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**ESTRATÉGIAS DE FORRAGEIO E REDE SOCIAL EM PRIMATAS DE VIDA  
LIVRE: UMA ABORDAGEM EXPERIMENTAL**

Recife

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Tese apresentada ao Programa de Pós-Graduação em Etnobiologia e Conservação da Natureza da Universidade Federal Rural de Pernambuco como parte dos requisitos para obtenção do título de Doutora em Etnobiologia e Conservação da Natureza.

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A meus pais Júlio e Mayté,  
a minhas irmãs Mary e Titi,  
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## RESUMO

Primatas, incluindo o ser humano, possuem um grande tamanho de cérebro e habilidades cognitivas complexas que os possibilitam de armazenar, recuperar e integrar informações para resolver problemas. Duas hipóteses tentam explicar a evolução cerebral em primatas, a hipótese ecológica e a hipótese social. No entanto, esta pode ser uma falsa diferenciação, uma vez que ao viver em grupos estáveis e habitar ambientes dinâmicos, os primatas devem ser capazes de utilizar tanto informações ecológicas, como a disponibilidade de recursos no tempo e espaço, quanto informações sociais provenientes da identidade, comportamento e relações entre os membros do grupo, para tomar decisões. Neste contexto, a vida social pode oferecer uma série de vantagens e desvantagens para os animais que vivem em grupo. Em se tratando da procura e obtenção de alimento, viver em grupo pode apresentar custos associados ao aumento da competição pelos recursos, assim como benefícios relacionados a uma melhor localização, acesso e defesa destes recursos. Assim, nesta pesquisa, utilizamos o sagui comum (*Callithrix jacchus*), uma espécie de primata coesa e cooperativa, como modelo para investigar como diferentes contextos ecológicos de disponibilidade de alimento e fatores sociais como a posição hierárquica, idade e sexo, afetam as estratégias de forrageio, o sucesso alimentar e as redes sociais entre os membros do grupo durante o forrageio social. Para tanto, realizamos uma série de experimentos de campo nos quais a distribuição (concentrada ou dispersa), produtividade (alta, média ou baixa quantidade) e o tipo de alimento (fruta ou inseto) foram manipulados para simular diversas condições alimentares encontradas na natureza. Ao investigar o uso de estratégias e o sucesso alimentar dos indivíduos nas diferentes condições experimentais encontramos que, exceto quando se tratava da fêmea reprodutora, a posição hierárquica e as interações agressivas (competição direta) não foram fortes preditores do consumo alimentar em saguis. Em cada grupo, a fêmea reprodutora foi a mais dominante e obteve o maior sucesso alimentar. No entanto, os outros membros do grupo, incluindo adultos e juvenis, apresentaram sucesso relativamente similar entre eles. Nossos resultados apontam que isto foi alcançado através de um equilíbrio no uso de estratégias relacionadas com a competição direta (principalmente por parte da fêmea reprodutora), competição indireta (formas não agressivas de competição relacionadas com a vantagem do descobridor) e tolerância nos sítios de alimentação. Para examinar a rede social dos saguis durante o forrageio avaliamos as associações que ocorriam nos sítios de alimentação entre os membros do grupo (número de indivíduos e tempo compartilhando um sítio alimentar) e assim investigar mais a fundo a tolerância social desta espécie nas diferentes condições experimentais. De acordo com nossos resultados, associações mais fortes foram encontradas quando o alimento se encontrava concentrado. Juvenis compartilharam plataformas com um maior número de indivíduos e por mais tempo do que adultos. Observamos maior força nas associações entre díades (preferência de parceiros) compostas por indivíduos de posições hierárquicas próximas, por sexos diferentes (fêmea-macho) e por idades diferentes (adulto-juvenil). No entanto, estas associações de forrageio entre díades variaram de acordo com as distintas condições ecológicas, sendo mais fortes quando o alimento se encontrava concentrado em um único sítio de alimentação, independentemente da quantidade de alimento. Assim, nós evidenciamos que o sagui comum é

capaz de utilizar e integrar tanto informações ecológicas como informações sociais para tomar decisões durante o forrageio social, ajustando seus comportamentos e associações dentro do grupo para obter acesso aos recursos, maximizar seu sucesso alimentar e manter a coesão grupal tão importante para a espécie. Em conclusão, esta tese contribuiu para demonstrar que, considerando as características sociais da espécie estudada (cooperação e estrutura social piramidal), a mesma não se ajusta ao modelo socioecológico clássico com relação à competição alimentar intragrupo. Além disso, mostrou-se que dentro de um grupo social os indivíduos desta espécie formam relações afiliativas com todos os outros membros do grupo ao se associarem durante o forrageio, resultando em grupos coesos e tolerantes durante uma atividade potencialmente competitiva. Salientamos assim, a necessidade de considerar e incorporar em futuros estudos e modelos tanto os custos como os benefícios que a vida social traz tanto a nível individual como grupal. Finalmente, destacamos a relevância de utilizar experimentos em campo para investigar sistematicamente questões socioecológicas em grupos primatas habitando seu ambiente natural.

**Palavras-chave:** comportamento animal, forrageio social, competição, tolerância social, sagui comum, *Callithrix jacchus*.

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### **ABSTRACT**

Primates, including humans, have a large brain size and complex cognitive abilities that enable them to store, recover, and integrate information to overcome challenges. Two hypotheses attempt to explain the cerebral evolution in primates, the ecological hypothesis and the social hypothesis. However, this may be a false distinction, since by living in stable groups and inhabiting dynamic environments, primates must be able to use both ecological information, such as the availability of resources in time and space, and social information such as the identity, behavior, and social relationships among group members to make decisions. In this context, social life can offer a number of advantages and disadvantages for animals living in groups. When it comes to searching and obtaining food, living in a group may incur costs associated with an increased competition for resources, as well as benefits related to an enhanced localization, access, and defense of these resources. Therefore, in this research, we used the common marmoset (*Callithrix jacchus*), a cohesive and cooperative primate species, as a model to investigate how different ecological contexts of food availability, and social factors such as rank, age and sex, affect individual foraging strategies, feeding success, and social networks among group members during social foraging. To do so, we conducted a series of field experiments in which the distribution (concentrated or scattered), productivity (high, medium or low quantity), and type of resource (fruit or insect) were manipulated to simulate different food conditions naturally found in the wild. By investigating the use of foraging strategies and the feeding success of individuals under different experimental conditions we found that except for the breeding female, rank and aggressions (contest competition) were not strong predictors of feeding success on marmosets. In each study group, the breeding female was the highest ranked individual and obtained the higher feeding success. However, the other group members, including adults and juveniles, obtained relatively similar feeding success among them. Our results indicate that this was achieved through a balance in the use of strategies related with contest competition (mainly by the breeding female), scramble competition (non-aggressive forms of competition associated with a finder's advantage), and tolerance on feeding sites. To examine the social network of marmosets during foraging, we assess the foraging associations between group members (number of individuals and time spent sharing a feeding site) and further investigate marmosets' levels of social tolerance under different experimental conditions. We found stronger associations when food was concentrated on a single feeding site. Juveniles shared platforms with more individuals and for longer time than adults did. We found stronger associations between dyads composed by individuals of closer rank, of different sexes (female-male), and of different ages (adult-juveniles). However, foraging associations among partners (dyads) varied between experimental conditions, being stronger when food was clumped, regardless of the amount of food. Therefore, this study showed that common marmosets are able to use and integrate both ecological and social information to make decisions during social foraging, by adjusting their behaviors and associations with each other to obtain access to resources, maximize their feeding success, and maintain group cohesion necessary for cooperation. In conclusion, this thesis contributed in demonstrating that considering the social characteristics of the studied species (cooperation and

a pyramidal social structure), common marmosets do not fit the socioecological model regarding intra-group food competition. In addition, we showed that within a group, individuals build affiliative relationships with all other group members by associating during foraging, resulting in cohesive and tolerant groups during a potentially competitive activity. We stress that future studies and models should incorporate both cost and benefits of social life to individuals and to the group as a social unit. Finally, we highlight the importance of using field experiments to systematically investigate the socioecology of primates inhabiting their natural environment.

**Key words:** animal behavior, social foraging, competition, social tolerance, common marmoset, *Callithrix jacchus*.



## 1. INTRODUÇÃO

Um grupo social pode ser definido como um conjunto de indivíduos da mesma espécie que se encontram próximos uns aos outros, interagem entre si e realizam suas atividades de forma sincronizada no tempo e espaço (KUMMER, 1971). Neste sentido, a vida em grupo pode fornecer uma série de vantagens e desvantagens para seus integrantes (KRAUSE e RUXTON, 2002). Alguns dos benefícios da vida social estão associados à maior proteção contra predadores, maior eficiência na aquisição de alimentos, acesso facilitado a um parceiro sexual, cuidado aloparental e melhor defesa de território. Por sua vez, os custos de viver em grupo podem incluir: maior visibilidade para os predadores, aumento na competição por recursos e parceiros, assim como aumento na proliferação e transmissão de doenças e/ou parasitas (FLEAGLE, 1999; KRAUSE e RUXTON, 2002). Dessa forma, os indivíduos, quando em um grupo social, devem tomar decisões que lhes permitam equilibrar as vantagens e desvantagens da vida em grupo.

Para qualquer indivíduo, a sua sobrevivência e sucesso reprodutivo irão depender principalmente da sua habilidade em obter alimento suficiente para ele e sua prole (FLEAGLE, 1999). No entanto, na natureza, a distribuição e a disponibilidade de recursos não ocorrem de maneira uniforme e constante tanto no espaço como no tempo (GARBER, 2000). Dessa forma, a busca por alimento envolve desafios quanto à procura, localização, captura, manipulação e exploração de fontes alimentares (SCHIEL et al., 2010). Sendo assim, a capacidade dos indivíduos em utilizar informações ecológicas (espacial e temporal) torna-se um fator importante para o sucesso no forrageio (BICCA-MARQUES e GARBER, 2004). A maneira como os animais obtêm e selecionam seus recursos alimentares é conhecida como estratégia de forrageio (FLEAGLE, 1999). De modo geral, ao falarmos de forrageio social, no qual todos os membros do grupo realizam tal atividade ao mesmo tempo, viver em grupo pode ser tanto prejudicial como proveitoso para o sucesso do forrageio individual. Por um lado, cada indivíduo sofre um aumento na competição por recursos alimentares devido à presença dos outros membros. Assim, indivíduos que vivem em grupos precisariam encontrar maiores fontes de alimento, viajar maiores distâncias para encontrar estas fontes e/ou visitar mais fontes de alimento por dia para saciar as necessidades de todos. Por outro lado, viver em grupo pode fornecer melhor acesso à comida aos indivíduos: defendendo ativamente as fontes alimentares de outros grupos e aumentando as chances de localizar alimento pela presença de vários indivíduos forrageando simultaneamente (KRAUSE e RUXTON, 2002).

Especificamente em se tratando de primatas, quase todas as espécies, incluindo o ser humano, vivem em grupos sociais durante toda ou maior parte da sua vida. Dessa forma, desenvolvem e mantêm relações de longo prazo, estabelecendo redes sociais complexas entre

os distintos membros do grupo (SUEUR et al., 2011). Estas redes são compostas por associações e interações não aleatórias, a partir de uma variedade de comportamentos sociais (afiliativos e/ou agressivos) que podem conectar os indivíduos do grupo de diferentes maneiras e influenciar no seu sucesso na obtenção de determinados recursos e inclusive na sua sobrevivência (LEHMANN e ROSS, 2011). Para entender a complexidade da estrutura social, e vincular o comportamento dos indivíduos em determinado contexto com o funcionamento e a eficiência da dinâmica grupal, a conectividade social, isto é, as relações que ligam os membros do grupo, pode ser medida e modelada (SUEUR et al., 2011). Neste sentido, a análise de redes sociais vem a ser uma poderosa ferramenta para estudar os padrões de interação (por exemplo, comportamentos de afiliação, agonísticos e/ou cooperativos) entre múltiplos indivíduos viventes em um grupo social.

Os primatas se caracterizam por possuir grande tamanho de cérebro com relação ao seu tamanho corporal o que leva a habilidades cognitivas que parecem influenciar na capacidade de armazenar, acessar e integrar informações (BARRET e HENZI, 2005; BARTON, 2006; GARBER et al., 2009). Existem duas hipóteses que visam explicar a evolução cerebral em primatas: a hipótese ecológica e a hipótese social. A primeira pressupõe que os desafios associados à localização e exploração de recursos em um ambiente ecológico complexo teriam evoluído mecanismos cognitivos para maximizar a eficiência no forrageio (BARTON, 1996; JANSON, 2007). Por sua vez, a hipótese social sugere que os desafios associados a viver em grupo, como manter relações sociais, hierarquias de dominância, competição e interações afiliativas entre indivíduos, exerceram um papel importante na evolução dos mecanismos cognitivos, ao terem que acompanhar e avaliar tais relações, reconhecer membros do grupo e lembrar de suas interações passadas (DUNBAR, 1998). No entanto, considerando que a maioria das espécies de primatas vive em grupos sociais estáveis e em ambientes naturais estocásticos, em que os recursos alimentares podem variar quanto a sua disponibilidade temporal e distribuição espacial, alguns pesquisadores sugerem que ambas pressões seletivas, a ecológica e social, contribuíram para a evolução cerebral e cognitiva nesta ordem animal (GIRALDEAU e CARACO, 2000; BICCA-MARQUES e GARBER, 2005; GARBER et al., 2009). Assim, como forrageadores sociais, além de utilizar informações ecológicas para localizar sítios de alimentação, os primatas também contariam com a vantagem que a informação social, proveniente do comportamento de outros membros do grupo e as relações entre eles (BICCA-MARQUES e GARBER, 2005; KING et al., 2009).

Neste contexto, incorporamos, através de experimentos em campo, elementos que contemplassem ambas as hipóteses supracitadas. Nosso objetivo geral foi investigar se primatas de vida livre seriam capazes de utilizar e integrar tanto informações ecológicas, relacionadas

com a distribuição e produtividade de recursos no ambiente, como informações sociais da identidade e comportamento dos outros membros do grupo para tomar suas decisões afim de maximizar os benefícios e minimizar os custos da vida social em um contexto potencialmente competitivo, como é o forrageio. Para tanto, utilizamos um pequeno primata Neotropical, o sagui comum (*Callithrix jacchus*), que se apresenta como um ótimo modelo devido às suas características ecológicas e sociais. São animais altamente sociáveis, formando pequenos grupos coesos compostos por múltiplas fêmeas e múltiplos machos. Espécie onívora, se alimenta de uma ampla gama de recursos na natureza como, por exemplo, frutos, insetos, exsudatos, pequenos vertebrados, entre outros. O sagui comum faz parte dos calitriquídeos, uma radiação de primatas que se caracteriza por um alto rendimento reprodutivo, em que a fêmea reprodutora produz duas ninhadas de gêmeos por ano. Além disso, se distinguem por apresentar cuidado cooperativo da prole por parte de todos os membros do grupo, característica pouco comum entre os primatas. Ao usarmos um primata cooperativo como modelo podem-se fazer analogias e comparações com outros primatas que possuem diferentes sistemas sociais, incluindo a espécie humana, para tentar entender como a vida social evoluiu e de que maneira adotar um determinado comportamento em detrimento de outro é mais vantajoso para os indivíduos e/ou para o grupo como um todo.

A fim de atingir o objetivo geral acima exposto, a presente tese se dividiu em dois capítulos. O primeiro capítulo teve como objetivo investigar como fatores ecológicos (distribuição e produtividade de recursos alimentares) e fatores sociais (posição de dominância, idade e sexo) influenciam no uso de estratégias de forrageio e conseqüentemente no sucesso alimentar dos membros do grupo. Neste contexto, de maneira geral, estudos sobre a competição alimentar em primatas têm sido desenvolvidos com base a modelos teóricos que consideraram aquelas espécies que possuem estilos de dominância mais extremos, nos quais existe forte ou fraca relação hierárquica entre os indivíduos (despóticas vs. igualitárias) e formam grupos que possuem múltiplas fêmeas reprodutoras (WRANGHAM, 1980; JANSON e VAN SCHAIK, 1988; STERCK et al., 1997). No entanto, existe ainda uma lacuna no entendimento de como espécies com uma estrutura social que não se encaixe nestes parâmetros (por exemplo, que possuam uma relação hierárquica menos extrema e/ou apenas uma fêmea reprodutora), como os calitriquídeos por exemplo, se comportam mediante diferentes situações de competição. Dessa forma, investigar comportamentos chaves que levam a aptidão dos membros do grupo em relação às suas estratégias de forrageio e o sucesso alimentar neste tipo de espécies, vem a ser essencial para melhor compreender a ampla diversidade de sistemas sociais (que inclui a organização social, a estrutura social e o sistema de acasalamento) encontrada em primatas (KAPPELER e VAN SCHAIK, 2002).

Complementarmente, o segundo capítulo teve como objetivo examinar, através da análise de redes sociais compostas pelos indivíduos dos grupos de sagui e as relações que os vinculam, como os fatores ecológicos e sociais mencionados acima influenciam na estrutura e dinâmica das associações entre os indivíduos durante o forrageio, afim de investigar mais a fundo a tolerância social dentro do grupo neste contexto de competição alimentar. Até o momento, poucos estudos têm investigado os padrões de associação (número e força das conexões entre indivíduos dentro da sua rede) durante o forrageio em primatas (VENTURA et al., 2006; KING et al., 2011). Analisar a conectividade social entre membros do grupo durante o forrageio social se torna propício, uma vez que diversos fatores como idade, sexo, posição de dominância, parentesco, entre outros, podem afetar os padrões espaciais, o tipo e a força das associações e interações sociais entre os indivíduos. Além disso, ao enfrentarem diferentes condições ecológicas de disponibilidade de alimento, é possível examinar tais relações entre os membros do grupo e a influência que cada indivíduo tem dentro da sua rede social. Assim, podemos entender melhor como as relações de competição e/ou tolerância social entre os indivíduos influenciam os padrões e estratégias sociais utilizadas no forrageio.

## **2. FUNDAMENTAÇÃO TEÓRICA**

### *2.1. Forrageio social e competição*

Ao viver em ambientes não estáveis, os animais são forçados a tomar decisões sobre onde procurar por alimento, por quanto tempo procurar, qual tipo de recurso disponível explorar, entre outros. Neste contexto, a Teoria do Forrageio Ótimo tenta explicar estes comportamentos em termos de custos e benefícios (PYKE *et al.*, 1977). Neste caso, a aptidão de um animal dependeria de sua eficiência ao forragear. Isto é, o custo energético envolvido na procura, captura e manipulação do alimento não deve ser maior do que os benefícios energéticos contidos neles (BEGON *et al.*, 2006). Desta forma, os animais devem tomar decisões que lhes proporcionem uma aptidão elevada e maior sucesso na sobrevivência e reprodução (CHAVES e ALVES, 2010). No entanto, esta teoria não considera a influência que fatores sociais podem ter no forrageio, em que animais interagem entre si, afetando as decisões uns dos outros (GIRALDEAU e CARACO, 2000; GIRALDEAU e DUBOIS, 2008). Assim, ao longo das últimas décadas, a Teoria do Forrageio Social tem sido desenvolvida para analisar os custos e benefícios da cooperação social em animais (GIRALDEAU e CARACO, 2000). Esta teoria prediz que o comportamento de animais que vivem em grupos é influenciado pelo comportamento dos outros membros do grupo e se baseia na Teoria dos Jogos (MAYNARD SMITH, 1982; GIRALDEAU e CARACO, 2000). A Teoria dos Jogos foi desenvolvida inicialmente para entender matematicamente o comportamento econômico dos seres humanos

e estudar a tomada de decisões em que “jogadores” escolhem diferentes ações tentando melhorar seu retorno. Considerando que os animais também devem tomar decisões baseadas em custos e benefícios energéticos a teoria passou a ser utilizada para examinar o emprego de estratégias comportamentais utilizadas pelos animais quando interagem com outros indivíduos no forrageio social (MAYNARD SMITH, 1982; GIRALDEAU e CARACO, 2000). Neste caso, o sucesso da estratégia (comportamento) de um indivíduo (“jogador”) depende da estratégia usada pelo indivíduo com que ele está interagindo (“jogador adversário”) (MAYNARD SMITH, 1979). Segundo a Teoria do Forrageio Social, um indivíduo pode utilizar principalmente informações ecológicas para procurar ativamente, localizar e explorar o alimento antes dos outros (atuar como descobridor, em inglês: *finder*), e/ou utilizar informações sociais, monitorando e avaliando o comportamento de outros membros para localizar os recursos (atuar como usurpador, em inglês: *joiner*). Assim, o sucesso da estratégia usada por um indivíduo para obter acesso ao recurso alimentar, irá depender da identidade e estratégia utilizada pelo indivíduo com que ele está interagindo durante o forrageio (GIRALDEAU e CARACO, 2000).

Dessa forma, a tomada de decisões e os custos e benefícios (sucesso alimentar) dos indivíduos que forrageiam em grupo irão depender tanto de fatores ecológicos como de fatores sociais (BICCA-MARQUES e GARBER, 2005; GARBER *et al.*, 2009). Dentro dos fatores ecológicos podem-se mencionar: a distribuição de locais de alimentação, a quantidade ou produtividade de alimento, e a qualidade do recurso, seja ela nutricional ou energética. Por sua vez, alguns dos fatores sociais são: a posição social de um indivíduo dentro do grupo (hierarquia), parentesco, idade, sexo dos indivíduos e tamanho do grupo (KING *et al.*, 2009). Neste sentido, alguns estudos realizados na natureza indicam que tais fatores influenciam simultaneamente na adoção de determinado comportamento de forrageio (BICCA-MARQUES E GARBER, 2005; GUEDES, 2012).

Os primatas possuem uma grande variedade de sistemas sociais, não apenas entre espécies, mas também podendo variar dentro de uma mesma espécie (KAPPELER e VAN SCHAIK, 2002). Os modelos socioecológicos têm tentado identificar os custos e benefícios de viver em grupo e explicar como características ecológicas influenciam na sociabilidade das diferentes espécies de primatas. Dois tipos de modelos têm sido propostos. Por um lado, um conjunto de modelos foca nos custos da vida social (por exemplo: competição, predação, infanticídio) e têm como premissa que as características dos recursos alimentares determinam os tipos de competição, afetando por sua vez os comportamentos e as relações sociais intra e intergrupais (WRANGHAM, 1980, VAN SCHAIK, 1989, ISBELL, 1991, STERCK *et al.*, 1997). Por outro lado, o modelo alternativo foca nos benefícios de viver em grupo, relacionados

às vantagens de participar em ações coletivas e de cooperação entre os indivíduos (SUSSMAN e GARBER, 2011). Dentro de um grupo, tanto machos quanto fêmeas podem competir e/ou cooperar pelos recursos (JANSON, 1985; VOGEL, 2005). No entanto, uma vez que o acesso a recursos alimentares é de suma importância para a sobrevivência e reprodução, principalmente para fêmeas, que possuem maiores gastos energéticos na gestação e lactação; estes modelos destacam os impactos da distribuição, abundância e qualidade de recursos, assim como os impactos das interações sociais associadas à dominância, competição, parentesco, cooperação e formação de alianças, no sucesso reprodutivo das fêmeas (KAPPELER e VAN SCHAIK, 2006).

Em situações nas quais a disponibilidade de alimento não é suficiente para saciar as necessidades de todos os membros de um grupo, a sua exploração resulta em um aumento na competição pelo mesmo. A competição por alimento pode ser determinada pela abundância e distribuição dos recursos no ambiente (ISBELL, 1991), enquanto que o efeito da competição pode ser refletido nas diferenças no sucesso alimentar entre os membros do grupo (SAITO, 1996; VOGEL, 2005). Dentro de um grupo, a competição por recursos pode ocorrer de forma indireta e/ou direta (JANSON e VAN SCHAIK, 1988). Na competição indireta, também chamada de competição por exploração, um ou alguns membros do grupo exploram os recursos de uma mancha alimentar antes da chegada dos outros, reduzindo sua disponibilidade para os demais. Na competição direta, ou competição por interferência, alguns indivíduos limitam o acesso de outros membros do grupo ao recurso alimentar através de interações agonísticas.

Quando o recurso se encontra aglomerado e pode ser defendido ou monopolizado por alguns indivíduos, as relações de dominância podem restringir o acesso ao alimento por parte de subordinados (competição direta), resultando em indivíduos dominantes obtendo um maior sucesso alimentar (VAN SCHAIK, 1989; KOENIG, 2002). Para evitar agressões, membros subordinados podem utilizar diferentes estratégias como, por exemplo, esperar que o dominante se retire do local de alimentação para consumir o alimento restante; ou consumir alimento, mesmo que de menor qualidade, localizado perto do sítio de alimentação principal. No entanto, estas estratégias por membros subordinados podem levar a um baixo sucesso alimentar, ao consumir alimento em menor quantidade ou de menor qualidade (KOENIG *et al.*, 1998). Para evitar isto, os indivíduos podem utilizar a estratégia de chegar para o sítio de alimentação antes dos dominantes, se comportando como descobridor (competição indireta) (DUBUC e CHAPPAIS, 2007). Desta maneira, os subordinados podem aumentar o seu sucesso alimentar, pois ao chegar primeiro, a produtividade de alimento do sítio é máxima, e os riscos de agressões por parte dos dominantes são menores (BÉLISLE e CHAPPAIS, 2001; DI BITETI e JANSON, 2001). Contudo, a vantagem do uso desta estratégia irá depender do risco de predação, da

quantidade de alimento disponível no sítio de alimentação e da proporção de alimento obtida pelo indivíduo antes da chegada dos outros, conhecida como vantagem do descobridor (em inglês: *finder's advantage*) (DI BITETI e JANSON, 2001).

Neste contexto, espera-se que em espécies despóticas ou caracterizadas por uma forte hierarquia de dominância, a competição direta seja mais evidente e a posição social dos indivíduos seja um fator importante no sucesso alimentar, uma vez que indivíduos dominantes podem obter prioridade de acesso aos recursos (STERCK *et al.*, 1997; BARTA e GIRALDEAU, 1998). Por sua parte, espécies mais igualitárias apresentam maiores níveis de tolerância social e menores taxas de agressão durante o forrageio, podendo compartilhar sítios de alimentação, minimizando a diferença no sucesso alimentar entre os membros do grupo (SUSSMAN e GARBER, 2011). Dessa forma, dependendo do contexto ecológico, relacionado à disponibilidade de alimento no ambiente e do contexto social dentro do grupo, os indivíduos devem integrar informações e tomar decisões de forrageio que lhes permita ajustar suas estratégias para balancear os custos e benefícios da vida social.

## 2.2. Redes sociais

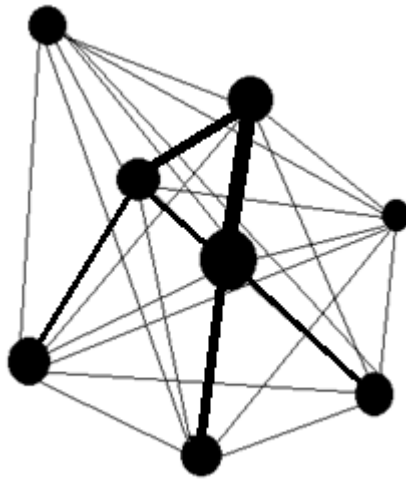
Uma consequência da vida em grupo é o desenvolvimento de conexões sociais entre seus membros e a presença de uma estrutura social. Especificamente, primatas são conhecidos por manter relações estáveis e de longo prazo com seus coespecíficos (THIERRY *et al.*, 2004). Os membros do grupo podem manter associações (condição passiva em que dois ou mais indivíduos compartilham do mesmo espaço e tempo) e interações (comportamento direcionado diretamente de um indivíduo a outro), através de comportamentos sociais afiliativos ou agonísticos, vinculando-os de diferentes maneiras (LEHMANN e ROSS, 2011). Além de comportamentos direcionados e associações espaciais e temporais, as relações entre indivíduos podem envolver eventos de transmissão (de conhecimento, de patógenos, de sinais), compartilhamento de recursos (alimentar, território, sítios de dormida) e de parentesco (WEY *et al.*, 2008). Tais associações e interações desenvolvem relações não aleatórias entre os membros de um grupo formando vínculos e ligações entre eles que são conhecidas como redes sociais. Ao serem analisadas, podemos entender melhor a estrutura e dinâmica social de diferentes espécies, trazer uma maior compreensão da complexidade social e da evolução e manutenção da sociabilidade (WEY *et al.*, 2008; KASPER e VOELKL, 2009, PINTER-WOLLMAN *et al.*, 2014; FARINE e WHITEHEAD, 2015).

A estrutura grupal pode influenciar todo tipo de comportamento dentro do grupo (cooperação no forrageio, acasalamento, aprendizagem social), podendo ser uma variável importante para entender as estratégias utilizadas por diferentes espécies em diversos contextos

(KASPER e VOELKL, 2009). Examinar as relações que um indivíduo específico mantém com todos os outros membros do grupo (WHITEHEAD, 2008) é de suma relevância para caracterizar grupos de primatas e suas diferentes estruturas organizacionais. Assim, a importância do estudo da organização estrutural de grupos de primatas recai em conhecer quais fatores ecológicos, sociais, pressões evolutivas e restrições individuais moldam os diferentes sistemas sociais das distintas espécies deste grupo animal (DUNBAR, 1988; KASPER e VOELKL, 2009). Por exemplo, um estudo realizado com babuínos (*Papio anubis*), os quais formam grandes grupos sociais, mostrou que os indivíduos mantêm relações sociais altamente diferenciadas e que as posições individuais dentro do grupo são fortemente determinadas pelo sexo (LEHMANN e ROSS, 2011). Por sua vez, um estudo realizado com chimpanzés (*Pan troglodytes*), revelou que as redes sociais nesta espécie são altamente dinâmicas ao longo do tempo e que o estado reprodutivo de fêmeas tem influência nas associações dentro do grupo (RUSHMORE *et al.*, 2013).

De tal modo, a Análise de Redes Sociais trata, principalmente, de uma coleção de instrumentos analíticos que visa investigar a conectividade social em diversos contextos e em diferentes níveis dentro do grupo (individual, díade, subgrupo, grupo) ou entre grupos e populações (e.g. NEWMAN, 2010, SUEUR *et al.*, 2011, MAKAGON *et al.*, 2012). Suas ferramentas gráficas permitem a inspeção visual das redes, ajudando no melhor entendimento dos padrões das associações e interações entre os indivíduos. Assim, as redes sociais podem ser retratadas visualmente em grafos (e.g. Figura 1) ou representadas em matrizes. Os modelos de redes são compostos pelos indivíduos (“nós” ou vértices) e suas conexões (“laços” ou arestas), que são as relações sociais entre dois indivíduos em um determinado momento. As conexões podem ter peso (força da conexão), direção (indicando o executor e o receptor da interação) e sinal (interação positiva ou negativa) provendo maiores detalhes sobre as interações.





**Figura 1.** Exemplo de representação gráfica de uma rede social para um grupo de 8 indivíduos. Cada ponto representa um membro do grupo e as linhas representam a conexão/relação entre dois indivíduos (associações ou interações). O tamanho dos pontos indica a força do indivíduo dentro da rede (se conecta com mais ou menos indivíduos). A espessura das linhas indica a força da conexão entre dois indivíduos. Ilustração: María Fernanda De la Fuente.

A análise de redes sociais permite relacionar o padrão, tipo e força das associações espaciais e das interações sociais entre os indivíduos durante um determinado contexto a fatores como idade, sexo, parentesco e hierarquia, para melhor entender como estes fatores afetam as diferentes relações sociais entre dois indivíduos (díades) e/ou entre vários indivíduos (subgrupos) dentro de um grupo maior (KASPER e VOELKL, 2009; CROFOOT *et al.*, 2011; JACOBS e PETIT, 2011). Se tratando de um contexto de forrageio social, é possível integrar e comparar as diferenças individuais nas estratégias de forrageio com base social (compartilhamento de sítios de alimentação) para examinar a estrutura, coesão e dinâmica das interações entre os membros do grupo ao longo de diferentes contextos ecológicos mais ou menos competitivos (JACOBS e PETIT, 2011; SUEUR *et al.*, 2011). Até o presente momento, pesquisas investigando especificamente as relações sociais de primatas durante o forrageio têm sido reduzidas (VENTURA *et al.*, 2006; KING *et al.*, 2011). Além disso, estudos com primatas não humanos que lidam com a análise de redes sociais, têm sido efetuados principalmente utilizando espécies do Velho Mundo e/ou que vivem em grandes grupos (> 20 indivíduos) (SUEUR e PETIT, 2008; SUEUR *et al.*, 2009; BORGEAUD *et al.*, 2017), deixando ainda pouco explorado como indivíduos de espécies de primatas que formam grupos menores se estruturam, relacionam e conectam. Dessa forma, ao utilizar o sagui comum como modelo, esperamos contribuir para um melhor entendimento sobre a grande diversidade de comportamentos, relações e sistemas sociais encontrados nesta ordem animal.

### 2.3. *Callithrix jacchus*

O sagui comum (*Callithrix jacchus*), é um pequeno primata Neotropical, endêmico do Nordeste do Brasil, pertencente ao gênero *Callithrix* e à família Callitrichidae (RYLANDS *et al.*, 2008; para uma revisão completa sobre a espécie, ver SCHIEL e SOUTO, 2017). O mesmo, destaca-se por sua grande capacidade de sobrevivência a diferentes tipos de ambientes (MODESTO e BERGALLO, 2008), habitando uma ampla variedade de biomas, desde florestas úmidas até ambientes semiáridos (Figura 2) (STEVENSON e RYLANDS, 1988; RYLANDS e FARIA, 1993). Acredita-se que o sucesso ecológico da sua distribuição geográfica e adaptação a estes diversos tipos de ambientes se deve à suas características morfofisiológicas para a eficiente exploração de exsudatos (goma e seiva de algumas espécies de árvores) como um importante recurso alimentar (dentição adaptada, ceco aumentado e unhas em forma de garras) (FERRARI, 1993), além de sua capacidade de ajustar suas estratégias comportamentais (DE LA FUENTE *et al.*, 2014, ABREU *et al.*, 2016). Esta espécie possui uma dieta onívora, se alimentando de uma ampla gama de recursos como goma, frutas, flores, sementes, insetos, aracnídeos, pequenos vertebrados, ovos de aves e cladódios de cactáceas (STEVENSON e RYLANDS, 1988; RYLANDS e FARIA, 1993; SOUTO *et al.*, 2007; AMORA *et al.*, 2013; ABREU *et al.*, 2016).



**Figura 2.** Sagui comum (*Callithrix jacchus*) em ambiente úmido de Mata Atlântica (A) e em ambiente semiárido de Caatinga (B), no nordeste brasileiro. Fotos: María Fernanda De la Fuente.

*Callithrix jacchus* é um animal social, forma grupos coesos que podem variar de tamanho entre 3 a 16 indivíduos, formados por múltiplas fêmeas e múltiplos machos. O grupo geralmente é constituído por animais de distintas faixas etárias (adultos reprodutores e não reprodutores, subadultos, juvenis e infantes), podendo ser aparentados ou não (DIGBY *et al.*, 2011). A composição do grupo permanece estável, exceto quando ocorre a imigração ou

emigração de algum indivíduo para outro grupo, e com o nascimento da prole (KINZEY, 1997). Em geral, os calitriquídeos são caracterizados por possuírem diversos atributos associados a um alto rendimento reprodutivo (produção de filhotes gêmeos duas vezes por ano) e um sistema de cuidado aloparental cooperativo, estas características os diferenciam de outras espécies de primatas.

O sistema de acasalamento dos calitriquídeos tem sido usualmente descrito como monogâmico, ocorrendo entre fêmea e macho reprodutores. No entanto, poliandria, na qual a fêmea reprodutora também acasala com outros machos; e poliginia, em que o macho reprodutor acasala com outras fêmeas, também podem ocorrer (FERRARI e LOPES FERRARI, 1989; ARRUDA *et al.*, 2005; YAMAMOTO *et al.*, 2009). Devido à capacidade da fêmea reprodutora de suprimir a ovulação de fêmeas subordinadas, habitualmente, apenas uma fêmea do grupo se reproduz (YAMAMOTO *et al.*, 2009). No entanto, alguns estudos de vida livre têm mostrado a presença de duas fêmeas reprodutoras em um mesmo grupo (DIGBY, 1995; ARRUDA *et al.*, 2005, YAMAMOTO *et al.*, 2009). Devido à ausência de anestro lactacional, o que permite que a fêmea reprodutora seja capaz de retomar a ovulação alguns dias após o parto, filhotes gêmeos são usualmente gerados duas vezes por ano (TARDIF *et al.*, 2003). A criação dos infantes é realizada através de cuidado aloparental, isto é, todos os integrantes do grupo, principalmente machos adultos, participam e cooperam no cuidado, transporte e provisão de alimento dos filhotes durante seus primeiros meses de vida (STEVENSON e RYLANDS, 1988; ROTHE *et al.*, 1993). Dessa forma, a sobrevivência da prole é fortemente dependente do número de ajudantes adultos presentes no grupo (KOENIG, 1995). Este tipo de cuidado cooperativo é extremamente raro em primatas e requer que os membros do grupo mantenham fortes laços sociais, monitorando o comportamento um dos outros e interagindo constantemente (GARBER, 1997).

Além do cuidado compartilhado e cooperativo da prole, outras atividades requerem cooperação entre os membros do grupo, como por exemplo: a defesa de território e parceiros sexuais de outros grupos (CASELLI *et al.*, 2018); e a vigilância e/ou defesa contra predadores (STOJAN-DOLAR e HEYMANN, 2010; FERRARI e FERRARI, 1990). De forma geral, os calitriquídeos se caracterizam por realizar a maioria das suas atividades de forma conjunta e coesa, se deslocando e forrageando em grupo, compartilhando sítios de alimentação e sítios de dormida (ABREU *et al.*, 2016; DUARTE e YOUNG, 2011). No entanto, fêmeas adultas investem mais tempo procurando e consumindo alimentos, enquanto machos investem mais tempo na vigilância contra predadores e no cuidado da prole (BICCA-MARQUES, 2003).

As características ecológicas e sociais do sagui comum fazem com que a espécie se apresente como um ótimo modelo para examinar os custos e benefícios do forrageio social. Ao

realizar experimentos de campo e manipular sistematicamente a produtividade e distribuição de sítios de alimentação podemos investigar como fatores ecológicos e fatores sociais, influenciam no uso de estratégias de forrageio para obter acesso aos recursos, no sucesso alimentar dos indivíduos e nas relações sociais entre os membros do grupo.

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#### 4. CAPÍTULO 1

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

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Foto: María Fernanda De la Fuente.

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

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**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.

**Key Words:** foraging strategies, feeding success, rank, finder's share, co-feeding.

## **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, 1986). 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 Schaik, 1989; Wrangham, 1980). An alternative model focuses on the benefits to individuals of collective action, co-feeding, 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 Schaik, 1989). Scramble competition is an indirect form of competition in which one individual (i.e., finder) encounters and exploits a food patch prior to 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., the 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, 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 & Caracao, 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 co-feeding, 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, 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 semi-arid scrubland habitat. In the wild, common marmosets live in multimale multifemale groups that range in size from three to 16 individuals (for a review, see Schiel & Souto, 2017). *Callithrix 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 and 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 non-breeding 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. Since 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**

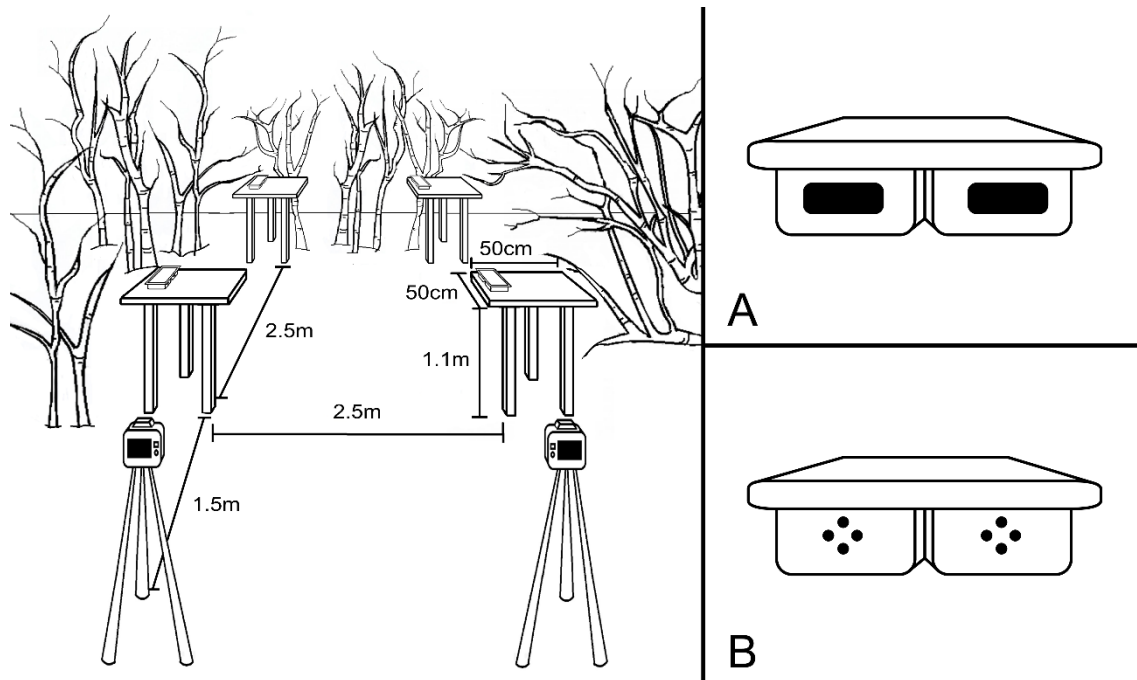
We conducted the study at the Baracuhy Biological Field Station (Fazenda Marimbondo, 7°31'42"S, 36°17'50"W), a 400-ha privately owned area characterized by a semiarid thorn-scrub Caatinga habitat (De la Fuente, Souto, Sampaio, & Schiel, 2014), located ca. 4 km from the municipality of Cabaceiras, state 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 mm and 10.3 mm in the rainy and dry season, respectively (INMET, 2017).

### **2.2 Study groups**

We studied four habituated groups of wild *Callithrix 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 in Supporting information for the composition of groups). Several months prior to 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 cm x 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 x 13.0 cm width x 6.0 cm height) with two separate and identical compartments on each platform (Fig. 1). Containers with accessible rewards had two openings (5 cm x 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 meters 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 one-week feeding trial (21 test sessions for each food type) prior to 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 in Supporting information for amount of food available). Before running the experimental conditions, we conducted a “pre-condition” 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 one-week feeding trial). We used the pre-condition 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.

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

<b>Experimental condition</b>	<b>Food distribution</b>	<b>Patch productivity</b>	<b>Amount of food at the feeding station</b>	<b>Amount of food in each platform</b>
S+	Scattered	Medium	Mean amount consumed by the group during one-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 one-week feeding trials	Enough to satiate approximately half of the group members
S-	Scattered	Low		Not enough to satiate one group member

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 SX 50) mounted on a tripod placed 1.5 m from the nearest platforms (Fig. 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 am, 10:30 am, and 3:00 pm), 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 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, 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 in Supporting information 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 in Supporting information 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 zero (a completely egalitarian hierarchy in which contest outcomes are unpredictable, the hierarchy is shallow) to one (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 ( $p\text{-value} > 0.05$ ) (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Whenever the best-fitted model include interactions among predictor variables, we conducted pairwise comparisons (Tukey 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  $R^2\text{s} > 0.6$  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:  $F_{(3, 671)} = 24.01$ ,  $p < 0.0001$ ; Mealworm:  $F_{(3, 555)} = 49.02$ ,  $p < 0.0001$ ), 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 *Individual Daily Consumption* (IDC) as the mean amount of food that a given individual consumed per day during the S++ “pre-condition” trial (resources present on the platforms were more than enough to satiate all group members; see Table-S1 in Supporting information 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 zero (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 results), 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 am and 10:30 am sessions) by acting as finders (i.e., engaging in scramble competition) to increase feeding success later in the same day (3:00 pm session). First, we examined if finders indeed had higher feeding success during a session compared to non-finders 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 pm 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  $27 \pm 3$  sessions per experimental condition (see Table-S4 in Supporting information 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 members co-foraged on  $63 \pm 5\%$  of visits. During conditions in which food was scattered on three reward platforms, two or more group members co-foraged on  $34 \pm 10\%$  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  $< 1$  to 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 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 in Supporting information), he was the third highest-ranking individual. Juveniles, irrespective of sex, occupied the lowest ranks in all groups.

**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)
<b>Banana</b>	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
	<b>Total</b>	7,149	1,248	0.174	0.066	0.035
<b>Mealworm</b>	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
	<b>Total</b>	5,548	388	0.069	0.023	0.010

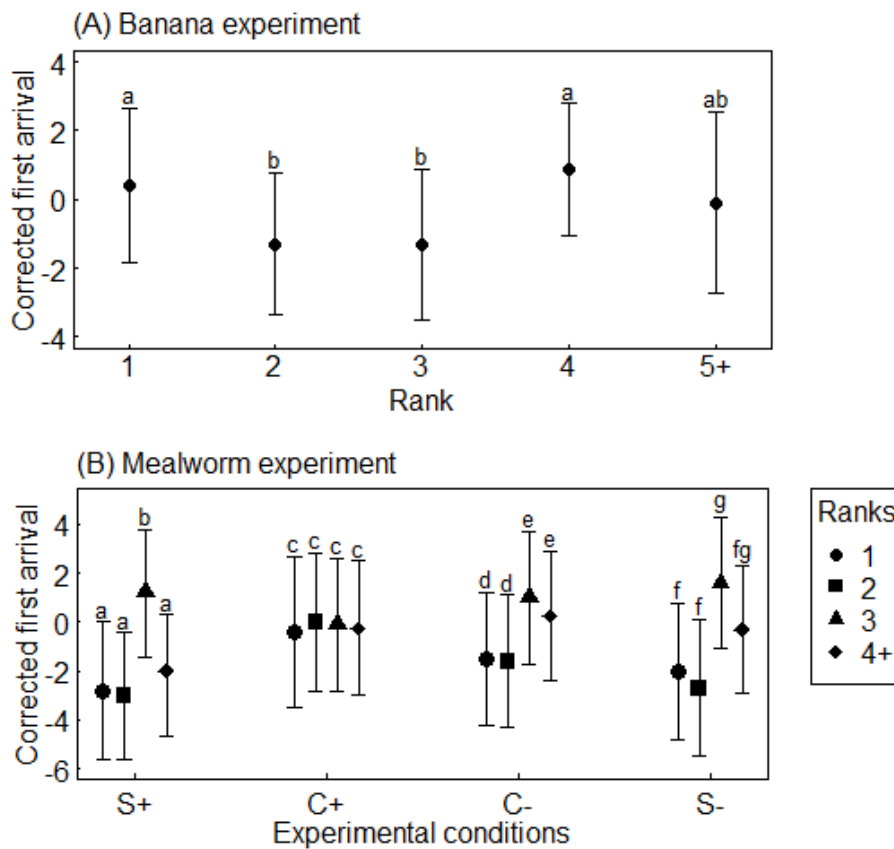
† Breeding females, see Supporting information for rank positions of group members.

### 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 to S9 in Supporting information for all model comparisons throughout the manuscript). However, contrary to H1 expectations, when food was concentrated on a single platform, 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  $p < 0.005$ ; Fig. 2.A). 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 (Fig. 2.B). 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 (Fig. 2.B). Therefore, we found support for H1 when a limited amount of mealworms was concentrated on a single reward platform. However, we did not find support for H1 when a larger amount of mealworms was concentrated, as individuals of all ranks acted equally as finders.



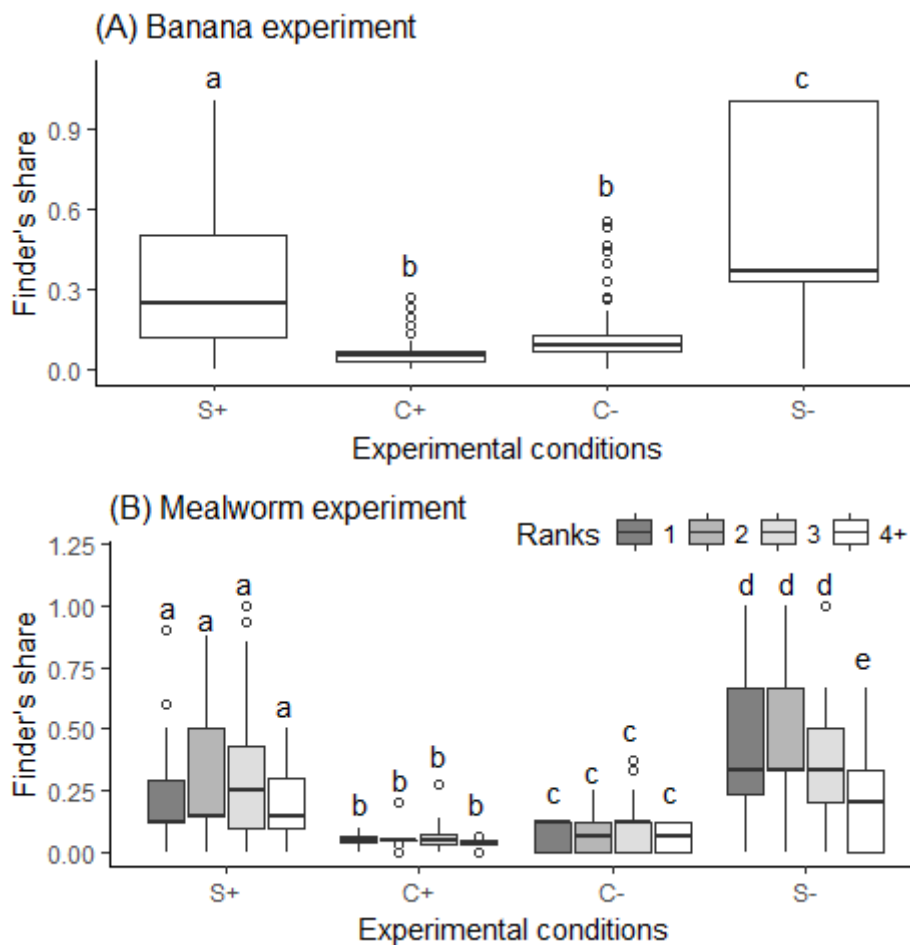
**Figure 2.** Mean  $\pm$  standard deviation of rank's *corrected first arrival* during (A) banana experiment, and (B) mealworm experiment (interaction among predictor variables: experimental conditions and rank). Tukey pairwise comparisons: different letters indicate significant differences ( $p < 0.05$ ) (A) among ranks, or (B) within each experimental condition.

### 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 to 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:  $0.56 \pm 0.3$ ) 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:  $0.31 \pm 0.26$ ) 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- =  $0.13 \pm 0.12$ ; C+ =  $0.06 \pm 0.05$ ), and not significantly different among them ( $p = 0.253$ ) (Fig. 3.A). 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 (Fig. 3.B). 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:  $0.44 \pm 0.32$ ;  $0.48 \pm 0.36$ ;  $0.34 \pm 0.28$ , respectively) than for individuals ranked fourth+ (mean:  $0.22 \pm 0.2$ ,  $p < 0.05$ ). 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+ =  $0.05 \pm 0.03$ , C- =  $0.08 \pm 0.07$ , 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.



**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 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.

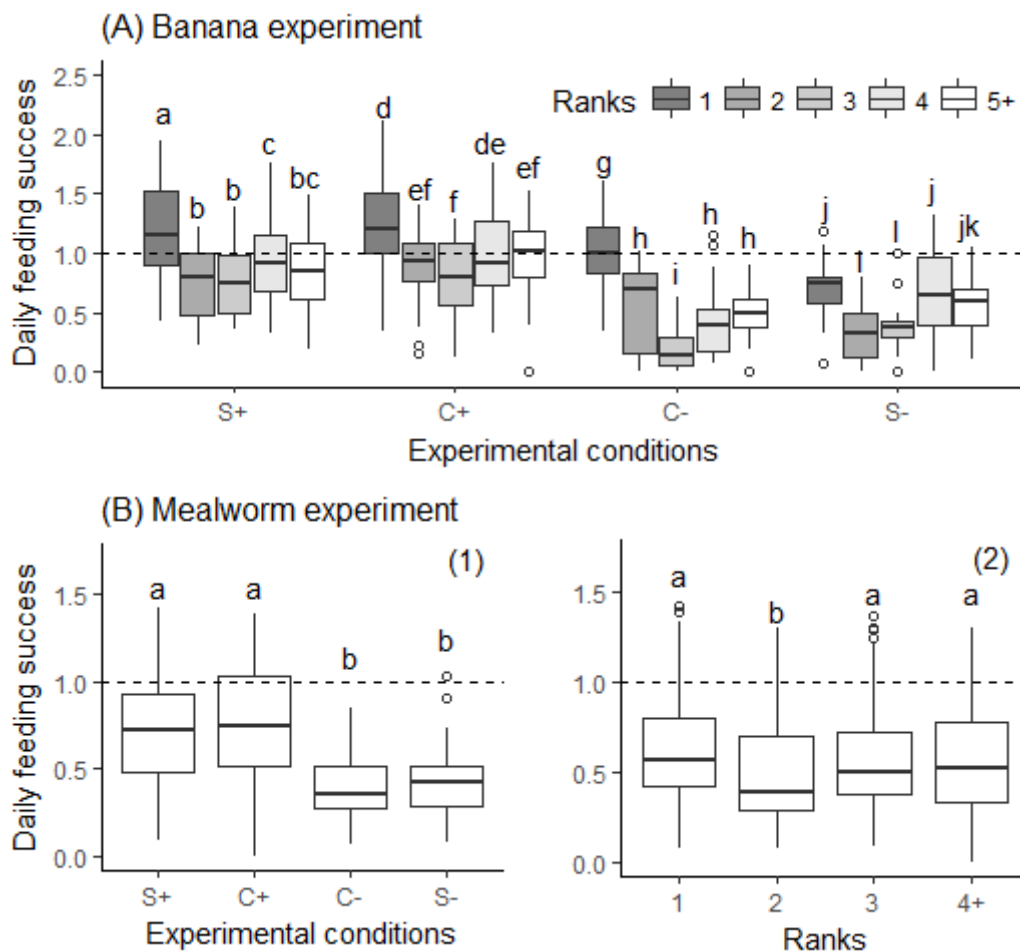
### 3.4 H3 - Daily feeding success

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 those in which food was limited (Fig. 4.A). 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 ( $p > 0.05$ ; Fig. 4.A). 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  $p < 0.0001$ ; Fig. 4.B.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  $p < 0.0001$ ; Fig 4.B.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.



**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 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* (IDC). Boxplots represent the median, first, and third quartiles, with superior and inferior limits, and outliers when present.

### 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 2/3 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 prior to 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 (*Sapajus 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 co-foraged 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: 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*, *P. 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 co-feeding 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 appears 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, while among all other group members, agonistic interactions were less frequent and winning outcomes were not consistently unidirectional (see Table-S3 in Supporting information). 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 non-aggressive forms of feeding competition (scramble) and social tolerance (e.g., co-feeding 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 Schaik, 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 similar 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 & 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 co-feeders. 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 non-aggressive 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 interest**

The authors of this manuscript have no conflict of interest to declare.

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Supporting information

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

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## Methods

**Table S1.** Size and composition of study groups. Normalized David's Score (NDS), rank, and Individual Daily Consumption (IDC) for each study subject in the banana and mealworm experiments.

Group	Ind.	Age	Sex	NDS (Rank)		IDC (Mean $\pm$ standard deviation)	
				Banana	Mealworm	Banana (3-g pieces)	Mealworm (1-g units)
COQ	FEC	A	BF	3.75 (1)	3.75 (1)	12 $\pm$ 3	17 $\pm$ 4
	MAC	A	M	2.78 (2)	2.63 (2)	13 $\pm$ 3	14 $\pm$ 2
	VRM	A	M	1.56 (3)	1.29 (4)	16 $\pm$ 2	14 $\pm$ 5
	AZL	A	M	1.16 (4)	1.49 (3)	12 $\pm$ 2	10 $\pm$ 4
	BEC	J/A	M	0.75 (5)	0.85 (5)	10 $\pm$ 2	11 $\pm$ 5
	†FR	I	F	-	-	-	-
	†FV	I	F	-	-	-	-
PRI	‡PSA	A	BF	4.78 (1)	¶-	13 $\pm$ 2	-
	‡PRI	A	M	3.52 (2)	¶-	10 $\pm$ 2	-
	ZNG	A	M	2.40 (3)	2.00 (2)	8 $\pm$ 3	13 $\pm$ 3
	POR	A	F	2.18 (4)	2.62 (1)	11 $\pm$ 4	16 $\pm$ 5
	BNR	A	F	1.14 (5)	0.92 (3)	10 $\pm$ 2	15 $\pm$ 4
	‡ILL	A	F	0.98 (6)	¶-	13 $\pm$ 2	-
	¶AND	I/J	M	†-	-	-	-
	§SAM	I/J	M	†-	0.46 (4)	-	10 $\pm$ 3
‡VAC	BRA	A	BF	3.35 (1)	-	12 $\pm$ 3	-
	FOG	A	M	3.05 (2)	-	14 $\pm$ 3	-
	LIL	A	M	1.54 (4)	-	12 $\pm$ 3	-
	COT	A	M	1.60 (3)	-	14 $\pm$ 2	-
	TRI	J	M	0.45 (5)	-	10 $\pm$ 1	-
§CAS	EST	A	BF	-	2.35 (1)	-	14 $\pm$ 2
	MAH	A	M	-	1.74 (2)	-	13 $\pm$ 3
	VEH	A	M	-	1.48 (3)	-	12 $\pm$ 4
	RAB	J	M	-	0.42 (4)	-	10 $\pm$ 3

A: adult; J: juvenile; I: infant; F: female; M: male; BF: breeding female. † Not included in the analyzes because individual could not actively obtain food rewards from the containers. ‡ Participated only in banana conditions; § Participated only in mealworm conditions; ¶ Not included in the analysis because of emigration or disappearance.

**Table S2.** Amount of food available per session for study group, during each experimental condition, and “pre-condition” trial (S++).

Group (size)	Total food amount available per session in each condition									
	Banana pieces (3 g each)					Mealworm units (1 g each)				
	S++	S+	C+	C-	S-	S++	S+	C+	C-	S-
COQ (5)	36	18	18	9	9	60	30	30	15	15
PRI (6/4)	60	30	30	15	15/12 <sup>†</sup>	50	25	25/22 <sup>†</sup>	8 <sup>§</sup>	8
VAC (5/4)	44	22	22	11	9 <sup>†</sup>	-	-	-	-	-
CAS (4)	-	-	-	-	-	50	25/20 <sup>‡</sup>	20	8 <sup>§</sup>	8

<sup>†</sup> Quantity adjusted after an individual left the group. <sup>‡</sup> Quantity adjusted after two individuals left the group and were replaced by one new individual. <sup>§</sup> Quantity adjusted prior to beginning this condition because not all mealworms were consumed in the previous condition.

**Table S3.** Dyadic agonistic interaction matrices built to estimate the NDS and rank order for each study group. Matrices include all agonistic interactions (low + high intensity) registered during each experimental condition, including the “pre-condition” S++.

		Winner	Loser				
<b>COQ</b>			FEC	MAC	VRM	AZL	BEC
Banana	FEC	-	69	116	72	130	
	MAC	16	-	24	14	10	
	VRM	1	0	-	4	15	
	AZL	0	1	1	-	10	
	BEC	4	4	4	2	-	
Mealworm		FEC	MAC	AZL	VRM	BEC	
	FEC	-	14	26	31	37	
	MAC	2	-	4	1	2	
	AZL	1	0	-	1	3	
	VRM	0	0	0	-	8	
BEC	1	0	2	2	-		
<b>PRI</b>		PSA	PRI	ZNG	POR	BNR	ILL
Banana	PSA	-	84	12	79	54	94
	PRI	11	-	6	18	41	13
	ZNG	0	0	-	6	17	18
	POR	0	1	3	-	51	33
	BNR	2	10	3	15	-	6
	ILL	1	4	4	0	6	-
Mealworm		POR	ZNG	BNR	SAM		
	POR	-	20	77	24		
	ZNG	9	-	11	9		
	BNR	3	0	-	7		
	SAM	0	3	1	-		
<b>VAC</b>		BRA	FOG	COT	LIL	TRI	
Banana	BRA	-	26	37	12	29	
	FOG	14	-	27	9	38	
	COT	3	9	-	12	42	
	LIL	2	0	15	-	15	
	TRI	1	3	4	4	-	
<b>CAS</b>		EST	MAH	VEH	RAB		
Mealworm	EST	-	12	25	15		
	MAH	3	-	4	11		
	VEH	10	2	-	12		
	RAB	2	1	2	-		

## Results

**Table S4.** Number of sessions that free-living common marmoset groups participated in each experimental condition.

Group	Banana conditions				Mealworm conditions			
	S+	C+	C-	S-	S+	C+	C-	S-
COQ	28	30	28	30	25	29	27	29
PRI	25	27	30	29	25	25	26	29
†VAC	29	28	29	29	-	-	-	-
‡CAS	-	-	-	-	21	22	20	20

† We could not use the VAC group for the mealworm conditions because group members would not eat mealworms or other insect prey that was offered (e.g. crickets and cockroaches, alive and dry). Therefore, we used the CAS group for the mealworm conditions. ‡ CAS group participated in only 20 sessions. This was likely due to social instability associated with a turnover in the reproductive female prior to the start of condition S+.



H1 – First arrival to reward platforms

**Table S5.** Sequential model comparisons of null-full and reduced models. *Corrected first arrival* as the response variable. Experimental conditions, rank, and their interaction (\*) as predictor variables. Group identity and sessions of the day as random effects. In italic: model selected between comparisons. In bold: final (best-fit) model selected.

<b>Food type</b>	<sup>†</sup> <b>Model comparisons</b>	<b>df</b>	<b>L</b>	<b>p-value</b>
<b>Banana</b>	Null model, <i>Full model (Experimental conditions * Rank)</i>	26	65.77	<0.0001
	Full model, <i>Model 1 (Experimental conditions + Rank)</i>	14	15.26	0.227
	Model 1, <b>Model 2 (Rank)</b>	11	4.99	0.172
	<i>Model 1</i> , Model 3 (Experimental conditions)	10	31.93	<0.0001
<b>Mealworm</b>	Null model, <i>Full model (Experimental conditions * Rank)</i>	22	91.68	<0.0001
	<i>Full model</i> , Model 1 (Experimental conditions + Rank)	13	19.93	0.018

<sup>†</sup> Following Zuur et al. (2009), we selected the simpler/reduced model whenever model comparisons indicated that model simplification would result in no significant loss of explanatory power (p-value > 0.05).

H2 – Finder’s share

**Table S6.** Sequential model comparisons of null-full and reduced models. Finder’s share as the response variable. Experimental conditions, rank, and their interaction (\*) as predictor variables. Group identity and sessions as random effects. In italic: model selected between comparisons. In bold: final (best-fit) model selected.

<b>Food type</b>	<sup>†</sup> <b>Model comparisons</b>	<b>df</b>	<b>L</b>	<b>p-value</b>
	Null model, <i>Full model (Experimental conditions * Rank)</i>	27	296.83	<0.0001
<b>Banana</b>	Full model, <i>Model 1 (Experimental conditions + Rank)</i>	15	11.38	0.496
	Model 1, <b><i>Model 2 (Experimental conditions)</i></b>	11	7.44	0.114
	<i>Model 1, Model 3 (Rank)</i>	12	274.06	<0.0001
<b>Mealworm</b>	Null model, <b><i>Full model (Experimental conditions * Rank)</i></b>	22	222.56	<0.0001
	<i>Full model, Model 1 (Experimental conditions + Rank)</i>	13	20.36	0.016

<sup>†</sup> Following Zuur et al. (2009), we selected the simpler/reduced model whenever model comparisons indicated that model simplification would result in no significant loss of explanatory power (p-value > 0.05).

H3 – Daily feeding success

**Table S7.** Sequential model comparisons of null-full and reduced models. Daily feeding success as the response variable. Experimental conditions, rank, and their interaction (\*) as predictor variables. Group identity as random effect. In italic: model selected between comparisons. In bold: final (best-fit) model selected.

<b>Food type</b>	<sup>†</sup> <b>Model comparisons</b>	<b>df</b>	<b>L</b>	<b>p-value</b>
<b>Banana</b>	Null, <i>Full model (Experimental conditions * Rank)</i>	26	416.59	<0.0001
	<i>Full model</i> , Model 1 (Experimental conditions + Rank)	14	37.48	<0.0001
<b>Mealworm</b>	Null, <i>Full model (Experimental conditions * Rank)</i>	21	316.62	<0.0001
	Full model, <i>Model 1 (Experimental conditions + Rank)</i>	12	11.06	0.271
	<i>Model 1</i> , Model 2 (Experimental conditions)	9	42.95	<0.0001
	<i>Model 1</i> , Model 3 (Rank)	9	183.64	<0.0001

<sup>†</sup> Following Zuur et al. (2009), we selected the simpler/reduced model whenever model comparisons indicated that model simplification would result in no significant loss of explanatory power (p-value > 0.05).

*Evidence of compensatory feeding strategies*

**Table S8.** Sequential model comparisons of null-full and reduced models. Session feeding success as the response variable. Experimental conditions, rank, acting as a finder or not, and their interactions (\*) as predictor variables. Group identity as random effect. In italic: model selected between comparisons. In bold: final (best-fit) model selected.

<b>Food type</b>	<b>† Model comparisons</b>	<b>df</b>	<b>L</b>	<b>p-value</b>
<b>Banana</b>	Null, <i>Full model (Experimental conditions * Rank * Acting as a finder or not)</i>	45	189.92	<0.0001
	Full model, <i>Model 1 (Experimental conditions * Rank + Experimental condition * Acting as a finder or not + Rank * Acting as a finder or not)</i>	33	11.76	0.464
	Model 1, <i>Model 2 (Experimental condition * Rank + Experimental condition * Acting as a finder or not)</i>	29	2.95	0.566
	Model 2, <b>Model 3 (Experimental condition * Acting as a finder or not + Rank)</b>	17	9.78	0.635
	<i>Model 3, Model 4 (Experimental condition + Rank + Acting as a finder or not)</i>	14	8.65	0.034
<b>Mealworm</b>	Null, <i>Full model (Experimental conditions * Rank * Acting as a finder or not)</i>	37	160.20	<0.0001
	Full model, <i>Model 1 (Experimental conditions * Rank + Experimental condition * Acting as a finder or not + Rank * Acting as a finder or not)</i>	28	7.17	0.619
	Model 1, <i>Model 2 (Experimental condition * Rank + Experimental condition * Acting as a finder or not)</i>	25	0.46	0.925
	Model 2, <i>Model 3 (Experimental condition * Acting as a finder or not + Rank)</i>	16	9.53	0.389
	Model 3, <i>Model 4 (Experimental condition + Rank + Acting as a finder or not)</i>	13	5.16	0.160
	Model 4, <b>Model 5 (Experimental condition + Acting as a finder or not)</b>	10	5.48	0.139
	<i>Model 5, Model 6 (Experimental condition)</i>	9	30.44	<0.0001

*Model 5, Model 7 (Acting as a finder or not)*    7    120.03    <0.0001

† Following Zuur et al. (2009), we selected the simpler/reduced model whenever model comparisons indicated that model simplification would result in no significant loss of explanatory power (p-value > 0.05).

**Table S9.** Sequential model comparisons of null-full and reduced models. Frequency of acting as finder during the 3 pm session as the response variable. Rank and *compensatory status*, and their interaction (\*) as predictor variables. Experimental conditions as a random effect. In italic: model selected between comparisons. In bold: final (best-fit) model selected.

<b>Food type</b>	† <b>Model comparisons</b>	<b>df</b>	<b>L</b>	<b>p-value</b>
<b>Banana</b>	Null, <i>Full model (Rank * Compensatory status)</i>	16	33.51	<0.0001
	Full model, <i>Model 1 (Rank + Compensatory status)</i>	12	7.84	0.097
	Model 1, <b><i>Model 2 (Compensatory status)</i></b>	5	13.80	0.055
	<i>Model 1</i> , Model 3 (Rank)	11	23.17	<0.0001
<b>Mealworm</b>	Null, <i>Full model (Rank * Compensatory status)</i>	13	37.60	<0.0001
	Full model, <i>Model 1 (Rank + Compensatory status)</i>	10	4.32	0.228
	Model 1, <b><i>Model 2 (Compensatory status)</i></b>	7	4.18	0.242
	<i>Model 1</i> , Model 3 (Rank)	11	23.17	<0.0001

† Following Zuur et al. (2009), we selected the simpler/reduced model whenever model comparisons indicated that model simplification would result in no significant loss of explanatory power (p-value > 0.05).

## 5. CAPÍTULO 2

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

Artigo submetido na revista científica *PNAS*.

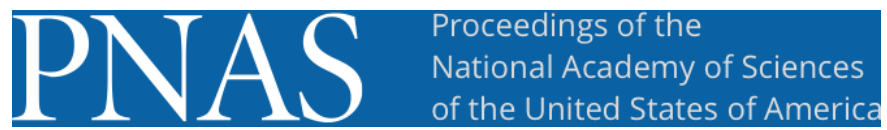


Foto: María Fernanda De la Fuente.

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

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**Key words:** social network, associations, common marmoset, field experiment, group  
cohesion

**Abstract**

Social living can impose costs and benefits to group members. In the wild, foragers are confronted with social and ecological challenges that affect their foraging decisions and tolerance among conspecifics. Developing social relationships can be a strategy to reduce opportunities for contest competition. To investigate within-group social tolerance in a cooperatively breeding primate species, we conducted a field experiment and used social network analysis to examine how rank, sex, age, and food availability influence the structure and dynamics of foraging associations in wild common marmosets (*Callithrix*

*jacchus*). Overall, we found stronger associations when food was concentrated in a single feeding site, regardless of food productivity. Juveniles and higher-ranking individuals associated for longer than adults and lower-ranking individuals, respectively. Foraging associations of dyads composed of an adult and a juvenile were strongest than dyads composed of two adults during all experimental conditions of food availability. In contrast, associations among dyads composed of individuals with diverse rank and sex varied across experimental conditions. Marmosets used different socially mediated behavioral strategies to obtain food rewards. Over time, the strength of associations at a previous foraging experience positively influenced the next one. Based on these results, common marmosets can adjust their foraging partner choices and regulate the intensity of their associations based on the ecological context. The cooperative infant caregiving system requires that all group members maintain strong social bonds to engage in coordinated behaviors. Therefore, social tolerance is crucial to promote group cohesion, social stability and benefits to all individuals in the group.

## **1 Introduction**

Socially living animals face a trade-off between the advantages and disadvantages of being part of a group, such as participating in collective or cooperative actions and dealing with competition over resources (1, 2). Behavioral strategies that allow individuals to accomplish a balance between the costs and benefits of social living can shape interactions and associations between group members and result in non-random relationships (3). The patterns of these relationships characterize the social network structure of a group or species and have been examined in different taxa (e.g., fishes: 4; birds: 5; non-primate mammals, such as cetaceans: 6, ungulates: 7, rodents: 8, meerkats:



9; and primates: 10). By forming and developing predictable and affiliative social relationships, individuals can enhance their access to resources and maximize their fitness (11).

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 and feeding contexts) while displaying low levels or no perceived aggression (12). In primate societies, cohesive groups are composed of individuals who are more tolerant of each other than those that live in groups with strict dominance or despotic hierarchies (13, 14). However, even in species in which individuals compete aggressively for access to resources, cooperative behaviors and food sharing can occur under specific ecological and social contexts, such as cooperative hunting and during sexual consortship (e.g., chimpanzees [*Pan troglodytes*]: 15; rhesus macaques [*Macaca mulatta*]: 16). The benefits of within-group tolerance and prosocial behaviors include lower rates of agonistic interactions, reduced risk of injury, improved access to and sharing of resources, and the transmission of social and ecological information by observing and following conspecifics (10, 17). For example, food-related experimental studies have shown that individuals of more tolerant species tend to succeed more in cooperative tasks than those in less tolerant species (18, 19).

In the wild, foragers are commonly confronted with a range of social and ecological challenges associated with spatial and temporal changes in food availability (distribution and productivity), social relationships, as well as individual differences in nutritional requirements that affect foraging decisions and the degree to which individuals are tolerant or intolerant of conspecifics (14, 20). For example, at larger and more productive feeding sites, tolerance can increase food intake among group members and

reduce the likelihood of aggression that threatens group cohesion. In contrast, higher-ranking foragers are expected to be less tolerant and exclude others from defensible and depletable feeding sites to obtain more food (1, 21, 22).

Maintaining close spatial proximity to group mates who are likely to exhibit a greater predisposition to share resources at a feeding site is a strategy employed by social foragers to reduce opportunities for contest feeding competition (15, 23). Consequently, individuals may develop co-feeding partner preferences based on age, sex, dominance rank, and kinship (23-25). For instance, in some primate species, individuals who share a similar rank position establish stronger bonds and more commonly share feeding sites compared with individuals of more distant social rank positions (e.g., rhesus monkeys [*Macaca mulatta*]: 26; capuchin monkeys [*Sapajus* sp., formerly *Cebus apella*]: 27). Adults can be more tolerant of immature group members who are less efficient and less competitive foragers than other adults (28); young individuals, in turn, can benefit by obtaining food-related information from adults and developing foraging skills (17). In addition, social relationships among group members are dynamic. They can show stability or vary over time in response to changes in ecological and/or social contexts (29, 30). Therefore, assessing the dynamics of foraging associations can help to elucidate decision-making processes and how individuals keep track, manage, and adjust their feeding relationships over time.

Although there has been a considerable interest in investigating the connection between ecological factors and social relationships in primates over the last decades (1, 22, 32), only a limited number of studies had focus on the pattern of foraging associations among group members in the wild (e.g., 23, 33, 34). These studies were mostly conducted with Old World primates, especially Cercopithecidae species (i.e., *Macaca maura*,

*Macaca fuscata yakui*, *Papio ursinus*), characterized by female philopatry and societies structured by matrilineal related individuals. Until the moment, no such empirical study has been conducted in New World primates, limiting our understanding on the associations at feeding sites among group members in these species. Given callitrichines unique social system, they offer a great opportunity to examine how individuals in such cooperative societies interact during a potentially competitive activity, such as foraging.

Therefore, in the current research we conducted an experimental field study of foraging associations in wild common marmosets (*Callithrix jacchus*, Callitrichinae), a species of cooperatively breeding New World primate. Callitrichine primates are distinguished by their cooperative infant caregiving system (also referred to as cooperative breeding system), in which usually a single breeding female can produce two sets of twin infants per year and relies on other group members as helpers, principally adult males, to successfully rear her offspring (35). Helpers carry and provision offspring and there is evidence of a positive correlation between infant survivorship and the number of adult male helpers in the group (36). Reproductive competition among adult females can take several forms including physiological ovulatory suppression, and aggression directed from the breeding female to other female group members (37). However, in free-ranging callitrichines, intragroup agonistic interactions among females are normally rare and between males are practically absent (38).

Common marmosets (*Callithrix jacchus*) live in small groups (3-16 individuals) composed of multiple males and females (39). They occur in the humid Atlantic forest and the semiarid Caatinga scrub forest in northeastern Brazil and exploit a wide range of food items including plant exudates, fruits, flowers, invertebrate and vertebrate prey (40). In the wild, they are attracted to others' food discoveries and can concurrently occupy the

same feeding site as a foraging strategy to obtain access to food resources and improve their feeding success (17, 41).

Here, we investigate how social and ecological factors influence the structure and dynamics of within-group foraging associations (i.e., social tolerance at feeding sites) in wild common marmosets under controlled conditions of food productivity and distribution. Specifically, we asked the following research questions. (RQ1) How does different conditions of food availability and individual's rank, sex, or age influence individual levels of social tolerance at feeding sites (i.e., node degree and node strength, see methods)? (RQ2) Do common marmosets exhibit dyadic foraging partner preferences based on their rank, sex, or age and are these preferences consistent across different conditions of food availability? (RQ3) Is there evidence that individual levels of social tolerance, avoidance events performed, and agonistic events received at a feeding site positively or negatively influence food consumption? (RQ4) Do previous experiences during foraging (strength of foraging associations, avoidance events, agonistic events, and food consumption) affect individuals' (a) and dyads' (b) subsequent levels of social tolerance?

## **2 Methods**

### *2.1 Study site and study groups*

We studied four groups of common marmosets living in the semiarid Caatinga scrublands at the Baracuhy Biological Field Station (7°31'42"S, 36°17'50"W) in the state of Paraíba, northeast of Brazil (see 42 for more information of the study site). Each group (ALG, COQ, PRI, and VAC) was studied for a period of four months and were composed of five to eight individuals at the beginning of the study. Group size and composition

changed throughout the study due to emigrations and immigrations (see Table 1 for details). There were no births during the study. Group members were habituated to the presence of human observers. We individually identified group members by marking adults with colored beaded collars and by shaving different tail segments of juveniles.

**Table 1** Common marmoset study groups' composition and rank position

Groups												
ALG <sup>†</sup>				COQ			PRI			VAC		
Sex	Age	Rank		Sex	Age	Rank	Sex	Age	Rank	Sex	Age	Rank
M <sup>‡</sup>	A	1	-	F <sup>*</sup>	A	1	F <sup>*</sup>	A	1	F <sup>*</sup>	A	1
M <sup>‡</sup>	A	2	-	M	A	2	M <sup>‡</sup>	A	2	M	A	2
F <sup>‡</sup>	A	3	-	M	A	3	M	A	3	M <sup>‡</sup>	A	3
F	A	4	2	M	A	4	F	A	4	M	A	4
F <sup>‡</sup>	A	5	-	M	J	5	F	A	5	M	J	5
F	J/A	6	3	F <sup>¶</sup>	I	-	F	A	6			
F	J/A	7	4	F <sup>¶</sup>	I	-	M <sup>¶</sup>	I	-			
M <sup>§</sup>	A	-	1				M <sup>¶</sup>	I	-			

F: female, M: male. A: adult (>11 months of age), J: juvenile (>4-11 months of age), I: infants (<4 months of age). Rank: ascending order from the most dominant group member (1) to the least dominant group member (according to group size). \*Breeding female. <sup>†</sup> In ALG group, rank was assessed twice due to changes in group size and composition. The breeding female and one adult male left ALG prior the beginning of our experiment (which might explain the instability of the group's composition during the study, see 44). The decrease in ALG size from seven to four individuals resulted from the emigration of two adult males followed by the immigration of a new adult male two days later and the emigration of two adult females. <sup>‡</sup> Individual left the group during the experiment. <sup>§</sup> Individual entered the group during the experiment. <sup>¶</sup> Infants not included in the analyses because they were dependent and did not visit the platforms by themselves during this study.

We assessed group members' social rank using the frequency of agonistic interactions that occurred between dyads. We calculated the Normalized David's Score (NDS; 43) for each group member and constructed a ranking order based on won agonistic interactions; i.e., the higher the frequency of interactions won, the higher the rank (Table 1; see 41 for more details). The single breeding female of COQ, PRI, and VAC occupied the highest rank, followed by adult males, other adult females and juveniles, when present. We assessed the rank twice in ALG because of its changes in

adult composition; adult males occupied the highest ranks, followed by adult females, and juveniles.

## *2.2 Field experiments*

We established an experimental feeding station by placing four wooden feeding platforms (50 cm x 50 cm) in a square arrangement (2.5 m apart from each other) in each study group's home range (see a detailed illustration of the feeding station in 41). We fixed a clear plastic container with an accessible or inaccessible food reward (banana pieces each weighing 3 g) in each platform. Accessible containers had two openings (5 cm x 3 cm) enabling two or more group members to feed and share a platform. Inaccessible containers had small holes and therefore the marmosets were unable to obtain access to the food reward. Using these two types of containers, we could systematically manipulate food distribution at the feeding station.

We conducted five experimental conditions in which food was concentrated (C) on one feeding platform or scattered (S) among three of the four feeding platforms. The amount of food provided at the feeding station could be high (++), medium (+), or low (-). We calculated the amount of food offered to each study group based on its mean daily consumption during a one-week feeding trial (with three daily sessions) conducted prior to beginning the experiments (Table 2). 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 marmosets' daily activity (42), we conducted three experimental sessions per day, at 6:00 am, 10:30 am, and 3:00 pm, resulting in a maximum of 30 sessions per condition (3 sessions per day x 10 days). Food distribution and productivity remained constant throughout each condition. Our experimental design allowed us to simulate conditions of food availability

that are naturally encountered by marmosets in the wild and to observe how marmosets associate with each other when foraging under these conditions.

**Table 2** Description of the experimental conditions with different food distribution (S: scattered, C: concentrated) and productivity (++: high, +: medium, -: low)

<b>Experimental conditions</b>	<b>Description</b>
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 2/3 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 1/3 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 1/2 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.

### 2.3 Data collection

We carried out the experiments with COQ and ALG from July to October 2015 and with PRI and VAC from April to July 2016. Four trained observers collected the behavioral data. In addition, we videotaped all sessions with two Canon Powershot SX50 HS (Canon Inc., Tokyo, Japan) cameras placed 1.5 m from each feeding station. We simultaneously videoed and recorded the behaviors of all group members during the experiments using the “all occurrences” sampling method (45). During each session, we

recorded: all individual platform visits; individual time spent in a platform (in seconds); the amount of food consumed by each group member; the identity of individuals sharing a platform (two 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.

#### *2.4 Social network measures*

Social networks are composed of nodes (actors) and edges (connections between nodes). In this study, we constructed foraging association networks (FANs), in which nodes represent group members and edges represent their foraging associations on a feeding platform (i.e., platform sharing between two individuals, our measure for social tolerance at feeding sites). We considered that two individuals were sharing a platform when they spent  $\geq 3$  s together on it (in 28% of shared platform visits,  $\geq 3$ -10 s was sufficient time for a forager to enter a platform and obtain a reward while in close proximity to a conspecific). Due to our groups' sizes and to the fact that we could reliably identify all individuals throughout the entire experiment, we used two individual-based (node degree and node strength) and one dyad-based (dyad association strength) measures (46) per session to examine social tolerance of common marmosets at feeding sites. Calculating these measures per session allowed us to understand how patterns of association change according to the experimental conditions and over time (temporal network analysis). We defined these measures as follows:

Node degree: the number of group members with which the focal individual was observed sharing a or several platforms during a session (number of associations). Degree can vary from zero (if the individual did not share a platform with any other group



member) to the group size (as a marmoset can share a platform with all other group members) minus one (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 in 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 on a platform during a session with other individual(s).

Dyad association strength: the proportion of time that a dyad shared a platform relative to the total amount of time each member of the dyad spent on a platform during a session. Therefore, 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. It 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.

In addition, we calculated the frequency of avoidance events and the frequency of agonistic events that occurred on a platform during a session. Avoidance occurred when an individual left a feeding platform in response to the presence or arrival of other member to the same platform (in the absence of any detectable agonistic behavior). 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 it took to leave the platform after anticipating a

conspecific's approach. Agonism occurred when an individual directed an aggressive behavior toward another individual on a feeding platform. Agonistic events could be of low intensity (no physical contact, such as agonistic vocalizations or piloerection) or high intensity (physical contact or injury risk, such as attacks, fights, or chases).

## *2.5 Data analysis*

We used Generalized Linear Mixed Models (GLMM) with a Markov Chain Monte Carlo (MCMC) approach to account for the non-independence of network data (47) to answer our research questions. We adjusted GLMMs with Gaussian error distribution, and whenever data was not normally distributed, we used error distributions according to the response variable. We used Poisson distribution for count data and Binomial distribution for proportional data (48). We constructed two GLMMs to assess individual levels of social tolerance during experimental conditions that varied in food availability (RQ1). The first model had node degree as the response variable, and the second had node strength as the response variable. For both models, we used individual's age, sex, rank position, and the experimental conditions, as predictor variables. Groups' identity was included as a random 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 in which the dyad association strength was the response variable to investigate marmosets' foraging partner preferences (RQ2). 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 positions in the group with seven individuals), dyad sex composition (female-female, female-male, male-male), and dyad age composition (adult-adult and adult-juvenile, given that only the ALG group had more

than one juvenile during three experimental conditions, we did not include a juvenile-juvenile level in our analysis). We included group identity as a random effect. We adjusted the model using a Binomial error distribution.

We carried out a GLMM in which the amount of food consumed (banana pieces) by marmosets during a session was the response variable to test if food consumption was affected by individual levels of social tolerance, avoidance and agonistic events (RQ3). Node degree, node strength, the frequency of avoidance events performed, the frequency of agonistic events received, and experimental condition were included as predictor variables. As a random effect, we used individual identity. We adjusted the model with a Gaussian error distribution.

To examine if the previous foraging experience affected subsequent levels of social tolerance, we constructed two GLMMs, one at the individual level (RQ4a), and the second at the dyad level (RQ4b). We used node strength in a given session ( $n$ ) as the response variable for the first model (RQ4a). The predictor variables were node strength, frequency of avoidance events performed, frequency of agonistic events received, and food amount consumed by the individual in the previous session ( $n - 1$ ), as well as the experimental condition. We included individual identity as random effect. In the second model (RQ4b), the dyad association strength of  $n$  was the response variable, while predictor variables were dyad association strength, frequency of avoidance events, and frequency of agonistic events among dyads in  $n-1$ , as well as the experimental condition. Dyad identity was included as random effect. We adjusted both models using a Binomial error distribution.

We conducted all statistical analyses using the R software version 3.5.1 (49). Before constructing the models, we evaluated multicollinearity between predictor factors

by calculating the variance inflation factor (VIF, R package “car”, 50). There was no correlation between predictor variables (all VIF <2; 51). We adjusted all GLMM models using the R package “lme4” (52). For each GLMM, we conducted multi-model inferences to compare and order models according to their Akaike Information Criterion after correction for small sample sizes (AICc) and normalized Akaike weights (AICw) (53). We conducted model selection using the R package “MuMIn” (54). This approach allows formal inference to be based on more than a single best model with the lowest AIC.  $\Delta$ AIC is the AICc difference between a given model and the model with the lowest AICc, while weights indicate the probability of a given model being the best among others. We considered models with a  $\Delta$ AIC <2 as candidate models (following 55) and include all predictor variables present in these candidate models to construct our final models (see model inference in Tables S1 to S6).

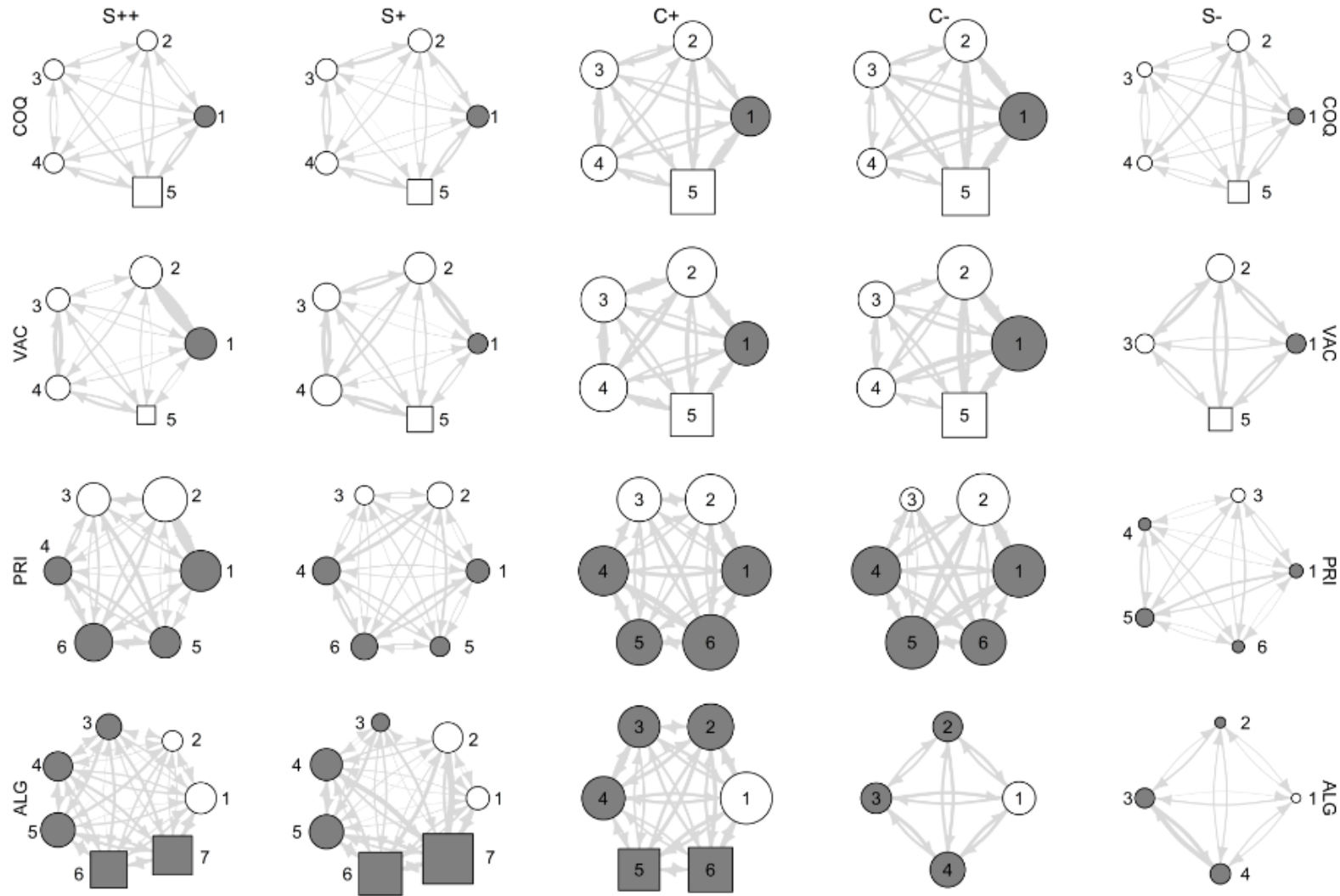
After this model selection, we applied a Markov Chain Monte Carlo (MCMC) approach to our final selected models to determine which predictor variables of the final models were significantly influencing our response variables, using the R package “MCMCglmm” (Bayesian method, 56). This approach is a strong and modern standard technique to compare statistical models based on the original data observed to a distribution of null models based on randomized data (57). 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). We based these parameters by checking the stability of the models. For all models, we assessed for approximate convergence of the MCMC chain (chain stability). We evaluated a final model’s validity by assessing residual distribution through residual

normality distribution plots. The significance level was set at 0.05. The 95% credible intervals are presented according to the Bayesian method we used (MCMCglmm).

This research adhered to the Brazilian laws governing wild animal research (SISBio n°46770-1). The study was approved by the Ethics Committee for Animal Use of the Federal Rural University of Pernambuco (CEUA n° 144/2014).

### **3 Results**

On average, group members participated in  $25 \pm 5$  out of a maximum of 30 sessions per experimental condition (Fig. 1). Common marmosets shared feeding platforms in  $81 \pm 15\%$  of these sessions, from which we recorded 5,407 shared platform visits by dyads. During these sessions, individuals shared platforms with 1 to 6 group members (depending on the maximum number of individuals in each group; most frequently observed [mode]: 2 individuals). Time spent sharing a platform ranged from 3 to 606 s (mean  $\pm$  SD:  $73 \pm 75$  s). During these shared visits, 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). 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 S7).



**Fig. 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, gray = females. Each individual (node) is identified by its rank position number. The links (edges) between individuals are dyadic associations. The size of nodes depends of node strength and the thickness of links depends on dyad association strength, with stronger associations indicated by thicker ties. Graphs were created using R package “igraph” (58).

### 3.1 Individual levels of social tolerance (RQ1)

Node degree was influenced by experimental condition and individual age, but not by individual rank or sex (Table 3). 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 (mode: C+: 4 individuals and C-: 3 individuals), and lowest under the condition in which a low amount of food was distributed on three platforms (mode: S-: 1 individual). In addition, juveniles shared a platform during a session with a greater number of group members than did adults (overall mode: juveniles: 3 individuals; adults: 2 individuals).

**Table 3** Results of the final model with node degree as the response variable to address RQ1. Estimates of posterior means and 95% credible intervals (CI) for the predictor variables reported. Significant p-MCMC ( $\leq 0.05$ ) values are in bold (MCMC: Markov Chain Monte Carlo)

Predictor variables	Posterior mean	Lower 95% CI	Upper 95% CI	p-MCMC
Intercept	0.44	0.23	0.68	<b>0.012</b>
Condition S+	-0.12	-0.33	0.08	0.26
Condition C+	0.34	0.13	0.54	<b>&lt;0.001</b>
Condition C-	0.35	0.14	0.56	<b>0.002</b>
Condition S-	-0.32	-0.54	-0.10	<b>0.002</b>
Sex (Male)	-0.20	-0.42	0.01	0.08
Age (Juvenile)	0.21	0.05	0.38	<b>0.01</b>
Rank	-0.01	-0.05	0.01	0.37
Condition S+:Sex (Male)	0.01	-0.24	0.31	0.94
Condition C+:Sex (Male)	0.28	0.002	0.58	0.08
Condition C-:Sex (Male)	0.14	-0.13	0.45	0.34
Condition S-:Sex (Male)	0.14	-0.21	0.43	0.36

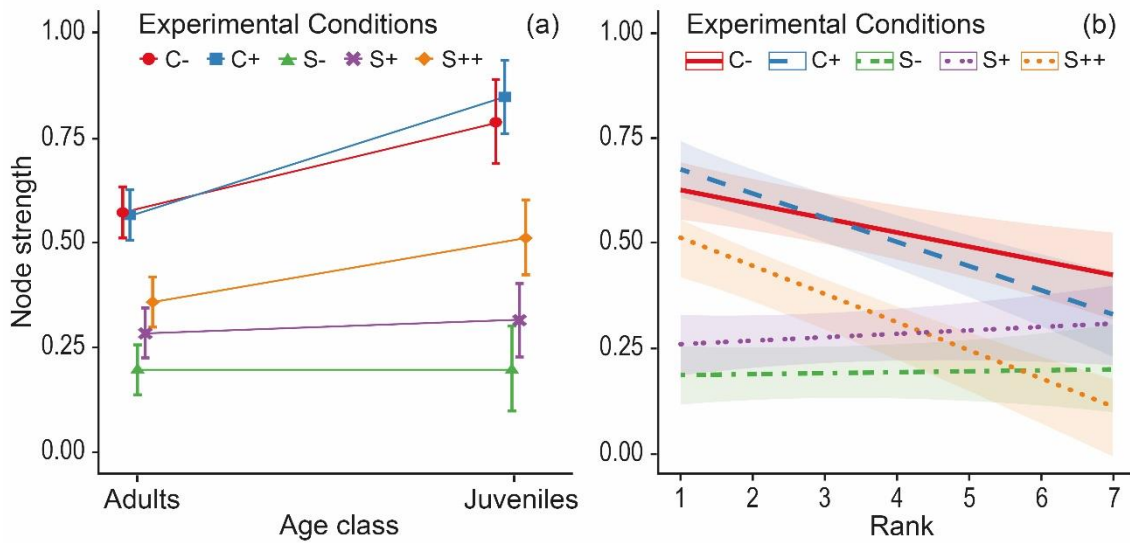
Node strength was affected by experimental condition, age, rank, and sex, as well as by the interactions between experimental condition and age, between experimental condition and rank, and between experimental condition and sex (Table 4). The proportion of time individuals shared a platform with other(s) during a session was higher

under conditions in which food was concentrated on a single platform (mean  $\pm$  SD: C+:  $0.59 \pm 0.32$  and C-:  $0.58 \pm 0.32$ ), and lower when food was scattered across three platforms (mean  $\pm$  SD: S++:  $0.35 \pm 0.31$ , S+:  $0.28 \pm 0.26$ , and S-:  $0.18 \pm 0.20$ ). Overall, juveniles presented a higher node strength than did adults; while rank was negatively related to node strength (Table 4). In addition, as revealed by the interaction effects, node strength varied according to individual age, rank, and sex among experimental conditions (as illustrated in Fig. 2a and Fig. 2b).

**Table 4** Results of the final model with node strength as the response variable to address RQ1. Estimates of posterior means and 95% credible intervals (CI) for the predictor variables reported. Significant p-MCMC ( $\leq 0.05$ ) values are in bold (MCMC: Markov Chain Monte Carlo)

Predictor variables	Posterior mean	Lower 95% CI	Upper 95% CI	p-MCMC
Intercept	-0.61	-0.99	-0.18	<b>&lt;0.001</b>
Condition S+	-1.59	-2.13	-1.13	<b>&lt;0.001</b>
Condition C+	0.16	-0.33	0.65	0.52
Condition C-	0.07	-0.44	0.50	0.75
Condition S-	-2.00	-2.52	-1.55	<b>&lt;0.001</b>
Age (Juvenile)	0.98	0.60	1.41	<b>&lt;0.001</b>
Rank	-0.32	-0.41	-0.23	<b>&lt;0.001</b>
Sex (Male)	-0.46	-0.72	-0.21	<b>0.002</b>
Condition S+: Age (Juvenile)	-0.84	-1.39	-0.30	<b>0.004</b>
Condition C+: Age (Juvenile)	0.16	-0.42	0.70	0.56
Condition C-: Age (Juvenile)	-0.22	-0.82	0.41	0.49
Condition S-: Age (Juvenile)	-0.86	-1.49	-0.20	<b>0.006</b>
Condition S+: Rank	0.38	0.26	0.51	<b>&lt;0.001</b>
Condition C+: Rank	0.07	-0.06	0.20	0.29
Condition C-: Rank	0.20	0.08	0.35	<b>&lt;0.001</b>
Condition S-: Rank	0.34	0.21	0.48	<b>&lt;0.001</b>
Condition S+: Sex (Male)	0.26	-0.09	0.58	0.128
Condition C+: Sex (Male)	0.65	0.34	1.00	<b>&lt;0.001</b>
Condition C-: Sex (Male)	0.33	-0.06	0.70	0.09
Condition S-: Sex (Male)	0.29	-0.08	0.67	0.15





**Fig. 2** Estimated node strength (proportion of time individuals spent sharing a platform with other(s) during a session) and standard error for adults and juveniles during each experimental condition **(a)**, and for individuals of different ranks (ascending order from the most to the least dominant group member) during each experimental condition **(b)**

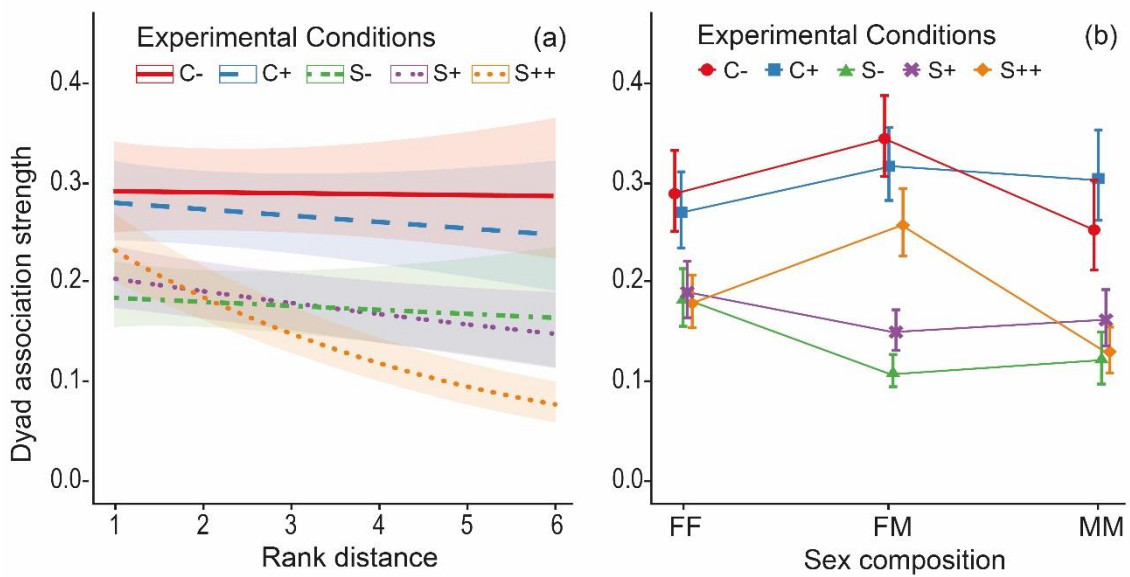
### 3.2 Partner preferences (RQ2)

When examining evidence of foraging partner preferences, dyad association strength was influenced by experimental condition, dyad's rank distance, sex composition, and age composition, as well as by the interactions between experimental condition and both rank distance and sex composition (Table 5). The proportion of time a dyad shared a feeding platform during a session was lower during all three conditions in which food was scattered (mean  $\pm$  SD: S++:  $0.21 \pm 0.20$ , S+:  $0.18 \pm 0.17$ , S-:  $0.13 \pm 0.17$ ), than when food was concentrated (mean  $\pm$  SD: C+:  $0.31 \pm 0.23$ , C-:  $0.33 \pm 0.26$ ). Overall, rank distance was negatively related to dyad association strength (dyads with closer rank positions spent more time together on a feeding platform than dyads composed of individuals of distant ranks; Table 5). However, as revealed by the interaction effects, this relationship was most evident in S++ than in all other conditions (Fig. 3a), indicating that individuals of different rank distances shared feeding platforms at similar levels.

Regarding the sex composition, the overall dyad association strength was highest for female-male dyads, followed by female-female dyads and lowest for male-male dyads (Table 5), but dyad association strength varied between experimental conditions without a clear pattern (Fig. 3b). Regarding dyad age composition, adult-adult dyad association strength was lower than that of adult-juvenile dyad association strength consistently throughout experimental conditions (no interaction; Table 5).

**Table 5** Results of the final model with dyad association strength as the response variable to address RQ2. Estimates of posterior means and 95% credible intervals (CI) for the predictor variables reported. Significant p-MCMC ( $\leq 0.05$ ) values are in bold (MCMC: Markov Chain Monte Carlo)

Predictor variables	Posterior mean	Lower 95% CI	Upper 95% CI	p-MCMC
Intercept	-1.82	-2.12	-1.47	< <b>0.001</b>
Condition S+	-0.30	-0.53	-0.08	<b>0.004</b>
Condition C+	0.11	-0.11	0.31	0.27
Condition C-	0.18	-0.04	0.43	0.11
Condition S-	-0.58	-0.84	-0.30	< <b>0.001</b>
Age (Adult-Juvenile)	0.24	0.92	0.40	<b>0.002</b>
Rank difference	-0.23	-0.29	-0.18	< <b>0.001</b>
Sex (Female-Male)	0.42	0.27	0.57	< <b>0.001</b>
Sex (Male-Male)	-0.33	-0.51	-0.15	< <b>0.001</b>
Condition S+: Age (A-J)	0.10	-0.11	0.33	0.35
Condition C+: Age (A-J)	-0.12	-0.32	0.07	0.22
Condition C-: Age (A-J)	0.13	-0.09	0.39	0.25
Condition S-: Age (A-J)	0.02	-0.27	0.33	0.91
Condition S+: Rank difference	0.18	0.09	0.25	< <b>0.001</b>
Condition C+: Rank difference	0.22	0.14	0.29	< <b>0.001</b>
Condition C-: Rank difference	0.21	0.13	0.31	< <b>0.001</b>
Condition S-: Rank difference	0.20	0.09	0.30	< <b>0.001</b>
Condition S+: Sex (F-M)	-0.66	-0.90	-0.46	< <b>0.001</b>
Condition C+: Sex (F-M)	-0.20	-0.41	0.01	0.09
Condition C-: Sex (F-M)	-0.21	-0.41	0.01	0.08
Condition S-: Sex (F-M)	-0.70	-0.94	-0.46	< <b>0.001</b>
Condition S+: Sex (M-M)	0.27	0.02	0.50	<b>0.024</b>
Condition C+: Sex (M-M)	0.51	0.28	0.74	< <b>0.001</b>
Condition C-: Sex (M-M)	0.11	-0.17	0.36	0.42
Condition S-: Sex (M-M)	-0.02	-0.33	0.30	0.89



**Fig. 3** Estimated 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 composition (FF: female-female, FM: female-male, MM: male-male) during each experimental condition **(b)**

### 3.3 Food consumption and levels of social tolerance (RQ3)

When investigating if individual levels of social tolerance influence food consumption, we found a positive relationship between node degree and amount of food consumed. However, food consumption was negatively related to node strength and positively related to the frequency of avoidance events (Table 6). In addition, as expected food consumption was directly influenced by the experimental conditions, depending on the amount of food offered in each condition. The frequency of agonistic events was not selected as a predictor variable for food consumption during model inference (see Table S4).

**Table 6** Results of the final model with food consumption as the response variable to address RQ3. Estimates of posterior means and 95% credible intervals (CI) for the predictor variables reported. Significant p-MCMC ( $\leq 0.05$ ) values are in bold (MCMC: Markov Chain Monte Carlo)

Predictor variables	Posterior mean	Lower 95% CI	Upper 95% CI	p-MCMC
Intercept	4.38	4.04	4.80	<b>&lt;0.001</b>
Node degree	0.13	0.08	0.19	<b>&lt;0.001</b>
Node strength	-0.28	-0.51	-0.04	<b>0.018</b>
Avoidance events	0.14	0.06	0.23	<b>0.004</b>
Condition S+	-0.47	-0.64	-0.30	<b>&lt;0.001</b>
Condition C+	-0.32	-0.49	-0.14	<b>0.002</b>
Condition C-	-2.16	-2.33	-1.94	<b>&lt;0.001</b>
Condition S-	-2.28	-2.47	-2.10	<b>&lt;0.001</b>

### 3.4 Previous foraging experience on subsequent levels of social tolerance (RQ4)

At the individual-based level, we found that node strength in a previous session positively affected node strength in a subsequent session (Table 7a), while avoidance events performed, agonistic events received, and food consumed by the individual during a previous session did not. Similarly, at a dyad-based level, only the dyad association strength of the previous session positively affected the dyad association strength during the subsequent session (Table 7b). Even though the frequency of avoidance and agonistic events among dyads during previous sessions were selected as predictor variables during model inference, they did not have a significant influence on the next dyad association strength.

**Table 7** Results of the final models with (a) node strength and (b) dyad association strength on a session as the response variables to address RQ4. Estimates of posterior means and 95% credible intervals (CI) for the predictor variables reported. Significant p-MCMC ( $\leq 0.05$ ) values are in bold (MCMC: Markov Chain Monte Carlo)

<b>Response variable</b>	<b>Predictor variables</b>	<b>Posterior mean</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>	<b>p-MCMC</b>
(a) Node strength	Intercept	-2.10	-2.37	-1.85	<b>&lt;0.001</b>
	Previous node strength	0.04	0.05	0.19	<b>&lt;0.001</b>
	Previous food consumption	0.03	-0.01	0.06	0.13
	Previous avoidance freq.	0.04	-0.05	0.13	0.42
	Previous aggression freq.	-0.01	-0.07	0.04	0.70
	Condition S+	-0.16	-0.33	0.01	0.08
	Condition C+	0.83	0.64	1.01	<b>&lt;0.001</b>
	Condition C-	0.89	0.69	1.11	<b>&lt;0.001</b>
Condition S-	-0.66	-0.88	-0.44	<b>&lt;0.001</b>	
(b) Dyad association strength	Intercept	-2.31	-2.41	-2.23	<b>&lt;0.001</b>
	Previous dyad association strength	0.87	0.75	0.99	<b>&lt;0.001</b>
	Previous avoidance freq.	-0.01	-0.07	0.06	0.83
	Previous aggression freq.	-0.01	-0.06	0.03	0.53
	Condition S+	-0.05	-0.14	0.04	0.22
	Condition C+	0.52	0.43	0.60	<b>&lt;0.001</b>
	Condition C-	0.49	0.40	0.58	<b>&lt;0.001</b>
	Condition S-	-0.45	-0.56	-0.35	<b>&lt;0.001</b>

#### 4 Discussion

In this experimental field study, we used social network analysis to examine foraging associations in wild common marmosets and investigate how social (rank, sex, age) and ecological factors (food distribution and productivity) influence within-group social tolerance. We found that associations were stronger (i.e. there were more associations and they lasted longer) when food was concentrated at a single feeding site regardless of whether that feeding site had small or medium amounts of food. At an individual-based level (node strength), both juveniles and higher-ranking marmosets associated for longer periods than did adults and lower-ranking group members, respectively, while no differences were found among sexes. Concordantly, at a dyadic-based level (dyad association strength) adult-juvenile dyads formed the strongest and

most consistent foraging partner preferences. However, associations among dyads composed of individuals of different rank and sex varied across experimental conditions. In general, individuals used different socially mediated behavioral strategies related to with whom, with how many individuals, and for how long to associate in a feeding site during a session to obtain and consume food rewards. Over time, the levels of social tolerance were modulated by the strength of previous foraging associations, but not previous avoidance and agonistic events at the experimental feeding platforms.

The socioecological model predicts that competition over scarce or limited food resources is a major cost of group living. The ability of certain group members to monopolize access to clumped and easily defensible resources is reported to result in increased levels of contest competition and high within-group variance in feeding success in several primate species (e.g., *Macaca fuscata*: 21; *Chlorocebus aethiops*, formerly *Cercopithecus aethiops*: 59; *Sapajus apella*, formerly *Cebus apella*: 60; *Cebus capucinus*: 61). However, we found that common marmosets associated with more group members and for a greater proportion of time when food was concentrated on a single platform, regardless of the amount of food available. This contradicts expectations of increased contest competition at monopolizable feeding sites (1). Moreover, under conditions in which food was scattered and individuals could feed on platforms not occupied by other group members, they continued to share feeding sites with others, although to a lesser extent than when only one of four platforms contained accessible food. Sharing feeding sites under conditions in which food is scattered could benefit all participants as a type of interaction that reinforces social bonds analogous to grooming (23) or alternatively represent a form of risk-sensitive foraging if co-feeders engage in cooperative vigilance against the threat of predators (62). As small-bodied primates (adult body mass

approximately 320 g; 63), common marmosets are susceptible to a range of aerial and arboreal predators, such as hawks and snakes (38).

The lowest strengths of foraging associations (i.e., social tolerance) occurred under conditions in which feeding sites could be quickly depleted and therefore the opportunities for feeding were limited. Higher-ranking marmosets (in our study groups the breeding female was the highest ranked individuals) were tolerant of lower-ranking individuals and shared feeding sites under conditions that, in other primate species, commonly results in contest feeding competition. In the absence of data on paternity, as each of a female's twin offspring can be sired by a different male (64, 65), tolerance at feeding sites by higher-ranking marmosets can be related to the cooperative infant caregiving system that characterizes common marmosets. In cooperatively breeding species, helpers are essential for offspring survival (66). Consequently, breeding individuals profit by forming close bonds with conspecifics whose efforts contribute to the group's reproductive success. Therefore, tolerance at feeding sites can serve as a mechanism of social reward to maintain helpers in the group (67).

We also found that juveniles associated with more group members (node degree) and for longer time (node strength) than adults did. Moreover, when investigating partner preferences (i.e., with whom individuals associated more during foraging, dyad association strength), dyads composed by an adult and a juvenile shared a feeding site for longer time than dyads composed by two adults, independent of food availability. This strengthens the idea that caregiving results in younger marmosets being tolerated by most or all other group members (breeding and non-breeding caretakers) (68). Callitrichine infants and juveniles usually associate and interact with older individuals during foraging to ensure access to hard to get and/or process resources and the adequate nutrition for

survival and growth (69), while also acquiring food-related and social information to gradually acquire proper competence to safely explore such resources (17, 70).

The trend we found of sharing a platform with a partner of closer rank was evident when a high amount of food was scattered. In all other conditions, group members were as likely to associate with most closely ranked individuals as they were with individuals of distant rank, supporting the importance of social tolerance to group cohesion and social stability in this species. Similarly, there was no evidence of a strong or consistent pattern of social tolerance between a particular sex composition dyad across all experimental conditions. Rather, foraging associations of dyads composed of either one or both sexes varied without a clear pattern between different contexts of food availability. Such absence of a strong sex related partner preference would not be expected among primates characterized as monogamous or pair bonded (71), but it is consistent with recent studies suggesting that common marmosets and other callitrichines are best described as exhibiting a non-monogamous single female breeding system (65). In addition, these findings suggest that social tolerance occurs at the group level (all group members are tolerant to each other) and can represent a social strategy in which individual marmosets adjust their foraging partner choices and regulate the intensity of their associations based on the current ecological context. Given that the number and strength of social bonds an individual maintains with other group members (i.e., the structure of the social network) can influence group stability, coordination, and cohesion (72), small group size presents the opportunity for all group members to build strong social relationships (72). The ability of marmosets and their close relatives, the tamarins (*Leontocebus*, *Saguinus*, and *Leontopithecus*), to establish and maintain strong associations and prosocial bonds among



all or most group members serve to increase opportunities for cooperative behavior and offspring survivorship (68).

Marmosets were able to make foraging decisions by using a range of behavioral patterns to obtain and consume food during feeding opportunities. These could be described as (i) individuals jointly occupied a platform and after one marmoset obtained and was consuming a food reward (banana slice) from the experimental container, the other individual would reach into the container to obtain a food reward and consume it or, (ii) one individual would occupy a platform and after obtaining a food reward could quickly leave the platform to consume the food item elsewhere (usually in trees nearby the feeding station). This strategy can enable group members to obtain food on the same platform and avoid potential agonistic encounters. Given that infant and juvenile common marmosets are reported to steal food (also called tolerated theft or tolerated scrounging; 73) from adult caretakers, consuming food 1 to 2 m away from the other group members may allow helpers to increase their feeding success. Or, (iii) a marmoset could remain on the platform for some extended period of time and consume food alone. These alternative strategies were found to be used by all group members and can allow individuals to balance the potential costs of feeding competition and the benefits of participating in associations that can improve access to resources (15, 16, 41).

Finally, we found that the proportion of time marmosets spent sharing a feeding site during a previous foraging session positively influenced the proportion of time they shared a feeding site in their subsequent foraging session. It seems that the strength of past foraging associations can mediate future levels of social tolerance at feeding sites and individuals may be able to track their foraging relationships with other group members over time (25, 29, 30). In our study groups, most agonistic interactions (65%)

were of low intensity (i.e., without physical contact and injury risk), such as agonistic vocalizations. These kinds of interactions, along with active avoidance, possibly serve as pre-conflict mechanisms to prevent the escalation of conflicts into potentially costly attacks or fights (74). It has been suggested that due to the cohesive and cooperative tendencies of marmosets and tamarins, “everyday” conflicts do not disturb their highly valuable and codependent relationships (75).

In conclusion, by using an experimental approach, we were able to quantitatively assess association patterns and social tolerance during foraging in free-ranging common marmoset groups under controlled conditions of food distribution and productivity. The cooperative breeding and cooperative infant caregiving system found in callitrichines is rare in mammals (e.g., marmots: 76; meerkats: 77; African wild dogs: 78) although common in a variety of bird species (79). This system requires that individuals maintain strong social relationships to engage in spatially and temporally coordinated behaviors in order to protect, transport and provision food for the young (66). As a cooperative species, common marmoset group members establish strong social bonds and high cohesion. Breeding individuals require helpers to successfully rear their offspring and enhance their reproductive success. Hence, they are tolerant of conspecifics at feeding sites and in other social contexts. In turn, non-breeding individuals can benefit from the joint or coordinated activities of conspecifics such as predator vigilance and territory defense. Moreover, by remaining in a group as helpers, nonbreeding individuals can also benefit by acquiring and accumulating experience in infant care needed if they ascend to occupy a breeding position (67). Therefore, social tolerance is crucial to promote group cohesion, and plays an important role in the cooperative infant caregiving in common marmosets. Given the complexity and variety of animal societies, field experiments and social network analyses

serve as important empirical instruments to systematically identify the patterns, quality, structure, and dynamics of social relationships. This approach allows researchers to manipulate and control certain ecologically relevant variables to investigate social behaviors that are rare, difficult to observe or quantify in the wild and can be applied to species with different social systems to achieve a comparative perspective.

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Supplementary Material

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

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**Table S1.** Model selection table for predictor factors influence on the node degree. Models are ranked according to the best AIC. In bold, candidate models retained.

Model	(Int)	Age	Exp. cond	Rank	Sex	Age:Exp con.	Rank: Exp. con	Sex: Exp con	df	logLik	AICc	ΔAIC	weight
<b>76</b>	<b>0.6777</b>	+	+		+			+	<b>12</b>	<b>-4383.7</b>	<b>8791.6</b>	<b>0.00</b>	<b>0.421</b>
<b>80</b>	<b>0.7011</b>	+	+	<b>-0.0073</b>	+			+	<b>13</b>	<b>-4383.4</b>	<b>8793.1</b>	<b>1.52</b>	<b>0.197</b>
12	0.6157	+	+		+				8	-4389.5	8795.2	3.60	0.070
92	0.6601	+	+		+	+		+	16	-4381.7	8795.7	4.10	0.054
112	0.5885	+	+	0.0213	+		+	+	17	-4380.7	8795.7	4.18	0.052
128	0.5913	+	+	0.0205	+	+	+	+	21	-4377.0	8796.4	4.89	0.036
16	0.6301	+	+	-0.0047	+				9	-4389.4	8797.0	5.40	0.028
96	0.6837	+	+	-0.0074	+	+		+	17	-4381.4	8797.2	5.61	0.026
4	0.5783	+	+						7	-4391.5	8797.2	5.66	0.025
48	0.5073	+	+	0.0295	+		+		13	-4385.6	8797.5	5.91	0.022
64	0.4963	+	+	0.0334	+	+	+		17	-4381.6	8797.5	5.96	0.021
8	0.5899	+	+	-0.0039					8	-4391.5	8799.1	7.53	0.010
56	0.4556	+	+	0.0350		+	+		16	-4383.4	8799.2	7.62	0.009
40	0.4646	+	+	0.0310			+		12	-4387.6	8799.4	7.79	0.009
28	0.5969	+	+		+	+			12	-4387.6	8799.5	7.90	0.008
32	0.6117	+	+	-0.0048	+	+			13	-4387.5	8801.3	9.70	0.003
20	0.5592	+	+			+			11	-4389.6	8801.4	0.81	0.003
79	0.6468		+	0.0140	+			+	12	-4389.4	8803.0	11.45	0.001
24	0.5714	+	+	-0.0042		+			12	-4389.5	8803.2	11.68	0.001
75	0.7001		+		+			+	11	-4390.8	8803.8	12.29	0.001
111	0.5237		+	0.0455	+		+	+	16	-4386.9	8806.0	14.48	0.000
15	0.5745		+	0.0163	+				8	-4395.1	8806.4	14.89	0.000
7	0.5462		+	0.0167					7	-4396.4	8806.9	15.33	0.000
47	0.4425		+	0.0532	+		+		12	-4391.5	8807.1	15.59	0.000
39	0.4129		+	0.0542			+		11	-4392.6	8807.4	15.81	0.000
11	0.6322		+		+				7	-4397.1	8808.3	16.79	0.000
3	0.6042		+						6	-4398.4	8808.9	17.35	0.000
14	0.7700	+		-0.0149	+				5	-4564.2	9138.6	347.04	0.000
10	0.7280	+			+				4	-4565.3	9138.6	347.07	0.000

2	0.6936	+							3	-4567.2	9140.4	348.88	0.000
6	0.7348	+		-0.0149					4	-4566.2	9140.5	348.94	0.000
9	0.7432				+				3	-4573.9	9153.9	362.38	0.000
13	0.7059			0.0113	+				4	-4573.0	9154.0	362.48	0.000
1	0.7183								2	-4575.1	9254.2	362.65	0.000
5	0.6807			0.0115					3	-4574.1	9154.2	362.68	0.000

**Table S2.** Model selection table for predictor factors influence on the node strength. Models are ranked according to the best AIC. In bold, candidate models retained.

Model	(Int)	Age	Exp. cond	Rank	Sex	Age:Exp con.	Rank: Exp. con	Sex: Exp con	df	logLik	AICc	ΔAIC	weight
<b>128</b>	<b>-0.3479</b>	+	+	<b>-0.18430</b>	+	+	+	+	<b>21</b>	<b>-42592.89</b>	<b>85228.1</b>	<b>0.00</b>	<b>1</b>
112	-0.3731	+	+	-0.17280	+		+	+	17	-42821.35	85676.9	448.80	0
64	-0.4737	+	+	-0.16930	+	+	+		17	-43043.86	86121.9	893.82	0
56	-0.5080	+	+	-0.16870		+	+		16	-43079.81	86191.8	963.70	0
96	-0.6853	+	+	-0.08224	+	+		+	17	-43274.96	86584.1	1356.02	0
111	-0.4678		+	-0.12810	+		+	+	16	-43320.22	86672.6	1444.52	0
48	-0.4949	+	+	-0.15.530	+		+		13	-43509.36	87044.9	1816.74	0
80	-0.7374	+	+	-0.08276	+			+	13	-43553.56	87133.2	1905.12	0
40	-0.5358	+	+	-0.15390			+		12	-43557.00	87138.1	1909.99	0
32	-0.7428	+	+	-0.07838	+	+			13	-43720.07	87466.3	2238.16	0
24	-0.7747	+	+	-0.07784		+			12	-43751.37	87526.9	2298.73	0
92	-0.9513	+	+		+	+		+	16	-43870.96	87774.1	2545.99	0
47	-0.5833		+	-0.11640	+		+		12	-43883.39	87790.9	2562.77	0
39	-0.6202		+	-0.11550			+		11	-43923.46	87869.0	2640.89	0
79	-0.8432		+	-0.03488	+			+	12	-44083.55	88191.2	2963.09	0
16	-0.7725	+	+	-0.07855	+				9	-44150.81	88319.7	3091.57	0
76	-1.0080	+	+		+			+	12	-44157.39	88338.9	3110.77	0
8	-0.8071	+	+	-0.07792					8	-44189.83	88395.7	3167.58	0
75	-0.9803		+		+			+	11	-44256.96	88536.0	3307.89	0
28	-0.9843	+	+		+	+			12	-44264.04	88552.2	3324.07	0
20	-1.0110	+	+			+			11	-44287.42	88596.9	3368.81	0
15	-0.8707		+	-0.03608	+				8	-44557.55	89131.2	3903.03	0
7	-0.9125		+	-0.03569					7	-44591.11	89196.3	3968.14	0
12	-1.0180	+	+		+				8	-44698.17	89412.4	4184.26	0
4	-1.0470	+	+						7	-44727.91	89469.9	4241.73	0
11	-1.0020		+		+				7	-44747.88	89509.8	4281.67	0
3	-1.0310		+						6	-44777.36	89566.7	4338.62	0
14	-0.6497	+		-0.10000	+				5	-50898.82	101807.7	16579.53	0
6	-0.6665	+		-0.09971					4	-50908.40	101824.8	16596.69	0

13	-0.7555		-0.05138	+					4	-51448.22	102904.5	17676.33	0
5	-0.7685		-0.05126						3	-51454.08	102914.2	17686.04	0
10	-0.9404	+		+					4	-51824.02	103656.1	18427.93	0
2	-0.9513	+							3	-51828.30	103662.6	18434.48	0
9	-0.9299			+					3	-51854.06	103714.1	18486.01	0
1	-0.9405								2	-51858.08	103720.2	18492.03	0

**Table S3.** Model selection table for predictor factors influence on the edge or dyad association strength. Models are ranked according to the best AIC. In bold, candidate models retained.

Model	(Int)	Exp. cond	Rank difference	Age comp.	Sex comp.	Exp con.:Rank dif	Exp. con:Age comp	Exp con: Sex comp	df	logLik	AICc	ΔAIC	weight
<b>128</b>	<b>-1.0260</b>	+	<b>-0.38440</b>	+	+	+	+	+	<b>26</b>	<b>-79109.97</b>	<b>158272.2</b>	<b>0.00</b>	<b>0</b>
96	-1.0030	+	-0.36440	+	+	+		+	22	-79382.96	158810.1	537.90	0
92	-0.9753	+	-0.33230		+	+		+	21	-79774.84	159591.8	1319.64	0
112	-1.2800	+	-0.15240	+	+		+	+	22	-81216.69	162477.6	4205.37	0
80	-1.3640	+	-0.15240	+	+			+	18	-81566.96	163170.0	4897.84	0
76	-1.3430	+	-0.11250		+			+	17	-82060.33	164154.8	5882.57	0
64	-0.9590	+	-0.29860	+	+	+	+		18	-82409.72	164855.6	6583.36	0
32	-0.9707	+	-0.31310	+	+	+			14	-82721.37	165470.8	7198.61	0
28	-0.9613	+	-0.28950		+	+			13	-82956.53	165939.1	7666.93	0
110	-1.4680	+		+	+		+	+	21	-83056.97	166156.1	7883.91	0
56	-1.0350	+	-0.28030	+		+	+		16	-83085.47	166203.0	7930.84	0
24	-1.0470	+	-0.29330	+		+			12	-83431.25	166886.5	8614.35	0
74	-1.5520	+			+			+	16	-83431.15	166894.4	8622.20	0
78	-1.5530	+		+	+			+	17	-83431.08	166896.3	8624.07	0
20	-1.0410	+	-0.28500			+			11	-83476.98	166976.0	8703.81	0
48	-1.1660	+	-0.15120	+	+		+		14	-83983.06	167994.2	9722.01	0
16	-1.2470	+	-0.15250	+	+				10	-84749.13	169518.3	11246.11	0
40	-1.2980	+	-0.12120	+			+		12	-84829.47	169683.0	11410.79	0
12	-1.2450	+	-0.12320		+				9	-85017.52	170053.1	11780.88	0
8	-1.3830	+	-0.12200	+					8	-85631.17	171278.4	13006.16	0
4	-1.3790	+	-0.11110						7	-85692.68	171399.4	13127.18	0
46	-1.3820	+		+	+		+		13	-85821.55	171669.2	13396.98	0
38	-1.4990	+		+			+		11	-86203.54	172429.1	14156.94	0
14	-1.4620	+		+	+				9	-86635.38	173288.8	15016.60	0
10	-1.4810	+			+				8	-86679.93	173375.9	15103.69	0
6	-1.5810	+		+					7	-87037.83	174089.7	15817.48	0
2	-1.6100	+							6	-87124.95	174261.9	15989.71	0
15	-1.1700		-0.13800	+	+				6	-90449.94	180528.7	22256.48	0



11	-1.1770		-0.11370		+				5	-90449.94	180909.9	22637.69	0
7	-1.2790		-0.10620	+					4	-91054.80	182117.6	23845.42	0
3	-1.2790		-0.09987						3	-91076.55	182159.1	23886.92	0
13	-1.3760			+	+				5	-91838.22	183686.4	25414.25	0
9	-1.3930				+				4	-91890.98	183790.0	25517.77	0
5	-1.4600			+					3	-92146.70	184299.4	26027.21	0
1	-1.4870								2	-92256.78	184517.6	26245.36	0

**Table S4.** Model selection table for predictor factors influence on the food consumption. Models are ranked according to the best AIC. In bold, candidate models retained.

Model	(Int)	Aggression	Avoidance	Exp. condition	Node degree	Node strength	df	logLik	AICc	ΔAIC	weight
<b>31</b>	<b>4.402</b>		<b>0.1468000</b>	+	<b>0.13780</b>	<b>-0.28030</b>	<b>10</b>	<b>-4567.491</b>	<b>9155.1</b>	<b>0.00</b>	<b>0.502</b>
<b>15</b>	<b>4.369</b>		<b>0.1592000</b>	+	<b>0.09923</b>		<b>9</b>	<b>-4568.899</b>	<b>9155.9</b>	<b>0.80</b>	<b>0.336</b>
29	4.402			+	0.16450	-0.32680	9	-4570.411	9158.9	3.83	0.074
32	4.395	-0.038980	0.1537000	+	0.14420	-0.26990	11	-4569.238	9160.6	5.51	0.032
16	4.363	-0.043280	0.1663000	+	0.10790		10	-4570.451	9161.0	5.92	0.026
13	4.364			+	0.12150		8	-4572.777	9161.6	6.54	0.019
7	4.538		0.2059000	+			8	-4574.016	9164.1	9.02	0.006
30	4.397	-0.027570		+	0.16990	-0.32090	10	-4572.577	9165.2	10.17	0.003
14	4.359	-0.031630		+	0.12850		9	-4574.809	9167.7	12.62	0.001
23	4.525		0.2051000	+		0.03701	9	-4575.312	9168.7	13.63	0.001
8	4.540	-0.013670	0.2094000	+			9	-4576.517	9171.1	16.04	0.000
24	4.524	-0.016170	0.2091000	+		0.04738	10	-4577.757	9175.6	20.53	0.000
5	4.582			+			7	-4582.558	9179.2	24.09	0.000
21	4.561			+		0.05962	8	-4583.747	9183.6	28.48	0.000
6	4.580	0.009303		+			8	-4585.126	9186.3	31.24	0.000
22	4.561	0.006330		+		0.05540	9	-4586.325	9190.7	35.65	0.000
10	3.416	-0.152900			0.19400		5	-4979.497	9969.0	813.95	0.000
26	3.422	-0.151000			0.20680	-0.08346	6	-4980.381	9972.8	817.73	0.000
12	3.415	-0.155100	0.0284700		0.19040		6	-4981.359	9974.8	819.68	0.000
28	3.420	-0.153200	0.0249800		0.20250	-0.07605	7	-4982.270	9978.6	823.51	0.000
9	3.421				0.15420		4	-4986.745	9981.5	826.44	0.000
25	3.431				0.17560	-0.13510	5	-4987.328	9984.7	829.61	0.000
11	3.421		-0.0005643		0.15430		5	-4988.751	9987.5	832.46	0.000
27	3.432		-0.0061910		0.17680	-0.13670	6	-4989.322	9990.7	835.61	0.000
18	3.622	-0.107800				0.41210	5	-4995.699	10001.4	846.35	0.000
20	3.599	-0.120500	0.1050000			0.40000	6	-4995.740	10003.5	848.44	0.000
17	3.607					0.31790	4	-4998.185	10004.4	849.32	0.000
19	3.589		0.0715800			0.30200	5	-4999.274	10008.6	853.50	0.000
1	3.732						3	-5001.364	10008.7	853.67	0.000

2	3.767	-0.072730					4	-5001.436	10010.9	855.82	0.000
3	3.703		0.0875200				4	-5001.976	10012.0	856.90	0.000
4	3.736	-0.087880	0.1157000				5	-5001.059	10012.1	857.07	0.000

**Table S5.** Model selection table for predictor factors influence on the individual previous experiences. Models are ranked according to the best AIC. In bold, candidate models retained.

Model	(Int)	Aggression N-1	Avoidance N-1	Exp. condition	Food consumed N-1	Node strength N-1	df	logLik	AICc	ΔAIC	weight
<b>32</b>	<b>-1.2860</b>	<b>0.01568</b>	<b>-0.0079330</b>	+	<b>0.02822</b>	<b>0.2322</b>	<b>10</b>	<b>-39629.57</b>	<b>79279.2</b>	<b>0.00</b>	<b>0.564</b>
<b>30</b>	<b>-1.2870</b>	<b>0.01489</b>		+	<b>0.02797</b>	<b>0.2320</b>	<b>9</b>	<b>-39630.84</b>	<b>79279.7</b>	<b>0.52</b>	<b>0.436</b>
29	-1.2880			+	0.02838	0.2423	8	-39641.37	79298.8	19.56	0.000
31	-1.2880		-0.0043130	+	0.02853	0.2427	9	-39640.98	79300.0	20.81	0.000
22	-1.1560	0.01679		+		0.2351	8	-39721.05	79462.1	182.92	0.000
24	-1.1550	0.01708	-0.0028100	+		0.2352	9	-39722.89	79463.8	184.61	0.000
21	-1.1550			+		0.2467	7	-39736.47	79487.0	207.76	0.000
23	-1.1550		0.0012100	+		0.2466	8	-39736.44	79488.9	209.71	0.000
14	-1.2060	0.02869		+	0.02893		8	-39850.10	79716.3	437.02	0.000
16	-1.2060	0.02935	-0.0064330	+	0.02913		9	-39849.26	79716.6	437.37	0.000
13	-1.2020			+	0.02983		7	-39890.82	79795.7	516.47	0.000
15	-1.2020		0.0007933	+	0.02980		8	-39890.81	79797.7	518.45	0.000
6	-1.0700	0.03087		+			7	-39949.04	79912.1	632.90	0.000
8	-1.0690	0.03099	-0.0011400	+			8	-39949.02	79914.1	634.86	0.000
5	-1.0610			+			6	-39996.32	80004.7	725.45	0.000
7	-1.0620		0.0066520	+			7	-39995.40	80004.9	725.62	0.000
28	-1.3600	0.02872	0.0436900		0.03122	0.6126	6	-43008.86	86029.7	6750.51	0.000
27	-1.3550		0.0512200		0.03068	0.6331	5	-43048.16	86106.3	6827.11	0.000
26	-1.3520	0.03373			0.03174	0.6179	5	-43048.68	86107.4	6828.15	0.000
25	-1.3450				0.03121	0.6439	4	-43104.52	86217.0	6937.82	0.000
20	-1.2390	0.02677	0.0464800			0.6240	5	-43160.76	86331.6	7052.32	0.000
19	-1.2370		0.0534800			0.6430	4	-43195.00	86398.0	7118.78	0.000
18	-1.2290	0.03208				0.6298	4	-43205.93	86419.9	7140.65	0.000
17	-1.2240					0.6543	3	-43256.56	86519.1	7239.89	0.000
12	-1.1700	0.07506	0.0619900		0.03891		5	-44875.34	89760.7	10481.45	0.000
10	-1.1560	0.08296			0.03967		4	-44955.83	89919.7	10640.45	0.000
4	-1.0140	0.07384	0.0656000				4	-45114.86	90237.7	10958.50	0.000
11	-1.1410		0.0848300	0.03823			4	-45157.36	90322.7	11043.51	0.000
2	-0.9964	0.08219					3	-45205.18	90416.4	11137.13	0.000

9	-1.1160			0.03921			3	-45313.79	90633.6	11354.36	0.000
3	-0.9884		0.0880700				3	-45388.57	90783.2	11503.93	0.000
1	-0.9592						2	-45557.48	91119.0	11839.74	0.000

**Table S6.** Model selection table for predictor factors influence on the dyad previous experiences. Models are ranked according to the best AIC. In bold, candidate models retained.

Model	(Int)	Aggression N-1	Avoidance N-1	Exp. condition	Dyad strength N-1	df	logLik	AICc	ΔAIC	weight
<b>15</b>	<b>-1.806</b>		<b>-0.014310</b>	+	<b>0.8942</b>	<b>8</b>	<b>-79718.25</b>	<b>159252.5</b>	<b>0.00</b>	<b>0.518</b>
<b>16</b>	<b>-1.806</b>	<b>-0.004014</b>	<b>-0.014220</b>	+	<b>0.8950</b>	<b>9</b>	<b>-79617.76</b>	<b>159253.6</b>	<b>1.03</b>	<b>0.310</b>
13	-1.809			+	0.8970	7	-79620.84	159255.7	3.17	0.106
14	-1.808	-0.004148		+	0.8977	8	-79620.32	159256.7	4.13	0.066
9	-1.768				1.0480	3	-81871.97	163749.9	4497.42	0.000
11	-1.770		0.008700		1.0500	4	-81871.01	163750.0	4497.49	0.000
10	-1.769	0.004084			1.0480	4	-81871.46	163750.9	4498.40	0.000
12	-1.770	0.003967	0.008569		1.0490	5	-81870.52	163751.1	4498.53	0.000
8	-1.568	0.021630	-0.076790	+		8	-83351.82	166719.7	7467.14	0.000
7	-1.565		-0.076590	+		7	-83366.13	166746.3	7493.75	0.000
6	-1.578	0.023320		+		7	-83428.22	166870.5	7617.92	0.000
5	-1.574			+		6	-83442.12	166896.3	7643.72	0.000
4	-1.486	0.038870	-0.063600			4	-87325.01	174658.0	15405.50	0.000
3	-1.477		-0.062880			3	-87371.91	174749.8	15497.30	0.000
2	-1.496	0.038360				3	-87377.88	174761.8	15509.23	0.000
1	-1.487					2	-87423.58	174851.2	15598.63	0.000

**Table S7.** Number of shared platform visits, frequency of avoidance and agonistic events that occurred during platform sharing in each experimental condition

Experimental conditions	Number of shared platform visits	Frequency of avoidance events	Frequency of agonistic events		
			Low + High intensity	Low intensity	High intensity
S++	984	139	152	113	39
S+	775	115	168	88	80
C+	1,904	282	434	329	105
C-	1,215	242	514	288	226
S-	529	177	181	123	58
<b>Total</b>	<b>5,407</b>	<b>955</b>	<b>1,449</b>	<b>941</b>	<b>508</b>

## 6. CONSIDERAÇÕES FINAIS

A presente tese contribuiu para o melhor entendimento da sociabilidade em primatas, assim como dos custos e benefícios da vida em grupo. A abordagem realizada, através do uso de experimentos em campo para responder questões socioecológicas, confere ao trabalho um caráter inovador e gera informações sobre o comportamento, ecologia e sistema social de uma espécie de primata do Novo Mundo que se distingue por apresentar apenas uma fêmea reprodutora e reprodução cooperativa. Ao investigar como fatores ecológicos (diferentes contextos de distribuição e produtividade de alimento) e fatores sociais (status social, sexo e idade) afetam as estratégias de forrageio, o sucesso alimentar, a estrutura e dinâmica das relações sociais (redes sociais de associação em sítios de alimentação) entre membros do grupo durante o forrageio social em saguis comum de vida livre (*Callithrix jacchus*), obtivemos os seguintes principais resultados:

1. Saguis comum usam e integram informações ecológicas da disponibilidade de recursos no ambiente e informações sociais da identidade e comportamento dos outros membros do grupo para tomar suas decisões de forrageio;
2. Durante nossos experimentos, tanto saguis dominantes como subordinados empregaram uma série de estratégias de forrageio para ter acesso ao alimento nos diferentes contextos ecológicos. Sendo aquelas relacionadas à: (a) competição por exploração (chegar ao sítio de alimentação antes dos outros membros do grupo e utilizar este comportamento ao longo do dia como uma estratégia alimentar compensatória), utilizadas por todos os membros do grupo; (b) competição por interferência (emitindo vocalizações e comportamentos agonísticos), utilizada principalmente pela fêmea reprodutora; e (c) tolerância social (compartilhando sítios de alimentação com outros indivíduos), por parte de todos os membros do grupo;
3. A única fêmea reprodutora de cada grupo obteve a posição hierárquica mais alta e o maior sucesso alimentar na maioria dos contextos de disponibilidade de alimento. No entanto, indivíduos ranqueados na segunda e terceira posição não apresentaram sucesso alimentar maior do que animais mais subordinados, mas sim relativamente similar entre eles;
4. Em base às interações agonísticas e o sucesso alimentar dos indivíduos, sugerimos que a estrutura social (hierarquia) dos grupos estudados é piramidal, na qual a única fêmea reprodutora é dominante sobre todos os outros membros do grupo;

5. Os grupos de sagui comum apresentaram redes de associação de forrageio estruturalmente coesas e dinamicamente estáveis ao longo dos experimentos. Indivíduos com diferentes posições hierárquicas, idade e sexo utilizaram simultaneamente sítios de alimentação mesmo em contextos alimentares mais competitivos (recurso concentrado), caracterizando altos níveis de tolerância social a nível de grupo.

De uma maneira geral, estes achados indicam que o sagui comum não se ajusta exatamente às previsões do modelo socioecológico com relação à competição alimentar dentro do grupo. As discrepâncias entre os padrões observados na presente pesquisa e aqueles previstos pelo modelo podem estar relacionadas ao fato de que o modelo foi construído e baseado em espécies de primatas do Velho Mundo, principalmente da família Cercopithecoidea. Estas espécies são caracterizadas por possuírem sistemas sociais com estilos de dominância mais extremos (despótico ou com uma forte hierarquia linear) e várias fêmeas reprodutoras. Por sua parte, o sagui comum se caracteriza por ser uma espécie coesa, cooperativa, e por apresentar, usualmente, apenas uma fêmea reprodutora dentro do grupo. Dessa forma, o atual modelo não é suficiente para explicar a ampla diversidade de sistemas sociais (que incluem a organização social, estrutura social e sistema de acasalamento) encontrada em primatas. Destacamos que comportamentos afiliativos, ações coletivas, de cooperação e relações sociais mutuamente benéficas entre os indivíduos do grupo devem ser considerados nos modelos como fatores que podem limitar os potenciais custos da competição por recursos alimentares dentro do grupo.

O presente estudo evidenciou, portanto, a natureza complexa e dinâmica das relações sociais de primatas em locais de alimentação (competição vs. tolerância), resultando no acesso e obtenção de recursos alimentares por parte de todos os indivíduos e na manutenção da estabilidade e união do grupo. O acentuado grau de tolerância por parte de todos os membros do grupo encontrado nesta pesquisa contradiz expectativas da competição principalmente em fontes aglomeradas, mas pode ser esperado para a espécie por facilitar os comportamentos cooperativos característicos da espécie, como o cuidado da prole. Por sua parte, o fato de trabalharmos com grupos pequenos (naturalmente encontrados em ambiente de Caatinga) pode ter colaborado para uma alta coesão dentro do grupo, uma vez que os membros possuiriam um número limitado de outros indivíduos com os quais se relacionar. Futuras comparações dos resultados aqui encontrados com grupos maiores tanto de *Callithrix jacchus* (por exemplo, aqueles que habitam na Mata Atlântica) como de outras espécies de calitriquídeos, poderão revelar diferenças ou semelhanças no que se refere ao tipo de associações e interações sociais durante o forrageio e possíveis variações no sistema social intra e entre espécies e gêneros.



Finalmente, a abordagem utilizada e os resultados obtidos neste estudo corroboram a importância que experimentos de campo possuem como uma poderosa ferramenta empírica para investigar de forma sistemática questões relacionadas com a competição, estratégias comportamentais, sucesso alimentar e relações sociais em grupos de primatas de vida livre. Ao utilizar experimentos de campo, pode-se manipular e controlar certas variáveis de interesse para investigar padrões comportamentais que são raros ou difíceis de observar e quantificar em estudos observacionais. Além disso, sem negar a importância dos estudos em laboratório, os experimentos de campo permitem investigar grupos de primatas em seu ambiente natural sem alterar ou restringir seus comportamentos naturais através de testes artificiais e do manejo necessário para a manutenção dos indivíduos no cativeiro. No entanto, esta abordagem também possui certas limitações, como por exemplo a impossibilidade de controlar certos fatores como as condições climáticas e a disponibilidade de recursos no ambiente, as quais poderiam ser controladas em ambiente de cativeiro e que podem influenciar no comportamento dos animais. Não obstante, utilizar experimentos de campo com primatas de vida livre se mostra como um instrumento relevante para investigar o repertório comportamental natural de uma espécie, entender o uso de diferentes estratégias e suas consequências para a aptidão dos indivíduos. Este enfoque pode ser aplicado em futuras pesquisas para investigar as questões aqui abordadas em uma diversidade de espécies com diferentes sistemas sociais, alcançando uma perspectiva comparativa.