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RESEARCH ARTICLE

Balancing contest competition, scramble competition, and social tolerance at feeding sites in wild common marmosets (*Callithrix jacchus*)

María Fernanda De laFuente[1] | Nicola Schiel[1] | Júlio César Bicca-Marques[2] | Christini B. Caselli[1] | Antonio Souto[3] | Paul A. Garber[4]

[1]Departamento de Biologia, Universidade Federal Rural de Pernambuco, Recife, Brazil

[2]Laboratório de Primatologia, Escola de Ciências, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil

[3]Departamento de Zoologia, Universidade Federal de Pernambuco, Recife, Brazil

[4]Department of Anthropology, Program in Ecology, Evolution, and Conservation Biology, University of Illinois, Urbana, Illinois

Correspondence
María Fernanda De la Fuente, Departamento de Biologia, Universidade Federal Rural de Pernambuco, Rua Manuel de Medeiros, s/n, Dois Irmãos, Recife, PE 52171-900, Brazil.
Email: ferni211@yahoo.com.ar

Abstract

Models of primate sociality focus on the costs and benefits of group living and how factors such as rank, feeding competition, alliance formation, and cooperative behavior shape within-group social relationships. We conducted a series of controlled field experiments designed to investigate how resource distribution (one or three of four reward platforms) and amount of food on a reward platform affected foraging strategies and individual feeding success in four groups of wild common marmosets (*Callithrix jacchus*) living in the Caatinga of northeastern Brazil. At our field site, common marmoset groups are characterized by a single breeding female who can produce twin litters twice per year, strong social cohesion, and cooperative infant care provided principally by several adult male helpers. We found that except for the dominant breeding female, rank (based on aggression) was not a strong predictor of feeding success. Although the breeding female in each group occupied the highest rank position and obtained the greatest daily feeding success, all other group members, including adults and juveniles experienced relatively equal feeding success across most experimental conditions. This was accomplished using a balance of behavioral strategies related to contest competition, scramble competition (associated with a finder's advantage), and social tolerance (sharing the same feeding platform). Based on these results, the social structure of common marmosets is best described as "single female dominance," with the breeding female maximizing food intake needed to offset the energetic costs associated with reproductive twinning and the ability to produce two litters per year. Cooperative infant caregiving, in which the number of helpers is positively correlated with offspring survivorship, requires a set of behavioral strategies that serve to reduce contest competition and promote prosocial behaviors at feeding sites.

RESEARCH HIGHLIGHTS

- Common marmosets balance competition and tolerance to equalize feeding success.
- Except for the breeding female, rank did not predict food intake.

1 | INTRODUCTION

Socioecological models aim to identify the costs and benefits to individuals of living in groups and explain how ecological factors shape within-group and between-group social interactions (e.g., Crook, 1970; Sterck, Watts, & van Schaik, 1997; Terborgh & Janson, 1996). Two main types of models have been proposed. One set focuses on the costs to individuals of group living, such as inter- and intragroup feeding competition, mating competition, and infanticide (e.g., Isbell, 1991; Koenig, 2002; Sterck et al., 1997; van Shaik, 1989; Wrangham, 1980). An alternative model focuses on the benefits to individuals of collective action, cofeeding, and enhanced opportunities for resource and predator detection as a member of a social unit (Sussman & Garber, 2011). Because reduced access to food resources likely constrains reproductive success in females more so than in males (Fedigan, 1983), these models prioritize the impacts of resource distribution, abundance, and nutritional/energetic quality, and social interactions associated with rank, aggression, kinship, cooperation, and alliance formation on female reproductive success (Kappeler & van Schaik, 2006).

Two forms of feeding competition, scramble, and contest, have been proposed as primary mechanisms to explain differential access to resources (Sterck et al., 1997; van Shaik, 1989). Scramble competition is an indirect form of competition in which one individual (i.e., finder) encounters and exploits a food patch before the arrival of other group members, and thereby obtains a feeding advantage. Under conditions in which a single or a small number of group members can monopolize resources, lower-ranking individuals may benefit by arriving at the feeding site in advance of higher-ranking individuals (Barta & Giraldeau, 1998; Bicca-Marques & Garber, 2005). The benefits of arriving first at a patch depend on both predation risk and the size of the "finder's advantage" that is, the number of food items consumed by the finder before the arrival of others (Giraldeau & Caraco, 2000). The proportion of food items consumed in a patch (i.e., finder's share) is expected to be higher when food patches contain a small number of items that can be quickly depleted (e.g., solitary insects, small vertebrates, and trees producing a small amount of ripe fruits per day; Garber, Bicca-Marques, & Azevedo-Lopes, 2009; Giraldeau & Caraco, 2000). For example, in an experimental field study of wild Weddell's saddleback tamarins (*Leontocebus weddelli*) and emperor tamarins (*Saguinus imperator*), finders experienced greater feeding success than other group members when the amount of food on feeding platforms was small and/or monopolizable (Garber et al., 2009). Similarly, an experimental field study of wild black-horned capuchins (*Sapajus nigritus*, formerly *Cebus apella nigritus*) found that the number of food

items on a platform and the amount of time a finder spent alone at a feeding site affected the finder's share (Di Bitetti & Janson, 2001). Therefore, social strategies used by foragers in deciding where to forage and when to arrive first can contribute significantly to increase feeding success (Bicca-Marques & Garber, 2005; Garber et al., 2009; Giraldeau & Caraco, 2000).

In contrast, contest competition is a direct form of social interaction in which agonistic behaviors, typically directed from higher- to lower-ranking individuals result in a single or a small set of individuals maintaining priority access to food resources. In general, it is assumed that individuals of higher rank can more effectively monopolize spatially and temporally clumped food items, and will prioritize or defend resources that are of high nutritional/energetic value (Hanya, 2009; Vogel, 2005). In species characterized by a despotic or linear dominance hierarchy, rank is expected to be a strong predictor of overall feeding success (Barta & Giraldeau, 1998). Alternatively, rates of aggression at feeding sites are expected to be low in primate societies characterized by high levels of cooperation, tolerance at feeding sites, and food sharing, with all or most group members cofeeding, especially at large, productive, and clumped food patches, thereby minimizing the effects of rank on feeding success (Sussman & Garber, 2011; Watts & Mitani, 2002).

It is generally assumed that social rank is positively correlated with fitness benefits resulting in higher reproductive output and success (Majolo, Lehmann, de Bortoli Vizioli, & Schino, 2012). However, dominance hierarchies can be dynamic, include rank reversals, and an individual's position in the hierarchy can vary in response to changes in group membership. Moreover, dominance hierarchies may take a variety of forms, including linear (A > B > C > D), triangular (A > B, B > C, but C > A), pyramidal (A > [B = C = D = E]), or class-based ([A + B] > [C = D + E]; Preuschoft & van Schaik, 2000). In some species, competitive outcomes in dyadic contest are highly predictable and described as decided dominance relationships. In contrast, under conditions in which the predictability of winning a contest is highly variable, agonistic interactions are not expected to be unidirectional, resulting in undecided dominance relationships (Preuschoft & van Schaik, 2000). In primate species characterized by undecided dominance, access to resources (food and mates) is highly context dependent and therefore likely to be more equal among group members (Majolo et al., 2012; Preuschoft & van Schaik, 2000).

In the present study, we examine the effects of rank, social tolerance, and systematic changes in food distribution and productivity on individual feeding success in four groups of common marmosets (*Callithrix jacchus*) inhabiting a semiarid scrubland habitat. In the wild, common marmosets live in multimale multifemale groups that range in

size from 3 to 16 individuals (for a review, see Schiel & Souto, 2017). *C. jacchus* is part of a highly successful radiation of small-bodied New World monkeys, the Callitrichinae, characterized by several derived traits associated with high reproductive output and cooperative infant caregiving that distinguish them from other primate taxa. These traits include the production of dizygotic twin offspring and the absence of lactational anestrus such that a female can resume ovulating a few days after giving birth, successfully nurse her current offspring while gestating her next litter, and produce two litters per year (Tardif et al., 2003; but see Löttker, Huck, Heymann, & Heistermann, 2004; Savage et al., 1997, for evidence of ovarian inactivity after parturition in wild callitrichines); usually only one female breeds (but see Digby, 1995), a reproductive skew that has been explained either by the ability of a dominant female to suppress ovulation in subordinate females (Yamamoto, Arruda, Alencar, Sousa, & Araújo, 2009) or by a reproductive self-restraint in subordinate nonbreeding females (Saltzman, 2017; Saltzman, Digby, & Abbott, 2009); and the presence of helpers, principally adult males who carry, guard, and provision infants and young juveniles with food (Rothe, Darms, Koenig, Radespiel, & Juenemann, 1993). Given evidence in several marmoset and tamarin species that breeding females have priority access to food (Bicca-Marques, 2003; Tardif & Richter, 1981), and that the number of male helpers increases offspring survivorship (Garber, 1997; Koenig, 1995), group members may be expected to weigh the benefits of increased food intake on reproductive output against the costs of contest competition on within-group social cohesion and cooperative infant caregiving in their foraging decisions.

To understand relationships between social rank, feeding behavior, and feeding success, we presented wild common marmosets with a series of controlled field experiments. Food distribution and productivity were systematically manipulated to simulate different ecological conditions of food availability naturally encountered in the wild. We designed the field experiments to test the following hypotheses. Hypothesis 1 (H1), under conditions in which resources are concentrated and therefore potentially monopolizable by a dominant individual, lower-ranking marmosets will employ a scramble foraging strategy of arriving at a reward platform in advance of more dominant individuals (act as a finder). (H2A) Regardless of rank, the finder's share will be negatively related to the amount of food available on a feeding platform. However (H2B), under conditions in which food is concentrated, higher-ranking finders are expected to obtain a greater finder's share than lower-ranking individuals, whereas under conditions in which food is scattered, the finder's share is expected to be similar among individuals of different rank. (H3) Higher-ranking individuals will have greater overall daily feeding success (amount consumed) than lower-ranking individuals when the amount of food provided is insufficient to satiate all group members and/or can be monopolized by higher-ranking individuals. As common marmosets encounter and consume a diversity of food types in the wild (Abreu, De la Fuente, Schiel, & Souto, 2016), to test these hypotheses we presented them with two different food types (ripe fruit and insect) that represent major components of their natural diet.

2 | METHODS

2.1 | Study site

We conducted the study at the Baracuhy Biological Field Station (Fazenda Marimbondo, 7°31′42″S, 36°17′50″W), a 400-ha privately owned area characterized by a semiarid thorn-scrub Caatinga habitat (De la Fuente, Souto, Sampaio, & Schiel, 2014), located ca. 4 km from the municipality of Cabaceiras, state of Paraíba, Brazil. The climate—hot semiarid—is characterized by high temperatures, low precipitation, and the region is considered one of the driest in Brazil (yearly rainfall averaged 336.6 mm from 1926 to 2011; Medeiros, Brito, & Borges, 2012). Mean monthly maximum temperature during the study ranged from 25°C to 29°C in the rainy season months (February to July) and from 26°C to 30°C in dry season months (August to January). Mean monthly rainfall was 32.0 and 10.3 mm in the rainy and dry season, respectively (Instituto Nacional de Meteorologia, 2017).

2.2 | Study groups

We studied four habituated groups of wild *C. jacchus* ranging in size from four to seven individuals, including infants (total = 24 individuals), from July 2015 to November 2016. One group (PRI) contained multiple adult females (four), although only one female in each group gave birth during the study. All groups contained multiple adult males (from two to three) at the beginning of the study. Group composition changed due to births and emigrations (see Table S1 for the composition of groups). Several months before initiating our field experiments, group members were trapped using the Peruvian method (Encarnación, Moya, Soini, Tapia, & Aquino, 1990) and adults were marked with a uniquely colored beaded collar. Juveniles and infants were not fitted with collars. Instead, we shaved different segments of their tails (upper, middle, or lower) for field identification.

2.3 | Field experiments

We established an experimental feeding station composed of four visually identical wooden platforms (50 × 50 cm) in the home range of each study group. We distributed the platforms in a square arrangement with each platform 2.5 m apart from its neighboring platform and at a height of 1.1 m above the ground. We placed a fixed transparent plastic container (21.5 cm length × 13.0 cm width × 6.0 cm height) with two separate and identical compartments on each platform (Figure 1). Containers with accessible rewards had two openings (5 × 3 cm) such that more than one group member could simultaneously feed from the same platform by inserting its hands and extracting a food item. Containers with inaccessible rewards were identical except for a series of small holes rather than an opening. These holes were too small for the marmosets to insert their hands, but served to equalize olfactory information among all platforms.
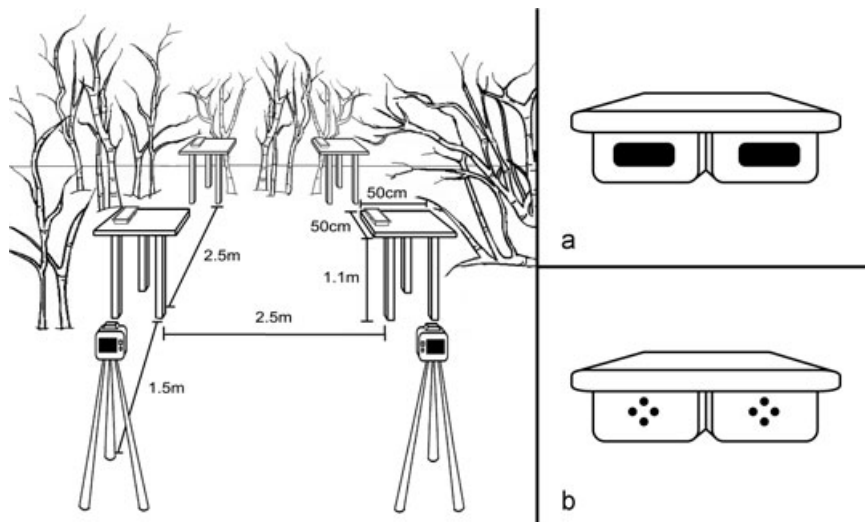
FIGURE 1 Representation of the feeding station with its four platforms distributed in a square arrangement. Two video cameras located 1.5 m from the platforms to record every session. Plastic containers placed at each platform could be (a) accessible, with openings large enough for marmosets to reach in and extract food, or (b) inaccessible, with small holes to equalize olfactory information among platforms

We simulated four conditions of food patch distribution and productivity by manipulating the number of reward platforms and the amount of food available on a reward platform. Accessible food was distributed on either one platform (concentrated food reward: C) or three platforms (scattered food reward: S). Rather than providing a standard amount of food based on group size and composition, we conducted a 1-week feeding trial (21 test sessions for each food type) before the beginning of the experiments to estimate the average amount of food consumed by each group per day. We used this estimate to determine values of medium (+), and low (−) food productivity for each group (Table 1). If group size changed during a condition, we adjusted the amount of available food accordingly (see Table S2 for the amount of food available). Before running the experimental conditions, we conducted a "precondition" trial (S++), in which food was scattered, and productivity was high (++: total amount in the feeding station was twice the mean amount of food consumed by the group during the 1-week feeding trial). We used the precondition trial to calculate Individual Daily Consumption (IDC), which represents the mean amount of food that each individual group member consumed per day (see below). We did this to control for individual differences in age, body size, or reproductive status on food intake.

In each condition, we presented banana slices or live mealworms to the marmosets as a food reward. We designed our experiments in a way that allowed us to reliably count each piece of banana or mealworm consumed by each marmoset. We standardized the weight of food items (half slice of banana = 3 g, ~5 cm giant mealworm [*Zophobas morio*, hereafter referred as mealworm] = 1 g) to increase the accuracy of our estimates of individual food intake. We kept food type, distribution, and productivity constant throughout a given condition. Therefore, marmosets had access to spatial information, quantity information (amount of food at each reward platform), distribution information (number of reward platforms) and food type after their initial visit to the feeding site. Marmosets could also use social information, such as the presence, absence, identity, and behavior of other group members in making foraging decisions.

2.4 | Data collection

From July 2015 to November 2016, four trained observers registered behavioral data on our marmoset study groups. We also recorded the behaviors of all group members visiting the platforms using two video cameras (Canon Powershot SX50 HS, Canon Inc., Tokyo, Japan) mounted on a tripod placed 1.5 m from the nearest platforms (Figure 1). After data collection, we transcribed the data onto an Excel spreadsheet and later M. F. De la Fuente reviewed the videos and verified the spreadsheet information. We conducted the experiments on each group at different times: COQ (July 2015 to February 2016), PRI (April to November 2016), VAC (April to July 2016), and CAS (August to November 2016). Each experimental condition lasted 10 consecutive days, with an interval of 11 days between conditions. We conducted sessions three times per day (6:00 a.m., 10:30 a.m., and 3:00 p.m.), totaling 30 sessions per condition. We recorded the behavioral data using the "all occurrences" sampling method (Martin & Bateson, 2007). Specifically, we recorded all feeding platform visits by each individual, the time and order of arrival, amount consumed, social interactions, the number of individuals jointly occupying the platform, and the time of departure from the platform.

This study adhered to the Brazilian laws governing wild animal research (SISBio n°46770-1). It was approved by the Ethics Committee for Animal Use of the Federal Rural University of Pernambuco (license n° 144/2014), and complied with the ethical requirements of the University of Illinois for Animal Research (IACUC n°14263). The research adhered to the American Society of Primatologist (ASP) Principles for the Ethical Treatment of Non-human Primates.

2.5 | Data analysis

We analyzed the data from the banana and mealworm experiments separately. Due to changes in groups' composition along the study period, we analyzed data from 16 individuals for the banana experiment, and 13 individuals for the mealworm experiment. We

TABLE 1 Design of field experiments simulating different conditions of food patch distribution and productivity using bananas and mealworms

Experimental conditions	Food distribution	Patch productivity	Amount of food at the feeding station	Amount of food in each platform
S+	Scattered	Medium	Mean amount consumed by the group during 1-week feeding trials	Enough to satiate approximately one-third of group members
C+	Concentrated	Medium		Enough to satiate almost all group members
C−	Concentrated	Low	Half of the mean amount consumed by the group during 1-week feeding trials	Enough to satiate approximately half of the group members
S−	Scattered	Low		Not enough to satiate one group member

did not analyze data on infants (0–4 months of age) because they were unable to reach and remove food from the containers.

2.5.1 | Rank

We determined the social rank of group members based on the frequency of agonistic interactions won during the experiments. We recorded all agonistic interactions that occurred between dyads, as low or high intensity. Low-intensity interactions comprised conflicts with no physical contact, such as visual and vocal threats (e.g., piloerection and agonistic vocalizations). High-intensity interactions included conflicts in which there was a risk of injury, such as unilateral attacks (hitting, pushing, biting, and grabbing), fights (both animals engage in mutual physical struggle), and chases. We considered that a marmoset was the winner of the agonistic encounter if it caused a submissive posture and/or vocalization from the recipient, and/or the recipient fled or withdrew from the interaction. We built dyadic agonistic interaction matrices for each group (see Table S3 for matrices) and estimated the Normalized David's Scores (NDS) for each group member. This score provides a measure of an individual's overall success considering the power of its opponent (de Vries, Stevens, & Vervaecke, 2006). From these data, we constructed a ranking order in which higher-ranking individuals won more agonistic interactions (see Table S1 for individuals' NDS and rank order). Given differences in the number of individuals per group, we pooled the lowest-ranked individual with the penultimate rank to perform statistical analyses whenever necessary. Therefore, we analyzed ranks 1, 2, 3, 4, and 5+ for the banana experiment, and 1, 2, 3, and 4+ for the mealworm experiment.

Based on NDS, we calculated hierarchy steepness for all groups, which denotes differences between individuals in winning dominance encounters (i.e., dominance success or the probability that a higher-ranked individual wins an agonistic interaction). Steepness measures can vary from 0 (a completely egalitarian hierarchy in which contest outcomes are unpredictable, the hierarchy is shallow) to 1 (a fully despotic hierarchy in which dominants always win, the hierarchy is steep; de Vries et al., 2006). We calculated NDS and steepness using the "steepness" R package (Leiva & de Vries, 2014).

2.5.2 | First arrival to reward platform

We considered the first individual to arrive at a reward platform as its finder to test H1. Given differences in group size and food distribution at the feeding station, we calculated the *corrected first arrival*; that is, the number of times that each group member arrived first at a platform in each condition minus the number of times that that individual was expected by chance to arrive first at a platform based on the number of reward platforms, group size, and the number of experimental sessions (30). If an individual left the group before completing the 30 sessions, we adjusted the group size and number of experimental sessions in which it participated.

To investigate differences in the use of a scramble foraging strategy (acting as finder) among ranks under different experimental

conditions, we constructed a generalized linear mixed model (GLMM) for each food type. We used the individuals' *corrected first arrival* as the response variable and the experimental conditions and the individuals' social rank as predictor variables. Group identity and sessions of the day were included as random effects. We conducted model comparisons through sequential analysis of variance using the *anova* function of "stats" package (R Core Team, 2017) starting with full models (fitting all predictor variables as fixed effects, including the interaction between them). We selected the simpler/reduced model whenever model comparisons indicated that model simplification would result in no significant loss of explanatory power ($P > 0.05$; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Whenever the best-fitted model include interactions among predictor variables, we conducted pairwise comparisons (Tukey's test), using the "lsmeans" R package (Lenth, 2016), to identify differences between ranks within each experimental condition. When the best-fitted model did not include interactions among predictor variables, we performed pairwise comparisons for each predictor variable independently.

2.5.3 | Finder's share

We calculated the finder's share as the proportion of food a finder consumed before the arrival of others, relative to the amount of food that was available on the feeding platform. Given that latency or the time that a finder spent alone at a reward platform is likely to influence the finder's share, before conducting analyses to assess H2, we examined this relationship using linear regression. We found a positive relationship for all conditions; that is, the longer (seconds) a finder spent alone on a reward platform, the more food it consumed (linear regressions, all R^2s > 0.6 for all conditions, all $P < 0.001$). However, given that latency was influenced by experimental condition (GLMMs, experimental condition as predictor variable, and group identity as random effect—banana: $F_{3,671} = 24.01$, $P < 0.0001$; meal-worm: $F_{3,555} = 49.02$, $P < 0.0001$), we did not include it as an extra predictor variable because its effect was already reflected by the experimental conditions in the models. Therefore, we tested H2 using GLMMs in which the finder's share was the response variable, experimental conditions and rank were included as predictor variables, and group identity and sessions were included as random effects. We performed model selection as described above.

2.5.4 | Feeding success

To control for the effects of age, sex, and reproductive condition on food intake, we first estimated IDC as the mean amount of food that a given individual consumed per day during the S++ "precondition" trial (resources present on the platforms were more than enough to satiate all group members; see Table S1 for IDC values). We assumed that the IDC represented the mean amount of food that each individual could reasonably consume during the three daily feeding sessions. We calculated the individual feeding success as the proportion of food consumed by a given individual during each day based on that individual's IDC. Feeding success can vary from 0 (individual did not

consume any food during the three daily sessions) to >1 (one was attained when an individual consumed its exact IDC, and greater than one when an individual consumed more than its IDC). To test H3, we evaluated marmosets' daily feeding success (sum of three daily sessions) rather than feeding success during each session to avoid that potential within-day between-session increase or decrease in feeding success bias the results. We used GLMMs with individual daily feeding success as the response variable, experimental conditions and rank as predictor variables, and group identity as a random effect. We performed model selection as described above.

2.5.5 | Evidence of compensatory feeding strategies

Given that marmosets of different ranks experienced relatively similar daily feeding success (see Section 3), to better understand the set of behavioral strategies used by marmosets to achieve this, we additionally examined whether individuals could compensate for lower food intake earlier in the day (6:00 a.m. and 10:30 a.m. sessions) by acting as finders (i.e., engaging in scramble competition) to increase feeding success later in the same day (3:00 p.m. session). First, we examined if finders indeed had higher feeding success during a session compared with nonfinders who fed during the session. We compared their performances by using GLMMs with the feeding success during a session as the response variable, experimental conditions, rank, and the status of acting as a finder or not as predictor variables, and group identity as a random effect. Next, to test for the occurrence of compensation, we used GLMMs in which the frequency of acting as a finder during the 3:00 p.m. session was the response variable, rank, and a new categorical variable named *compensatory status* were the predictor variables. The levels of this new variable indicated whether the animals that had obtained or not their expected 2/3 IDC by the second session of the day (yes or no) acted as finders in the last session of the day (yes), resulting in two levels: yes/yes and no/yes. We also included the experimental conditions as the random effect. We performed model selection as described above.

We carried out all statistical analyses using the R software version 3.3.3 (R Core Team, 2017). We adjusted all GLMM models with Gaussian error distribution using the "nlme" package (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2018). Before running models' comparisons, we evaluated the models with respect to the distribution of the residuals and the variance structure. Whenever necessary, we allowed heterogeneous variance among levels of nominal values (following Zuur et al., 2009). We set the statistical significance at the 5% level for all analyses.

3 | RESULTS

Each study group visited the feeding station in 27 ± 3 sessions per experimental condition (see Table S4 for details). Overall, we recorded 12,697 visits to a platform during the banana and mealworm experiments. During conditions in which food was concentrated on a single reward platform, two or more group

TABLE 2 Rates of agonism, number of platform visits, and number of agonistic interactions that occurred at the feeding station during each experimental condition

Experimental conditions	Number of platform visits	Total number of agonistic interactions	Overall rates of agonism (low + high agonistic interactions/visits)	Rates of high intensity agonistic interactions (high agonistic interactions/ visits)	
				All ranks	Without highest rank (1)[a]
Banana					
S+	1,904	187	0.098	0.050	0.035
C+	1,965	467	0.238	0.060	0.033
C−	1,623	428	0.264	0.125	0.055
S−	1,657	166	0.100	0.032	0.018
Total	7,149	1,248	0.174	0.066	0.035
Mealworm					
S+	1,562	19	0.012	0.006	0.003
C+	1,231	31	0.025	0.012	0.007
C−	1,337	172	0.128	0.047	0.019
S−	1,418	166	0.117	0.026	0.013
Total	5,548	388	0.069	0.023	0.010

[a]Breeding females, see Supporting Information for rank positions of group members.

members coforaged on 63 ± 5% of visits. During conditions in which food was scattered on three reward platforms, two or more group members coforaged on 34 ± 10% of visits.

3.1 | Rank

We recorded 1,636 dyadic agonistic interactions. Low-intensity interactions accounted for 63.5% of these events, whereas the remaining 36.5% were of high intensity. The rate of high-intensity agonism ranged from 3 to 12 events per 100 platform visits when bananas were present on reward platforms to <1–5 events per 100 platform visits during the mealworm experiments. The overall rate of agonism was highest when bananas and mealworms were concentrated on a single platform (Table 2). Based on the steepness index (probability that a higher-ranked individual wins an agonistic interaction), which ranged from 0.61 to 0.76 per group, higher-ranking individuals won most of the aggressive contests.

The highest-ranking individual in each group was always the lone breeding female, who engaged in the majority of high-intensity agonistic interactions (53%). Excluding breeding females, rates of high-intensity agonism ranged from 2 to 5 events and from <1 to 2 events per 100 platform visits during the banana and the mealworm experiments, respectively (Table 2). An adult male was the second highest-ranking individual in all groups, and when a second adult male was present (all groups except PRI during mealworm conditions, see Table S1), he was the third highest-ranking individual. Juveniles, irrespective of sex, occupied the lowest ranks in all groups.

3.2 | H1—First arrival to reward platforms

In the banana experiments, we found that rank (GLMM: $F_{4,161} = 8.69$, $P < 0.0001$), but not experimental conditions (GLMM: $F_{3,162} = 1.39$,

$P = 0.246$), influenced individual's likelihood to arrive first at a reward platform (*corrected first arrival*; see Tables S5–S9 for all model comparisons throughout the manuscript). However, contrary to H1 expectations, when food was concentrated on a single platform,
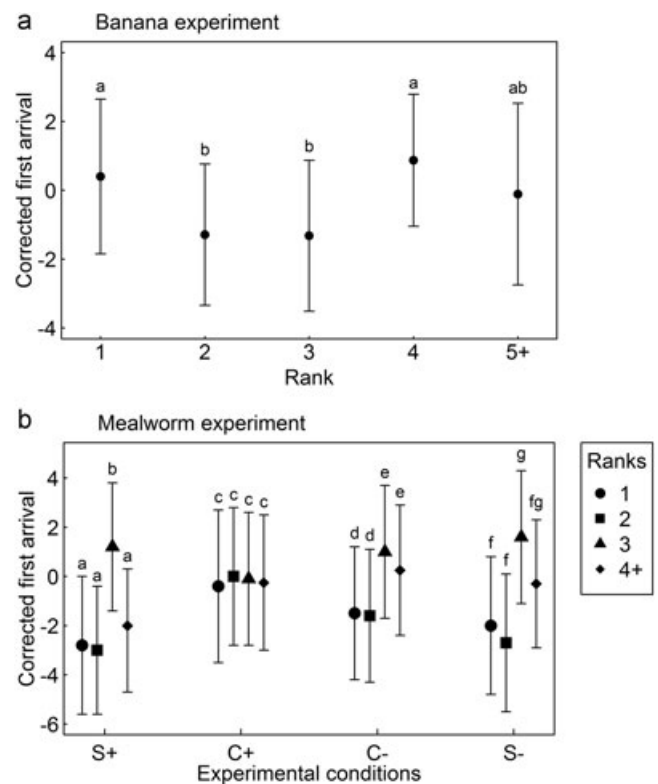

FIGURE 2 Mean ± standard deviation of rank's *corrected first arrival* during (a) banana experiment, and (b) mealworm experiment (interaction among predictor variables: experimental conditions and rank). Tukey's pairwise comparisons: Different letters indicate significant differences ($P < 0.05$) (a) among ranks or (b) within each experimental condition

lower-ranking individuals did not act as finders more often. Pairwise comparisons among ranks showed that the first- and fourth-ranking individuals arrived on a reward platform in advance of other group members more often than individuals who occupied the second and third ranks (all $P < 0.005$; Figure 2a). Moreover, there were no significant differences between the fifth + ranking individuals and all others in arriving first at a reward platform (all $P > 0.05$).

During the mealworm experiments, the interaction between rank and experimental conditions explained the patterns of first arrival at a reward platform (GLMM: $F_{9,132} = 2.17$, $P = 0.0278$). Pairwise comparisons among ranks within each condition revealed that marmosets showed considerable variation in the likelihood of arriving first (Figure 2b). For example, during condition C+, in which a single platform contained enough food to satiate almost all group members, first arrival to the reward platform was similar among individuals of all ranks (all $P > 0.05$). In contrast, during condition C−, when food contained on a single platform was sufficient to satiate approximately half of the group members, lower-ranking individuals arrived at a reward platform in advance of higher-ranking individuals (Figure 2b). Therefore, we found support for H1 when a limited amount of mealworms was concentrated on a single reward platform. However, we did not found support for H1 when a larger amount of mealworms was concentrated, as individuals of all ranks acted equally as finders.

3.3 | H2−Finder's share

During the banana experiments, only the experimental conditions had a significant influence on the finder's share (GLMM: $F_{3,580} = 114.93$, $P < 0.0001$). Overall, the finder's share was lower when resources were concentrated compared with when they were scattered, and it was negatively related to the amount of food available on a feeding platform. That is, marmosets obtained the largest finder's share (mean: $0.56 ± 0.3$) during condition S−, in which each platform contained the lowest amount of food (pairwise comparisons: all $P < 0.0001$). The second largest finder's share (mean: $0.31 ± 0.26$) was obtained during condition S+, when each platform contained enough food to satiate only one-third of group members (all $P < 0.0001$). Under conditions in which a platform contained larger amounts of food (i.e., C− and C+), the finder's share was lowest (means: C− = $0.13 ± 0.12$; C+ = $0.06 ± 0.05$), and not significantly different among them ($P = 0.253$; Figure 3a). Therefore, we found support for H2A. However, we failed to find support for H2B as rank was not a significant factor influencing the finder's share when bananas were offered as a food reward (GLMM: $F_{4,576} = 1.87$, $P = 0.114$).

In the mealworm experiment, the model containing the interaction between experimental conditions and rank best explained the finder's share (GLMM: $F_{9,420} = 2.27$, $P = 0.017$). Similar to the banana experiment, the finder's share was lowest when resources were concentrated on a single platform, and was negatively related to the amount of food available on a feeding platform, supporting H2A (Figure 3b). Pairwise comparisons indicate that on platforms with the

lowest amount of food (during S−), the finders' share was significantly greater for individuals of the three higher ranks (means: $0.44 ± 0.32$; $0.48 ± 0.36$; $0.34 ± 0.28$, respectively) than for individuals ranked fourth+ (mean: $0.22 ± 0.2$, $P < 0.05$). During condition S+, the finder's share was the second highest among conditions and it was not significantly different among marmosets of all ranks (all $P > 0.05$). In addition, during both conditions with the greatest amount of food on a single platform, the finder's share was the lowest and similar among individuals of all ranks (means: C+ = $0.05 ± 0.03$, C− = $0.08 ± 0.07$, all $P > 0.05$). Although during the mealworm experiments, rank had a significant effect on the finder's share, this was true for just one condition (S−) in which only the fourth + ranking individuals obtained a lower finder's share than the others. Therefore, we also did not find support for H2B when mealworms were offered as a food reward.

3.4 | H3−Daily feeding success

The interaction between experimental conditions and rank influenced individual daily feeding success in the banana experiment (GLMM: $F_{12,600} = 3.14$, $P < 0.0001$). Overall, marmosets tended to achieve greater daily feeding success during those experimental conditions in which there was a larger amount of food than during
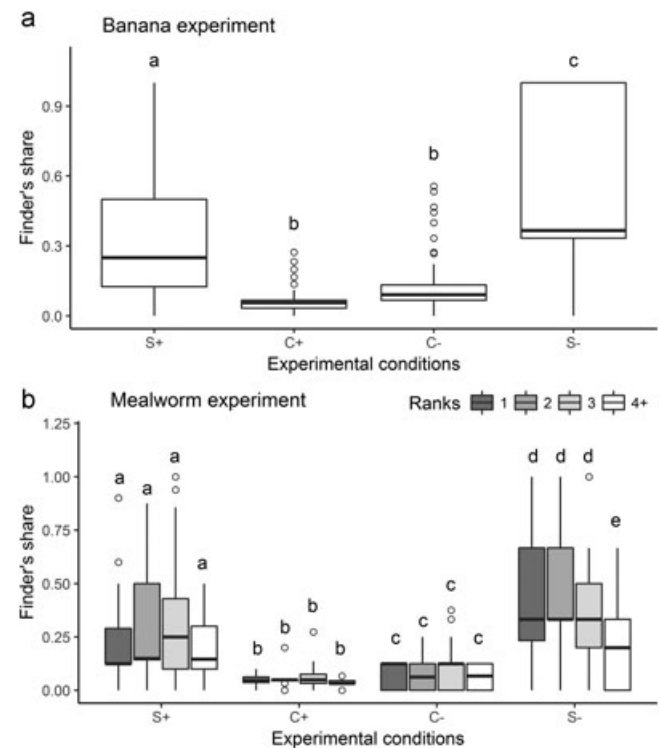

FIGURE 3 Finder's share of common marmosets during (a) banana experiment and (b) mealworm experiment (interaction between predictor variables: experimental conditions and rank). Tukey's pairwise comparisons: Different letters indicate significant differences ($P < 0.05$) (a) among experimental conditions or (b) within each experimental condition. Boxplots represent the median, first, and third quartiles with superior and inferior limits, and outliers when present
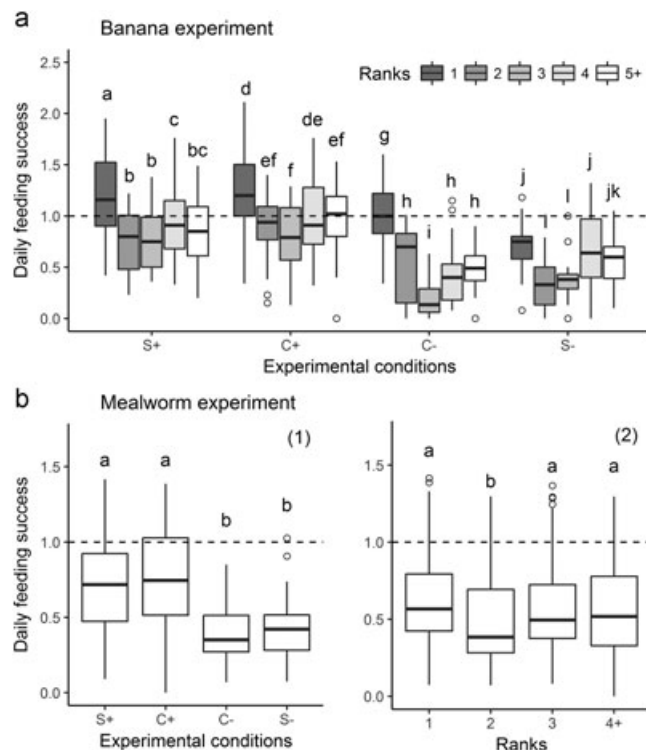
FIGURE 4 Daily feeding success of common marmosets during (a) banana experiment (interaction between predictor variables: experimental conditions and rank) and (b) mealworm experiment, no interaction among (1) experimental conditions and (2) ranks. Tukey's pairwise comparisons: Different letters indicate significant differences ($P < 0.05$) (a) within each experimental condition or (b) among (1) conditions and (2) ranks, independently. Dashed lines indicate the Individual Daily Consumption. Boxplots represent the median, first, and third quartiles, with superior and inferior limits, and outliers when present

those in which food was limited (Figure 4a). The highest-ranking individual (the breeding female) of each group exceeded or reached her expected IDC in three conditions (S+, C+, and C−), and pairwise comparisons revealed that during these conditions breeding females had higher daily feeding success than, virtually, all other group members (all $P < 0.04$, except for rank 4 during condition C+, $P = 0.628$). The only condition during which the breeding female did not reach her IDC was S−, when there was insufficient food to satiate a single forager on each of three platforms. During this condition, the daily feeding success of breeding females was similar to lower-ranking group members ($P > 0.05$; Figure 4a). Therefore, we partially supported H3 for the breeding female when we used bananas as rewards because they obtained higher feeding success when the food was monopolizable (C+ and C−). However, we did not find support for H3 for the other ranks, as marmosets ranked second and/or third did not have higher daily feeding success than individuals of lower rank during conditions C+, C−, and S−.

When mealworms were available on reward platforms, both experimental conditions (GLMM: $F_{3,510} = 77.57$, $P < 0.0001$) and rank (GLMM: $F_{3,510} = 15.59$, $P < 0.0001$) independently influenced individual daily feeding success, but not the interaction between these two

variables (GLMM: $F_{9,510} = 1.20$, $P = 0.288$). Pairwise comparisons revealed that feeding success was lower when there was less food at the feeding station (all $P < 0.0001$; Figure 4b[1]) and only the second-ranked individual (in all cases an adult male) experienced lower daily feeding success than individuals of all other ranks (all $P < 0.0001$; Figure 4b[2]). Moreover, the breeding female of each group did not have a higher feeding success than lower-ranking group members. Overall, we found no support for H3.

3.5 | Evidence of compensatory feeding strategies

We found during the banana experiment that, regardless of rank, the mean session feeding success of individuals was influenced by the interaction between experimental conditions and acting as finder (GLMM: $F_{3,103} = 2.79$, $P = 0.04$). During mealworm experiment, experimental conditions (GLMM: $F_{3,93} = 88.09$, $P < 0.0001$) and acting as finder (GLMM: $F_{1,93} = 36.60$, $P < 0.0001$) influenced the mean session feeding success independently. Overall, marmosets obtained a higher session feeding success when they acted as finders and during conditions with more food (pairwise comparisons: all $P < 0.05$). In addition, for experiments using both food types and independently of rank, individuals who obtained less than two-thirds of their IDC during the first two sessions of the day acted as finders more often during the last session of that day (GLMMs—banana: $F_{1,34} = 20.09$, $P < 0.0001$; mealworms: $F_{1,27} = 50.84$, $P < 0.0001$). The use of this type of compensatory foraging strategy enabled most group members to obtain a relatively similar daily feeding success at experimental platforms.

4 | DISCUSSION

In the present study, we conducted a series of controlled field experiments designed to investigate how social rank based differences in foraging strategies influenced individual feeding success in wild common marmosets, a primate species characterized by cooperative infant caregiving and high levels of female breeding competition (Garber, Porter, Spross, & Di Fiore, 2016). In our research design, we simulated changes in food availability naturally encountered by wild marmosets, and accurately recorded the total amount of food consumed by each individual during each platform visit. Given the cohesive nature of common marmoset groups and the fact that helpers are reported to be highly tolerant of the presence of conspecifics at feeding sites (Digby, 1995; Koenig, 1995; Schiel & Huber, 2006), we examined the degree to which contest competition, scramble competition, and/or social tolerance best explained feeding success.

We found that although rates of high-intensity aggression (i.e., contest competition) at reward platforms were generally low (from 0.006 to 0.125 depending on the experimental condition; Table 2), the single breeding female in each of our four study groups was responsible for most agonistic interactions and attained higher daily feeding success than all other group members. The breeding female

was dominant to adult males and nonbreeding females and maintained priority access to experimental feeding sites through a combination of contest competition, scramble competition, and feeding tolerance. In contrast, rank (based on aggression) was not a strong predictor of access to feeding sites or feeding success among all other group members. Across most experimental conditions, individuals ranked second through fifth+ were characterized by relatively equal daily feeding success. Therefore, we examined the behavioral strategies used by these group members to obtain access to feeding sites.

First, we tested whether subordinates acted as finders at monopolizable feeding sites to obtain an increased share of resources before being displaced by higher-ranking group members. However, in general, both higher- and lower-ranking marmosets acted as finders under conditions in which resources were scattered and under conditions in which resources were monopolizable. Next, we tested whether higher-ranking finders obtained a greater finder's share than lower-ranking finders when food was concentrated on a single reward platform. Regardless of the amount of food available on a feeding site, finders spending more time feeding alone are expected to have an increased share compared to finders who are quickly joined or displaced by other group member (Rita & Ranta, 1998). However, we found no evidence of a positive relationship between rank and the size of the finder's share across most experimental conditions. This is consistent with an experimental field study of wild capuchins (S. nigritus) that also reported no effect of dominance rank on the size of the finder's share (Di Bitetti & Janson, 2001).

Our results indicate that marmosets obtained greater overall feeding success in sessions when acting as finders. Similar results were found for spice finches (Lonchura punctulata) and zebra finches (Poephila guttata) in which birds consumed more seeds as finders than when arriving later and joining a conspecific at a feeding site (Giraldeau, Hogan, & Clinchy, 1990; Giraldeau, Soos, & Beauchamp, 1994). Thus, we examined whether marmosets who consumed less than their expected share of food during the first two daily feeding sessions acted as finders during the final session of the day as a compensatory strategy to increase feeding success and we confirmed our expectation. Finally, across all experimental conditions, we found that two or more marmosets shared and coforaged on the same feeding platform 48% of the time, demonstrating tolerance among group members. The results of our study highlight the complex and dynamic nature of primate social interactions at feeding sites and the ability of common marmosets to flexibly use a set of alternative behavioral strategies associated with contest competition, scramble competition, and social tolerance to balance the requirements of both individual feeding success while maintaining group stability and social cohesion.

Based on the predictions of the socioecological model, high levels of within-group contest competition, especially among adult females, are expected in primate species characterized by linear, nepotistic and despotic dominance hierarchies (Sterck et al., 1997). In the case of marmosets and tamarins, however, "dominance hierarchies based on aggression or access to resources are difficult to discern," except

for the breeding female "who maintains priority in access to food items" (Garber, 1997, p. 189; see also Bicca-Marques, 2003). Studies on the behavior and ecology of marmosets and tamarins indicate low levels of intragroup aggression and high levels of social cooperation associated with range and resource defense, predator vigilance, infant caregiving, and food sharing (Bicca-Marques, 2003; Bicca-Marques & Garber, 2005; Digby, 1995; Garber, 1997; Heymann, 1996). Moreover, there is evidence in several species that an increase in the number of helpers, principally adult males, is positively associated with increased infant survivorship (Garber, 1997; Koenig, 1995). Observations of unprovisioned common marmosets at our field site indicate that several individuals may jointly feed in the same food patch, often on the same food item or "take turns" feeding without any detectable signs of aggression or displacement. That is, one animal takes a part of a food item, moves away from the feeding site while others feed, then returns after it has consumed the food item (e.g., fruits, flowers, and/or cladodes from several cacti species such as *Pilosocereus pachycladus*, *Pilosocereus gounellei*, and *Cereus jamacaru*, as well as pods from *Prosopis juliflora*; Abreu et al., 2016). Similar evidence of cooperative food harvesting has been reported in other callitrichine species (Garber, 1997). Moreover, we have observed common marmosets on several occasions to simultaneously hunt relatively large vertebrate prey (lizards), with several individuals cofeeding on the carcass. Given the benefits that marmosets and tamarins receive as members of a highly cohesive social and reproductive unit, individuals appear to integrate a range of behavioral strategies to increase feeding success and reduce opportunities for within-group aggression at feeding sites (Garber, 1997; Sussman & Garber, 2011).

In the case of the breeding female, dominance and priority access to resources appear to be closely tied to female reproductive competition, the evolution of twinning and the ability to produce two litters per year. Studies by Digby (1995) and Yamamoto et al. (2009) indicate that in common marmoset groups containing two breeding females, the socially dominant female has higher reproductive success than the subordinate breeding female. A similar finding has been reported for golden lion tamarins (Dietz & Baker, 1993). Moreover, in golden lion tamarins, female body mass was the strongest predictor of reproductive success (number of infants born per litter; Bales, O'Herron, Baker, & Dietz, 2001). Relatedly, captive studies indicate that common marmoset females characterized by reduced body mass experience an increased likelihood of fetal loss as well as a reduction in the number of eggs produced per ovulatory cycle (Tardif & Jaquish, 1997). Therefore, priority access to feeding sites represents a critical component of female reproductive success. In the present study, we found that the breeding female in each group prevailed in decided agonistic contests, whereas among all other group members, agonistic interactions were less frequent and winning outcomes were not consistently unidirectional (see Table S3). Based on our results, the social structure of common marmosets may be best described as "single female dominance" and characterized by a pyramidal-like hierarchy (Preuschoft & van Schaik, 2000) in which the breeding female is dominant and other group members

maintain social relationships that result in relatively equal feeding benefits. A pyramidal structure in common marmosets appears to enhance the ability of the group's lone/dominant breeding female to maximize food intake required to successfully produce two sets of twin offspring per year (Bicca-Marques, 2003; Garber, 1997). While, in the case of other group members, the balance between nonaggressive forms of feeding competition (scramble) and social tolerance (e.g., cofeeding at the same platform) appears to limit aggression at feeding sites and maintain the high level of group cohesion required to facilitate cooperative infant caregiving by multiple helpers.

Among mammals, social structures characterized by female dominance are not common (Kappeler, 1993). However, forms of female dominance have been reported in several species of lemurs (in these species usually all females are dominant to all males, e.g., *Lemur catta*, Kappeler, 1990; *Eulemur coronatus*, Marolf, McElligott, & Müller, 2007; *Eulemur rubriventer*, Marolf et al., 2007; *Varecia variegata*, Overdorff, Erhart, & Mutschler, 2005; *Indri indri*, Pollock, 1979), and in some species of New World monkeys (e.g., *Saguinus mystax*, Garber, 1997; *Saimiri boliviensis*, Mitchell, Boinski, & van Shaik, 1991). In the case of Malagasy lemurs, female dominance occurs in both feeding and social contexts (Kappeler, 1990; Sauther, 1993) and has been explained in terms of the cost asymmetry hypothesis (Dunham, 2008). This hypothesis argues that in species characterized by body size monomorphism (although some lemur species exhibit male-biased canine dimorphism; Kappeler, 1996), males and females have similar fighting abilities but asymmetrical nutritional requirements associated with the cost of reproduction. Therefore, throughout their reproductive cycle (ovulation, gestation, and lactation), females are expected to aggressively control access to feeding sites also sought by similarly sized adult males (Dunham, 2008).

In this regard, the cost asymmetry hypothesis appears to offer an instructive conceptual framework to explain the single female dominance social structure reported in several species of callitrichines, including common marmosets. Many species of marmosets and tamarins are reported to be monomorphic or exhibit low levels of body size dimorphism (Araújo et al., 2000; Ford, 1994). However, given their potential for high reproductive output (four offspring per year), breeding females are likely to require greater amounts of food and/or priority access to high-quality feeding sites. For example, Garber and Leigh (1997) report that relative to maternal body mass, daily infant body mass gain during nursing in callitrichines was considerably higher than that found in other small-bodied New World primates such as night monkeys (*Aotus* sp.), titi monkeys (*Plecturocebus* sp., formerly, *Callicebus* sp.), and squirrel monkeys (*Saimiri* sp.). Therefore, the evolutionary demands for the potential to gestate and nurse two sets of twin infants per year and the requirements of cooperative infant caregiving (at 8–9 month of age juveniles may continue to steal food, such as vertebrates, from adult helpers; Ferrari, 1987) appear to have resulted in a callitrichine social structure characterized by single female dominance.

In conclusion, field experiments represent a powerful tool to address questions regarding social rank, feeding competition, foraging strategies, and feeding success in wild primates. The socioecological model offers a framework for understanding relationships between resource characteristics (e.g., productivity and distribution), social organization, dominance style, and the types of feeding competition a species exhibits. However, we found that common marmosets do not fit the model's predictions regarding intragroup feeding competition. Except for the sole breeding female, rank was not a strong predictor of contest competition and access to resources. The socioecological model may better describe species with extreme dominance styles (i.e., despotic societies) and species in which several females breed during the same period of the year. For other primate species, however, affiliation, cooperation, and mutually beneficial social relationships enhance the primary advantages of group living and serve to limit opportunities for contest competition at feeding sites (Sussman & Garber, 2011). Common marmosets are characterized by a social hierarchy that includes a single dominant female and high level of social affiliation among all group members. The strategies regulating within-group feeding behavior include a balance among contest competition, scramble competition associated with a finder's advantage, and tolerance of cofeeders. It appears that the evolution of cooperative infant caregiving in marmosets and tamarins is associated with a social system in which the potentially high costs of contest competition, leading to reduced social cohesion, are offset by the benefits of nonaggressive forms of competition and tolerance at feeding sites. In future studies, we plan to investigate the role of social networks in common marmoset foraging strategies and the degree of which the breeding female positively or negatively affects access to resources by other group members.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

ORCID

María Fernanda Fuente http://orcid.org/0000-0002-4137-2404
Nicola Schiel http://orcid.org/0000-0002-2454-0912
Júlio César Bicca-Marques http://orcid.org/0000-0002-5400-845X
Christini B. Caselli http://orcid.org/0000-0002-3058-7872
Antonio Souto http://orcid.org/0000-0003-1692-1958
Paul A. Garber http://orcid.org/0000-0003-0053-8356

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