sueur, C., Romano, V., Sosa, S., & Puga-Gonzalez, I. (2018). Mechanisms of network evolution: A focus on socioecological factors, intermediary mechanisms, and selection pressures. *Primates*, 1–15. <https://doi.org/10.1007/s10329-018-0682-7>
- Sussman, R. W., & Garber, P. A. (2011). Cooperation, collective action, and competition in primate social interactions. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.), *Primates in perspective* (pp. 587–599). Oxford University Press.
- Sweeney, C. G., Curran, E., Westmoreland, S. V., Mansfield, K. G., & Vallender, E. J. (2012). Quantitative molecular assessment of chimera across tissues in marmosets and tamarins. *BMC Genomics*, 13, 98. <https://doi.org/10.1186/1471-2164-13-98>
- Thornton, A., & Clutton-Brock, T. H. (2011). Social learning and the development of individual and group behavior in mammal societies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 978–987. <https://doi.org/10.1098/rstb.2010.0312>
- Vahl, W. K., Lok, T., van der Meer, J., Piersma, T., & Weissing, F. J. (2005). Spatial clumping of food and social dominance affect interference competition among ruddy turnstones. *Behavioral Ecology*, 16(5), 834–844. <https://doi.org/10.1093/beheco/ari067>

- van Schaik, C. P., & van Noordwijk, M. A. (1988). Scramble and contest feeding competition among female long-tailed macaques (*Macaca fascicularis*). *Behaviour*, 105, 77–98.
- Weiss, J. (2006). Foraging habitats and associated preferential foraging specializations of bottlenose dolphin (*Tursiops truncatus*) mother-calf pairs. *Aquatic Mammals*, 32(1), 10–19. <https://doi.org/10.1578/AM.32.1.2006.10>
- Weiss, M. N., Franks, D. W., Brent, L. J. N., Ellis, S., Silk, M. J., & Croft, D. P. (2021). Common datastream permutations of animal social network data are not appropriate for hypothesis testing using regression models. *Methods in Ecology and Evolution*, 12, 255–265. <https://doi.org/10.1111/2041-210X.13508>
- Whitten, P. L. (1983). Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *American Journal of Primatology*, 5(2), 139–159. <https://doi.org/10.1002/ajp.1350050205>
- Yamamoto, M. E., Arruda, M. F., Alencar, A. I., Sousa, M. B. C., & Araújo, A. (2009). Mating systems and female-female competition in the common marmoset, *Callithrix jacchus*. In S. M. Ford, L. M. Porter, & L. C. Davis (Eds.), *The smallest anthropoids: The marmoset/callimico radiation* (pp. 119–133). Springer.
- Zahavi, A. (1990). Arabian babblers: The quest for social status in a cooperative breeder. In P. B. Stacey & W. D. Koenig (Eds.), *Cooperative*

*breeding in birds* (pp. 103–130). Cambridge University Press. <https://doi.org/10.1017/CBO9780511752452.005>

- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer. <https://doi.org/10.1007/978-0-387-87458-6>

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**How to cite this article:** De la Fuente, M. F., Sueur, C., Garber, P. A., Bicca-Marques, J. C., Souto, A., & Schiel, N. (2022). Foraging networks and social tolerance in a cooperatively breeding primate (*Callithrix jacchus*). *Journal of Animal Ecology*, 91, 138–153. <https://doi.org/10.1111/1365-2656.13609>