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Social relationships in wild white-faced capuchin monkeys (*Cebus capucinus*): Insights from new modeling approaches

A dissertation submitted in partial satisfaction of the requirements for the degree

Doctor of Philosophy in Anthropology

by

Kotrina Kajokaite

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ABSTRACT OF THE DISSERTATION

Social relationships in wild white-faced capuchin monkeys (*Cebus capucinus*): Insights from new modeling approaches

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Kotrina Kajokaite
Doctor of Philosophy in Anthropology
University of California, Los Angeles, 2019
Professor Susan Emily Perry, Chair

Answers to many of the most important questions about the evolution of primate social strategies still elude us, due to the difficulties in extracting information about primates' decision-making processes and the fitness consequences of their behavioral choices. These sorts of questions cannot be answered experimentally: the answers must be inferred from the behavioral patterns of wild populations in long-term studies. It is only now that sufficiently sophisticated methods are being developed to allow us to make precise inferences from these messy observational data sets. In this thesis I will ask questions about how wild primates make decisions about allocations of favors to social partners, and about the fitness consequences of their behavioral choices.

In the following chapters, I examined: (1) reciprocity in capuchin monkeys' social relationships; (2) the relationship between adult female capuchins' sociality and longevity; and

(3) the decision rules that capuchins use when soliciting an ally in a coalitionary fight. I used behavioral, genetic, and demographic data of wild white-faced capuchin monkeys (*Cebus capucinus*). The data came from 11 capuchin social groups and were collected over a 19-year period at Lomas Barbudal Biological Reserve and surrounding private lands in Guanacaste, Costa Rica. To answer the questions above, I used innovative statistical techniques currently unrepresented in the primatological literature. To analyze reciprocity and the fitness benefits of dyadic relationships, I used the Social Relations Model (Kenny 1994). To model capuchin monkey choices of allies in coalitionary aggression, I employed conditional logistic regression. Both of these modeling techniques allow me to take into account the particularities of a dataset collected in the wild.

My findings show that capuchin monkeys reciprocate in grooming and coalitionary support exchanges. When choosing allies in coalitionary aggression, capuchins use both rank and relationship quality of the potential partner to make a decision. Finally, sociality is associated with fitness outcomes in female capuchins: More social females tend to live longer than less social ones. Together, these chapters will provide insights into capuchin monkeys' social relationships, decision making and social relationships' effects on fitness.

The dissertation of Kotrina Kajokaite is approved.

Harold Clark Barrett

Jacob Gates Foster

Joseph Howard Manson

Karthik Panchanathan

Brooke A. Scelza

Susan Emily Perry, Committee Chair

University of California, Los Angeles

2019

This work is dedicated to Danutė, Donaldas, Rūta and Ugnė who made it easy to foster our social bond despite the distance between us.

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Biographical Sketch

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Kajokaite K., Whalen A., Panchanathan K., and Perry S. (2019). "White-faced capuchin monkeys use both rank and relationship quality to recruit allies". Animal Behaviour 154: 161-169

Conference presentations

Kajokaite K., Koster J. (2019) You scratch my back and I'll scratch yours: grooming reciprocity in capuchin monkeys. *California Workshop on Evoliutionary Social Sciences (CSWESS).* Chino Hills, California

Kajokaite K., Whalen A., Panchanathan K., Perry S. (2018) Testing hypotheses of social cognition with observational data: coalitions in white-faced capuchin monkeys. *International Primatological Society Congress.* Nairobi, Kenya

Kajokaite K., Perry S. (2016) Flexibility in social relationships in female white-faced capuchins during takeovers. *International Primatological Society Congress*. Chicago, Illinois

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2019 Testing hypotheses about social cognition with observational data: coalitions in white-faced capuchin monkeys (Center for Behavior, Evolution, and Culture (BEC), University of California-Los Angeles, CA)

2019 Coalitions in white-faced capuchin monkeys (Evolution and Social Complexity Colloquium, Arizona State University, Tempe, AZ)

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Chapter 1

Reciprocity in capuchin monkeys: insights from Social Relations Model

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Keywords: reciprocity, social relationships, Social Relations Model, *Cebus capucinus*

ABSTRACT

One of the conditions for reciprocity is a long-lasting relationship between partners (Axelrod and Hamilton 1981). Rates of dyadic interactions typically are used to operationalize dyadic relationships in nonhuman primates. However, the link between observed interaction and a relationship is not always a direct one. Often the process that generates the observed exchanges of interactions is composed not only of special dyadic relationships, but also the individual actor's general tendencies to engage with anyone (Snijders and Kenny 1999). In order to evaluate whether some pairs of individuals have reciprocal relationships, we ought to take into account both of those processes. In this chapter, we present 17 years of data on grooming, coalitionary support, and foraging in close proximity for a population of white-faced capuchin monkeys, collected in 11 social groups at Lomas Barbudal Biological reserve. We used the Social Relations Model (Kenny 1994) to estimate individual tendencies to engage with anyone, as well as dyad-specific tendencies to engage in the behavior. We evaluate if dyad-specific exchanges of grooming and coalitionary support are reciprocal. In addition, we estimate how kinship, age, sex, dominance rank, and group size can explain the data. The results suggest that after accounting for individual tendencies, capuchin monkeys show high dyadic reciprocity in their grooming and coalitionary support exchanges. Kinship, age, sex, dominance rank, and group size also account for a lot of variation in grooming, coalitional support and foraging tolerance; however, even after accounting for all of these factors, the capuchin monkeys' dyadic reciprocity remains high in grooming and coalitionary support exchanges.

INTRODUCTION

Unlike in most mammalian societies, membership in the majority of primate groups is consistent; individuals recognize each other and base their social behavior on their memories of past interactions (Byrne and Bates 2010), generating differentiated social relationships, i.e. patterned sequences of dyadic interaction (Hinde, 1976). Only a small proportion of non-primate mammals (e.g. elephants, wild dogs, and bottlenosed dolphins) show sociality as complex as most primates (Byrne and Bates 2010). Primatologists have been long interested in social relationships, but currently there is no consensus regarding how to describe or measure social relationships in nonhuman primates (Silk et al. 2013).

One of the problems with studying social relationships in primates is that we are interested in understanding whether some pairs of individuals treat each other in a special way, but the data we typically use to answer this question is generated by several distinct processes (Snijders and Kenny 1999). The patterns of exchanging affiliative behaviors are a result not only of distinctive *dyadic relationships*, but also of the *individual tendencies* to engage in the behavior under study with *anyone* in general (Snijders and Kenny 1999). For example, if two individuals, *i* and *j,* have very different tendencies to engage in grooming in general, such that *i* grooms anyone whom they encounter whereas *j* almost never grooms, then, if we observe *i* and *j* exchanging grooming, we might conclude that this is a reciprocal exchange. However, if we take into account that *i* is behaving as per usual, but *j* is treating *i* in a special way (since *j* almost never grooms), then we might draw a different conclusion.

The psychology literature has well-developed methods for analyzing dyadic relationships while estimating individual tendencies and dyad-specific relationships using the Social Relations Model (Kenny 1994; Snijders and Kenny 1999). This approach assumes that dyadic exchanges of behaviors are generated by both individual tendencies and dyad-specific relationship tendencies (Back and Kenny 2010). The model estimates three major components: the general tendency of each individual to engage in the interaction, the general tendency of each individual to be the recipient of the interaction, and a dyad-specific relationship effect that is independent of the two previous effects.

How do we evaluate if the individuals treat their partners in a special way if we estimate their individual and partner specific tendencies? Estimating specific relationship effects after taking into account each individual's general tendencies, we can evaluate whether partners in pairs treat each other in a reciprocal way. I.e. if one of the individuals treats their partner in a special way, does that partner reciprocate?

The evidence for reciprocity in the primate literature, based on Trivers' (1971) proposed mechanism of direct reciprocity, is contentious. Jaeggi et al. (2013) distinguishes between *short-term behavioral contingency* and *long-term statistical contingency* reciprocity patterns in primates. *Short-term behavioral contingency* refers to a *tit-for-tat* strategy where individuals are expected to reciprocate immediately until their partner defects (Axelrod and Hamilton 1981). The evidence for this type of pattern in primate data is weak (reviewed in Silk 2007; Jaeggi et al. 2013). *Long-term statistical contingency* is based on statistical evidence that there is an association between service given and received over long periods of time (e.g. Manson et al. 2004; Frank and Silk 2009; Jaeggi and van Schaik 2011).

We propose that the evaluation of whether pairs of individuals behave reciprocally towards each other faces the same problem as described above: We should take into account that observations of exchanges are generated by *individual tendencies* to engage with *anyone* and by *dyad-specific relationships* (Snijders and Kenny 1999). Although we are interested in the latter, we need to take into account the former as well. The Social Relations Model estimates dyadic reciprocity by correlating dyad-specific relationship effects: (1) where individual *i* is providing a service to individual *j* and (2) where *j* is providing a service to *i*. Therefore, before estimating dyadic reciprocity correlation, the model "removes" the individual tendencies that "contaminate" the phenomenon of reciprocity that we are interested in evaluating (McElreath, forthcoming).

Apart from relationship specific effects, other factors like kinship, age, sex, dominance rank, and group size can explain reciprocal interactions. Primates show very strong kin biases in the distribution of affiliative and supportive social interactions (Chapais and Berman 2004). For example, in female baboons and male chimpanzees, most strong and long-lasting bonds are formed with close maternal kin (Mitani 2002; Silk et al. 2006 a,b, 2010). Other individual and dyadic factors that explain variation in rates of interaction are: (1) dominance, such that individuals are more attracted to higher-ranking social partners (Seyfarth 1977, Schino 2001), (2) age, such age-mates are typically more likely to form strong social relationships than individuals of disparate ages (e.g. Mitani 2002; Silk et al. 2006 a,b), and (3) sex, where individuals are assumed to pursue different strategies when forming social relationships with either males or females (e.g. Archie et al. 2014). The size of a social network also contributes to the patterns of variation in interaction rates and partner choice (e. g. Perry et al. 2008). The Social Relation Model allows for the inclusion of covariates like kinship, age, sex, dominance rank and group size, and estimates the extent to which they explain the variation in exchanges (Koster et al. 2015).

In this chapter, we analyze social interactions of white-faced capuchin monkeys (*Cebus capucinus*). We chose three behavioral domains: (a) grooming, (b) coalitionary support, and (c) foraging in close proximity. Our first aim is to evaluate whether capuchin monkeys show reciprocity in dyadic relationships after taking into account each partner's individual tendencies. Second, we aim to estimate how kinship, dominance rank, age, sex, and group size structure the choices of capuchin social partners, and whether dyadic reciprocity changes when we take these factors into account.

Capuchin monkeys live in multi-male/multi-female social groups (Jack 2007). The membership in such groups is largely stable, which means that individuals, and particularly females as the philopatric sex (Jack 2007; Perry 2012), have an opportunity to form and cultivate long-term social relationships. More closely related females are more likely to aid each other in coalitions and spend more time grooming together (Perry et al. 2008). Males of the Lomas Barbudal population disperse several times in their lifetime (Jack and Fedigan 2004; Perry 2012). We observe high rates of male co-migration and unusually long alpha male tenures, sometimes lasting up to 18 years (Perry 2012). Due to (1) parallel dispersal, which results in related males co-residing in the same social groups after transfer (Perry 2012; Wikberg et al. 2014), and (2) the potential for some males to co-reside with their maternal and paternal siblings due to long alpha male tenures, both male and female capuchins can form long-term relationships with same-sex kin.

Capuchin monkeys have very rich social lives and engage in many types of social behaviors. The highly social nature of capuchin monkeys and the co-residence patterns makes them an excellent species for the study of social relationships. Moreover, capuchin monkeys are New World primates, which means that they shared a common ancestor with humans about 35-40 MYA (Schrago and Russo 2003). Phylogenetically, capuchins are more distantly related to humans than are the Old World primates. Their evolutionary convergence with both humans and with Old World monkeys with regard to a diverse set of behavioral traits (Perry 2012) makes capuchin monkeys an important data point for understanding primate sociality across the entire clade.

METHODS

Study subjects

Here we analyze data collected between January 2002 and May 2018 at Lomas Barbudal Biological Reserve and surrounding private lands in Guanacaste, Costa Rica (Perry et al. 2012). We used behavioral and demographic records collected by experienced observers during observation periods that lasted at least 6 hours/day. The subjects were 218 adult male and female capuchins living in nine social groups over 106 group-years (average years per group = 11.8, range = 7 – 17 years), see Table 1.2 for final sample description. Individuals were added to the dataset when they reached the age of 5 years.

Behaviors

We chose three behavioral domains that represent different types of social interactions: grooming, coalitionary aggression, and foraging. When observing grooming and coalitionary aggression, we identified the individuals who were givers and who were recipients of the behavior in each interaction. Information about proximity during foraging was gleaned from scans, which meant that we lacked information about who was responsible for establishing and maintaining proximity during foraging; therefore, both members of the dyad were given equal "credit" for this behavior.

Grooming (groom give and groom receive)

We used focal follow data to estimate grooming rates, by calculating dyadic opportunities and dyadic counts of grooming. Dyadic opportunities to groom were equal to the number of focal follows in which one of the individuals within the dyad was the focal animal and the other individual was co-resident in the group. To estimate the number of instances of giving and receiving grooming, we assigned a "1" if monkey *i* groomed monkey *j,* and vice versa. Only one count per direction per focal follow was counted. Otherwise 0 was assigned for either direction.

Joining a coalitionary conflict (support give and support receive)

Support in a coalitionary conflict was defined as an individual intervening on one side of an ongoing aggressive conflict. This definition does not necessarily reflect intent to help a specific individual, but rather indicates a functional aspect of supporting a side. We used both *ad libitum* and focal follow data on aggressive interactions, because aggression is salient and harder to miss than other activities such as grooming or foraging in proximity. We divided the chronological sequence of aggressive behaviors into 5 min. segments. In order to identify instances of support in a coalitionary conflict, monkey *i* is identified as joining monkey *j*, if *i* performed an aggressive behavior to either monkey *j*'s opponent or victim within the context of the 5-minute segment. If multiple instances of monkey *i* joining monkey *j* were observed during the 5 min segment, we only counted one instance of *i* joining *j*. To count the opportunities to provide and receive support during coalitionary conflict, all individuals who were co-resident during the aggressive encounter were counted as having had an opportunity to join on either side during the conflict.

Foraging in proximity

To estimate foraging in close proximity rates, we used group scans that were performed in the foraging context. During a group scan, observers noted the identity of the focal individual, their activity and their proximity to other individuals within 10 monkey body lengths (~2 m). Individuals were considered to be foraging in close proximity if they were within 5 body lengths

(~1 m) of each other. The group scan data do not contain information about who initiated the approach; therefore the data on foraging in close proximity, unlike the data on grooming and coalitionary support, do not distinguish actor from receiver. For each dyad, we scored whether they were observed foraging within close proximity in a 10 min segment. If they were observed in proximity more than once within a 10 min. segment, only one instance was counted. The sum of group scans that were at least 10 min. apart, in which one of the individuals was the focal animal, was considered to be the number of opportunities that the dyad had to forage in close proximity of each other.

Analyses

We modeled rates of interactions using observed annual counts of interactions within each behavioral domain separately. We had two main goals: First, estimate how much of the variation is explained by age, dominance rank, sex, group size, and kinship. Second, for the grooming and coalitionary support interactions, we sought to answer whether or not (after accounting for the variation that is explained by the covariates) capuchins have reciprocal relationships.

Covariates

Table 1.1 provides a short description and summary statistics for all the covariates.

Table 1.1. Variable descriptions and summary statistics

Variable	Description	Model	Mean	SD	Min	Max
Continuous variables:						
Age	Age of either giver or recipient	groom, support	11.98	6.48	5	39
Age difference	Absolute age difference	forage	7.16	6.38	0	33
Rank	Average annual rank of either giver or recipient	groom, support	0.6	0.26	0	1
Rank difference	Absolute rank difference	forage	0.3	0.21	0	1
Group size	number of adults in the social group	groom, support	13	3.32	2	20.27
		forage	13.23	3.53	3.39	20.27
Binary variables:						
Sex	0 denotes females, 1 denotes males	groom, support			0	1
Female dyad	0 denotes mixed-sex dyad, 1 denotes female-female dyad	forage			0	1
Male dyad	0 denotes mixed-sex dyad, 1 denotes male-male dyad	forage			0	1
Mother-offspring	denotes mother-offspring dyad	groom, support, forage			0	1
Father-offspring	denotes father-offspring dyad	groom, support, forage			0	1
Full siblings	denotes full sibling dyad	groom, support, forage			0	1
Maternal half-siblings	denotes maternal half-sibling dyad	groom, support, forage			0	1
Paternal half-siblings	denotes paternal half-sibling dyad	groom, support, forage			0	1
Other kin	denotes kin (0.5 - 0.25) who are not one of 5 above categories	groom, support, forage			0	1
Co-migrants	denotes male-male dyad who immigrated into a social group together	groom, support, forage			0	1
Distant/non-kin	denotes distant kin dyad (>0.25)	groom, support, forage			0	1

Sex: For grooming and coalitionary support, we used both the sex of the giver and that of the recipient of the interaction as two separate fixed effects. For foraging in close proximity, we coded each dyad as female-female, male-male, or female-male.

Age: We used demographic records on births and deaths collected from 1990 – 2018 at the Lomas Barbudal Monkey project to estimate the age of individuals. Those born prior to the 1990s were assigned an age in part by retrospectively comparing photos taken with photos of known-aged individuals collected later in the study and in part by using reproductive histories via genetic maternity data. We assumed that, given a 2-year interbirth interval and the age of first birth of 6 years, that a female with 1 offspring had to be at least 6, while a female with at least 2 offspring would have to be at least 8, etc. For the grooming and coalitionary support interactions, we used the giver's and the recipient's ages as two separate fixed effects. For foraging in close proximity, we calculated the absolute age difference within each dyad.

Average annual number of adults in the group: This represents the mean number of adult females and adult males that resided in the group during the days when researchers spent at least 6 hours of observation with the group, averaged for the year.

Annual dominance index: The annual dominance index indicates the proportion of group members that the individual dominated that year, on average. For each observation day, we identified every individual that resided in a social group. For each individual in the group, everyone else is an alter that the focal individual can either dominate or be submissive to. To assess whether the focal individual was dominant to an alter on a particular observation day, we identified the two temporally closest dominance interactions of each focal-alter dyad: one immediately before and one immediately after the observation day. The number of opportunities for the focal to dominate another individual is equal to the total number of these interactions across all focal-alter dyads.

For each interaction, we scored that the focal individual was dominant if she was either the animal performing the supplanting, or being cowered at, or being avoided, or fled from. The daily dominance index, DDI_i, of a focal individual, i, is a sum of dominance interactions where the focal was dominant to their alters, w_{i-a}, divided by the total number of dominance interactions that the focal had with her alters, $s_{i\text{-a}}$:

$$DDI_i = \frac{\sum w_{i-a}}{\sum s_{i-a}} \tag{1}$$

The average annual dominance index, ADI_i, is an average of daily dominance indices:

$$ADI_i = \frac{1}{n}\sum_{i=1}^{n} DDI_i \tag{2}$$

In some cases, either one or no dominance interactions were observed for a focal-alter dyad. The individuals who did not have dominance interactions with the focal did not contribute to the calculation of the focal's daily dominance index.

Kinship: We treated kinship as a categorical variable and classified each dyad into one of eight kin categories. Father-offspring relationships were assigned, and mother-offspring relationships were confirmed, based on DNA obtained through non-invasively collected fecal sampling and through the occasional collection of tissue samples from dead capuchins (Muniz et al. 2006; Godoy et al. 2016). For other kin categories, we used additional information related to the pedigrees of the members of the dyad to assign kinship category. Each dyad was classified as belonging to one of the following categories: mother-offspring, father-offspring, full siblings, maternal half-siblings, paternal half-siblings, other kin (kinship categories, other than those listed, with estimated levels of relatedness between 0.25 and 0.5, e.g. full aunt/uncle-niece/nephew dyads, grandparent/grand-offspring), and distant kin/non-kin (kinship categories where r is estimated below 0.25). We created a separate category, co-migrants, for males who co-migrated together from outside of the study area. Although we are not able to identify their kinship category, it is likely that these male dyads are related (Perry 2012) and share a special relationship with each other, given the finding that males who co-emigrate from study groups in the Lomas population are related, on average, at approximately the level of half siblings (Perry 2012). Immigrant males were assumed to be unrelated to the other members of their new group, unless they were later known to be father-offspring pairs after genotyping. When pedigrees for a dyad were of insufficient depth to support the assignment of a kin category with high certainty, we dropped that dyad from the analysis. This resulted in an approximate 5% loss for each behavioral domain (Table 1.2).

Sample

There were 2721 dyads co-residing in nine social groups during the study period. Some of these dyads were never observed when both individuals were co-resident, or we lacked information about a dyad's kinship relationship (Table 1.2). For grooming interactions, there were 274 dyads (11%) for which no focal follows were conducted while the monkeys were co-resident, and out of the 2447 remaining, 121 dyads (5%) could not be assigned a kinship category with certainty. This resulted in a total of 15% loss of dyads, i.e. 2326 dyads were represented in the final sample for grooming interactions. For coalitionary support, there were 85 dyads (3%) that had no observations of aggressive behaviors while co-resident, and from those 2636 remaining, the kinship category was uncertain for 136 (5%). This resulted in the total of 8%

loss, i.e. a final sample size of 2500 dyads. For foraging in close proximity, 52 dyads (2%) had no group scans while they were co-resident, and of the 2530 remaining, 139 (5%) had no kinship category assigned. This resulted in a total of 9% loss, i.e. 2530 dyads were represented in the analyses of foraging in close proximity.

Table 1.2. Sample description. The Census column contains the number of individuals that were residing in the study group. The Groom, Support, and Forage columns contain the number of individuals that were used for each type of model.

	Census	Groom	Support	Forage
Total adults	218	217	217	217
Females	97	97	97	96
Males	121	120	120	121
Dyads	2721	2326	2500	2530
Groups	9	9	9	9

Modeling approach

To model the counts of grooming and coalitionary support exchanges, we analyzed the data using the Social Relations Model (SRM; Kenny and Le Voie 1984; Kenny 1994; Snijders and Kenny 1999). When using this modeling framework, we assume that each dyad- and direction-specific observed behavioral frequency (e.g. how much A grooms B) is a function of both (a) each individual's tendency to engage in these interactions with any partner (A's general tendency to groom, B's general tendency to be groomed), and (b) the individual's ability to behave differently depending on the identity of partner (the dyad-specific tendency of A to groom B) (Back and Kenny 2010). Social Relations Model is a statistical framework that accounts for these complexities by assuming that dyadic phenomena can be separated into components (Kenny et al. 2006). For example, consider the observed number of grooming interactions that a pair of monkeys exchange in one year. SRM decomposes this observed number of monkey A giving grooming to monkey B into the following components: (1) the overall mean number of grooming exchanges within dyads in the population; (2) the social group effect, which measures how the mean number of grooming exchanges within dyads in a particular year and social group deviates from the overall population mean; (3) the Monkey A giver effect, which measures how the mean number of grooming bouts provided by monkey A to other monkeys in his/her group deviates from the overall mean and his/her group and year mean; (4) the Monkey B receiver effect, which measures how the mean number of grooming bouts received by monkey B from other monkeys in his/her group deviates from the overall mean and his/her group and year mean; (5) the Monkey A and B relationship effect, which measures the number of grooming exchanges that monkey A provides to monkey B, over and above the estimated population mean, their group and specific year mean, the Monkey A giver effect, and the Monkey B receiver effect. As a result, SRM must analyzes a network of interactions since in order to evaluate the relationships between two specific monkeys, it must use information about each one of those monkeys' interactions with all of the other monkeys in the social network (Back and Kenny 2010).

Variance decomposition

The variance in the giver, receiver and relationship effects quantify the relative importance of monkeys as givers and receivers. Unique relationships with specific partners can be considered as an explanation for observed variance in grooming exchanges among monkeys (Koster and Leckie 2014). In other words, giver variance answers the question of how monkeys differ in the amount of grooming they generally provide to others (generalized giver effects). Receiver variance answers the question of how monkeys differ in the amount of grooming that they generally receive from others (generalized receiver effects). Unique relationship variance answers the question of how much monkeys differ with respect to their unique actions toward specific partners (relationship effects). To estimate the variances, giver and receiver effects estimates are computed for each individual, and three relationship effects are computed for each dyad.

Measuring reciprocity

The correlation between generalized giver effects and generalized receiver effects provides a measure of generalized reciprocity (Kenny and Nasby 1980; Miller and Kenny 1986): the degree to which the aggregate amount of grooming that an individual provides is related to the aggregate amount of grooming she receives. In the terminology of social network analysis, a positive generalized reciprocity implies a positive correlation between the in-degree centrality and out-degree centrality of a given individual (Koster and Aven 2018). The correlation between two unique relationship effects measures dyadic reciprocity: the degree to which an excess of grooming above the general tendency to groom by Monkey A is reciprocated by Monkey B. In other words, it tells us how much Monkey A treating Monkey B in a special way (or differently from Monkey A's general tendencies) is correlated with Monkey B treating Monkey A in a special way. This type of dyadic reciprocity correlation has a different interpretation from the simple unconditional pairwise correlation calculated on the raw data (Koster and Leckie 2014).

The model

We generally follow the specification of the SRM in Koster et al. (2015).[1] Here we describe the model using grooming interactions. The model specification from support in coalitionary aggression is identical to that for grooming. For foraging in close proximity

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[1] One difference is that whereas Koster et al. (2015) assumed generalized reciprocity to be zero, in our models we estimate this correlation.

interactions, the model specification is different due to the lack of directionality in the data. The model's modifications for foraging in close proximity are provided at the end of the section.

Let y_{ij} denote the total number of grooming bouts given by a monkey *i* $(i = 1, \ldots, N\,)$ to a monkey *j* $(j = 1, \ldots, N)$ over a calendar year. Our response variable is a count outcome, and we assume a likelihood distribution as Poisson

$$y_{ij} \sim Poisson\left(\lambda_{ij}\right) \qquad (3)$$

where λ_{ij} denotes the expected rate of grooming provided by monkey *i* to monkey *j*. The deviation of the observed counts from the expected counts is the error in this model. For the "intercept-only" model (empty model), we specify the log-linear model of λ_{ij}

$$\log\left(\lambda_{ij}\right) = \beta_0 + m_k + g_i + r_j + \underbrace{u_{|ij|} + e_{ij}}_{d_{ij}} \qquad (4)$$

The intercept, β_0, measures the average logged rate of expected grooming given by monkey *i* to monkey *j*, or a population base rate. The group effect, m_k, represents the extent to which the overall rate of grooming in group *k* differs from the baseline. The effect, g_i, is the individual-level giver effect, which, added to the base rate, β_0, measures the average logged rate individual *i* tendency to groom monkeys in his/her group. The effect, r_j, is the individual receiver effect, which, when added to the base rate, β_0, measures the average rate of individual *j* receiving grooming from other monkeys in his/her group. We modeled the relationship level effect, d_{ij}, as a sum of asymmetric (directed), e_{ij}, and symmetric (undirected), $\mathrm{u}_{|ij|}$ relationship effects. The variables are distinguished by using the ij and $|ij|$ subscripts, respectively (Koster et al. 2015).

SRM assumes co-variance across these components. The individual-level giver and receiver effects, g_i and r_i , are assumed to be bivariate normally distributed with zero means and a homogenous 2 × 2 giver-receiver covariance matrix

$$\left(\frac{g_i}{r_i}\right) \sim N \left\{ \left(\frac{0}{0}\right) , \left(\frac{\sigma_g^2}{\sigma_{gr} \quad \sigma_r^2}\right) \right\} \tag{5}$$

where σ_g^2 measures the giver variance, σ_r^2 measures the receiver variance, and σ_{gr}^2 measures the giver-receiver co-variance. The giver-receiver correlation, $\rho_{gr} = \sigma_{gr}/\sqrt{\sigma_g^2\sigma_r^2}$, measures the degree of generalized reciprocity in a monkey group.

Both the symmetric and directed dyadic effects are assumed to be normally distributed around zero means:

$$u_{|ij|} \sim N(0, \sigma_u^2) \tag{6}$$

$$e_{ij} \sim N(0, \sigma_e^2) \tag{7}$$

The symmetric effect, $u_{|ij|}$, reflects the extent to which both members of the dyad (*i* and *j*) deviate from the average in the same direction. For instance, when *i* grooms *j* and *j* grooms *i* substantially more than average, then the symmetric effect will be strongly positive. Meanwhile, the directed effect, e_{ij}, represents the extent to which unidirectional assistance is heterogeneous. If *i* assists *j* considerably whereas *j* hardly ever assists *i*, then there may be large positive and negative directed effects, respectively.

We can obtain an estimate of overall dyadic variance, σ_d^2, and dyadic reciprocity, ρ_{dd}, as follows:

$$\sigma_d^2 = \sigma_u^2 + \sigma_e^2 \tag{8}$$

$$\rho_{dd} = \frac{\sigma_u^2}{\sigma_d^2} \tag{9}$$

This estimate of dyadic reciprocity implicity assumes $0 \leq \rho_{dd} \leq 1$ since $\sigma_u^2 \geq 0$ and $\sigma_e^2 \geq 0$. High dyadic reciprocity implies that both individuals in the dyad exchange roughly comparable amounts of grooming after adjusting for their general predispositions toward giving and receiving.

Finally, the group-level effect is estimated as a conventional varying intercept, with effects assumed to be distributed normally around a mean of zero with variance σ_m^2.

$$m_k \sim N(0, \sigma_m^2) \tag{10}$$

There was a lot of variation in how many opportunities each dyad had to be observed grooming. To account for the variation among dyads in opportunities to groom, we enter a natural logarithm of this annual exposure as an offset in the model. This allows us to estimate annual rates of grooming rather than the expected rates of grooming for the period that each dyad co-resided together.

Drawing on this statistical framework, the dyadic data from each group-year were incorporated into a joint model with a unique likelihood function for each group-year. Each function fit parameters that are common across all of the functions in the model. For instance, the variances and covariances of the random effects were assumed to be constant across group-years. The fixed effect parameters were likewise assumed to have constant effects across group-years. The random effects for each group-year were modeled separately, however, making no attempt to model correlations between individuals and dyads when they appear in multiple group-years.

Full model

The full model includes the specification of the empty model as well as individual- and dyad-level covariates: age, sex, rank, group size, kinship (Table 1.1).

Forage in close proximity

The foraging in close proximity data did not contain directional information, therefore we did not estimate individual giver and receiver effects, but rather the individual's tendency to be observed in foraging in close proximity. Therefore, the log-linear model of λ_{ij}

$$log\left(\lambda_{ij}\right) = \beta_0 + v_i + v_j \quad (11)$$

$$v_i \sim N(0, \sigma_v^2) \quad (12)$$

$$v_j \sim N(0, \sigma_v^2) \quad (13)$$

where the intercept, β_0, measures the average logged rate of expected rate of observing monkey *i* foraging next to monkey *j,* or a population base rate. The effect, v_i, is the individual level effect, which added to the base rate, β_0, measures the average logged rate individual i forages near monkeys in his/her group. The effect, v_j, is the individual effect for individual *j*.

For the forage full model, we added the dyad-level covariates (Table 1.1).

RESULTS

For each behavioral domain – grooming, support in coalitionary aggression, and foraging in close proximity of others – we present two models: an "intercept-only" model (empty model), and a model with covariates (full model). The empty model includes only the intercept and the random effects. The full model includes covariates as fixed effects in addition to the intercept and the random effects. The results for six models, empty and full for each of the three behavioral domains, are presented in Table 1.3 and Table 1.4. We present the results from all six models and then we discuss the findings related to covariates from the three full models.

Table 1.3. Random effects in Groom, Support, and Forage models. The empty model includes only the intercept and the random effects. The full model includes covariates as fixed effects in addition to the intercept and the random effects. The parameter estimates are posterior means and SD (in parentheses).

		Groom models	
Parameter		empty	full
σ^2_{Gm}	Group variance	0.22 (0.20)	0.11 (0.10)
σ^2_{Gg}	Giver variance	1.12 (0.07)	0.26 (0.02)
σ^2_{Gr}	Receiver variance	0.14 (0.02)	0.10 (0.02)
σ^2_{Gu}	Symmetric relationship variance	0.89 (0.04)	0.67 (0.03)
σ^2_{Ge}	Asymmetric relationship variance	0.00 (0.00)	0.00 (0.00)
ρ_{Ggr}	Generalized reciprocity correlation	0.50 (0.05)	0.43 (0.06)
ρ_{Gdd}	Dyadic reciprocity correlation	0.99 (0.00)	0.99 (0.00)

		Support models	
Parameter		empty	full
σ^2_{Sm}	Group variance	0.16 (0.14)	0.12 (0.10)
σ^2_{Sg}	Giver variance	0.66 (0.04)	0.38 (0.03)
σ^2_{Sr}	Receiver variance	0.22 (0.02)	0.12 (0.01)
σ^2_{Su}	Symmetric relationship variance	0.33 (0.02)	0.29 (0.02)
σ^2_{Se}	Asymmetric relationship variance	0.00 (0.00)	0.00 (0.00)
ρ_{Sgr}	Generalized reciprocity correlation	0.92 (0.01)	0.94 (0.02)
ρ_{Sdd}	Dyadic reciprocity correlation	0.99 (0.00)	0.99 (0.00)

		Forage models	
Parameter		empty	full
σ^2_{Fm}	Group variance	8.86 (8.48)	13.05 (9.82)
σ^2_{Fv}	Individual variance	0.29 (0.02)	0.20 (0.01)

Table 1.4. Fixed effects in Groom and Support models. The empty model includes only the intercept and the random effects. The full model includes covariates as fixed effects in addition to the intercept and the random effects. The parameter estimates are posterior means and SD (in parentheses).

	Groom models				Support models		
Parameter		empty	full	Parameter		empty	full
β_{G0}	base rate	-5.06 (0.17)	-4.43 (0.13)	β_{S0}	base rate	-4.27 (0.15)	-3.92 (0.14)
β_{G1}	male (*i*)	-	-1.85 (0.06)	β_{S1}	male (*i*)	-	-0.73 (0.06)
β_{G2}	male (*j*)	-	-0.28 (0.05)	β_{S2}	male (*j*)	-	-0.49 (0.04)
β_{G3}	age (*i*)	-	-0.34 (0.02)	β_{S3}	age (*i*)	-	-0.16 (0.03)
β_{G4}	age (*j*)	-	-0.02 (0.02)	β_{S4}	age (*j*)	-	0.03 (0.02)
β_{G5}	rank (*i*)	-	0.32 (0.03)	β_{S5}	rank (i)	-	0.69 (0.03)
β_{G6}	rank (*j*)	-	0.28 (0.02)	β_{S6}	rank (*j*)	-	0.30 (0.02)
β_{G7}	number of adults	-	-0.16 (0.04)	β_{S7}	number of adults	-	-0.10 (0.05)
β_{G8}	mother-offspring	-	1.41 (0.07)	β_{S8}	mother-offspring	-	0.52 (0.05)
β_{G9}	father-offspring	-	0.44 (0.12)	β_{S9}	father-offspring	-	-0.02 (0.08)
β_{G10}	full siblings	-	0.92 (0.09)	β_{S10}	full siblings	-	0.49 (0.07)
β_{G11}	maternal half sibling	-	0.07 (0.06)	β_{S11}	maternal half sibling	-	0.12 (0.05)
β_{G12}	paternal half siblings	-	0.80 (0.08)	β_{S12}	paternal half siblings	-	0.39 (0.07)
β_{G13}	other kin	-	0.37 (0.07)	β_{S13}	other kin	-	0.27 (0.06)
β_{G14}	co-migrant males	-	0.68 (0.22)	β_{S14}	co-migrant males	-	0.12 (0.17)

Table 1.5. Fixed effects in forage models. The empty model includes only the intercept and the random effects. The full model includes covariates as fixed effects in addition to the intercept and the random effects. The parameter estimates are posterior means and SD (in parentheses).

		Forage models	
Parameter		empty	full
β_{F0}	base rate	-0.73 (1.05)	-0.62 (1.04)
β_{F1}	female dyad	-	-0.26 (0.04)
β_{F2}	male dyad	-	0.73 (0.05)
β_{F3}	age difference	-	-0.09 (0.02)
β_{F4}	rank difference	-	-0.41 (0.01)
β_{F5}	number of adults	-	-1.62 (0.16)
β_{F6}	mother-offspring	-	0.53 (0.04)
β_{F7}	father-offspring	-	0.01 (0.99)
β_{F8}	full siblings	-	-0.48 (0.04)
β_{F9}	maternal half sibling	-	-0.74 (0.05)
β_{F10}	paternal half siblings	-	0.00 (1.00)
β_{F11}	other kin	-	-0.58 (0.04)
β_{F12}	co-migrant males	-	0.00 (0.99)

Generalized individual effect: Empty models

When not taking into account any of the covariates, capuchins vary the most in how much grooming they provide to others. The giver variance, σ_{Gg}^2, in the empty groom model is 1.12. In their roles as receivers of grooming, the estimated variance, σ_{Gr}^2, is 0.14.

In support for coalitionary aggression, capuchins also vary more in their roles as providers of support ($\sigma_{Sg}^2 = 0.66$) than as receivers of support ($\sigma_{Sr}^2 = 0.22$). The foraging in close proximity data does not contain directional information and therefore the estimated variance, $\sigma_{Fv}^2 = 0.29$, represents the variance in how likely an individual is to be observed foraging in close proximity of others.

Generalized individual effects: full models

The empty models provide estimates of the variance among individuals in their roles as givers and receivers of the interactions. The full models estimate that same variance after taking into account how much of it is explained by the covariates.

After taking into account age, sex, rank, group size, and kinship, individuals vary noticeably less in how much grooming they provide ($\sigma_{Gg}^2 = 0.26$), suggesting that a lot of variation in grooming rates is explained by the covariates. However, there is still more residual variation in how much grooming monkeys provide ($\sigma_{Gg}^2 = 0.26$) than in how much they receive ($\sigma_{Gr}^2 = 0.10$). The same pattern is true in the full support model: after some of the variation in support provided and received is explained by the covariates, monkeys vary more in how much support they provide ($\sigma_{Sg}^2 = 0.38$) than in how much support they receive ($\sigma_{Sr}^2 = 0.12$), a pattern suggesting a somewhat even distribution of grooming and coalitionary support across the group members.

The full foraging model shows that the variation in how likely the dyad is to be observed foraging near others also shrinks to $\sigma_{Fv}^2 = 0.20$ in comparison to the empty foraging model.

Generalized reciprocity

For grooming and support in coalitionary aggression models, which contain directional information on giving and receiving, we can estimate generalized reciprocity, ρ_{gr}. This measure is roughly analogous to the correlation between in-degree and out-degree in social network analyses (Freeman 1978). The generalized reciprocity measure provides information about how an individual's role as a giver of the behavior correlates with their role as a receiver, e.g. do those individuals who groom others a lot also tend to receive a lot of grooming?

For grooming, there is a moderate positive correlation between individual's groom giving rates and groom receiving rates. Generalized reciprocity in the null groom model is estimated to be $\rho_{Ggr} = 0.50$. In the full groom model, this estimate shrinks to $\rho_{Ggr} = 0.43$.

For support in coalitionary aggression, there is a very strong correlation between support given and received, reflecting that the subset of individuals that often participate in fights on behalf of each other is small. The null support model generalized reciprocity is estimated to be $\rho_{Sgr} = 0.92$, while for the full support model it increases to $\rho_{Sgr} = 0.94$.

To better illustrate the generalized reciprocity results, we plotted the individual giver against individual receiver generalized effects for the full groom model in Figure 1.1, and for the full support in coalitionary aggression model in Figure 1.2.

Figure 1.1. Generalized reciprocity in groom full model

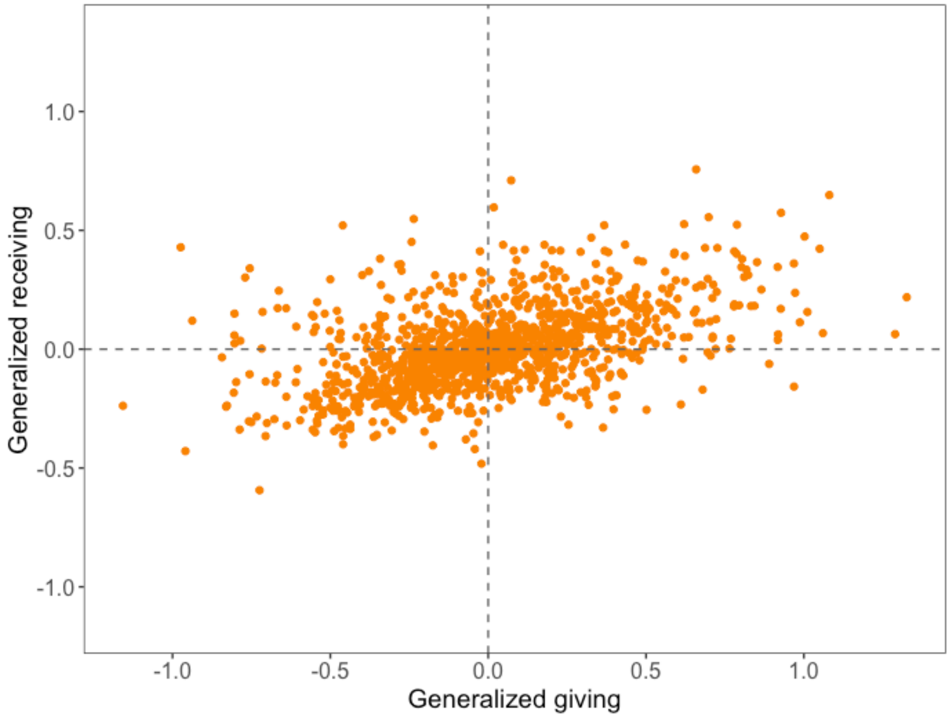
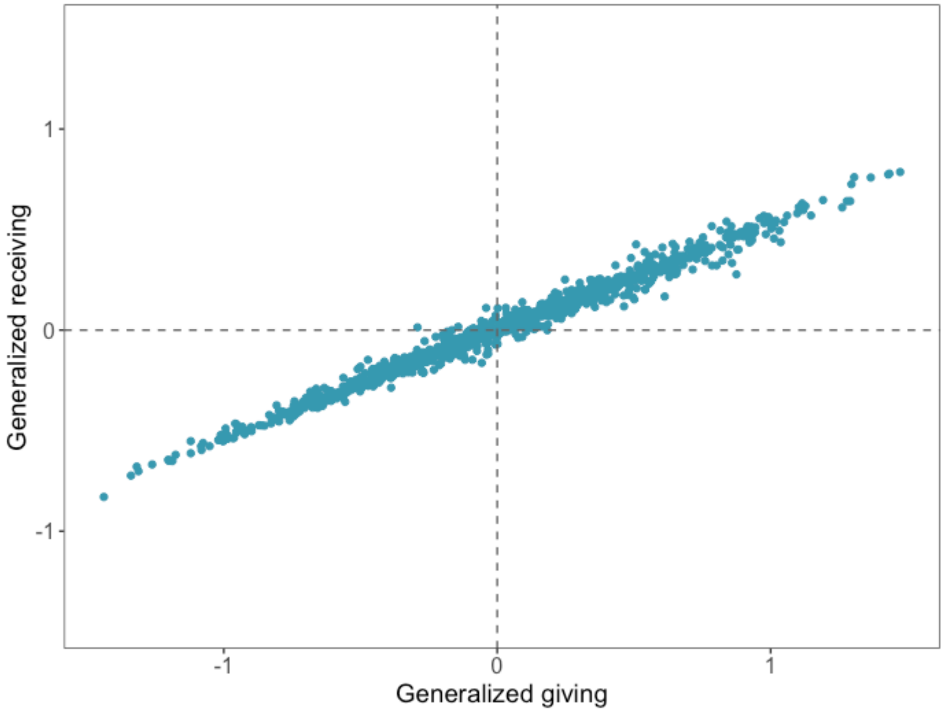


Figure 1.2. Generalized reciprocity in support in coalitionary aggression full model



Dyadic reciprocity

Dyadic reciprocity, ρ_{dd}, measures dyad specific rates after accounting for each individual's generalized propensities as givers and receivers. High estimates for dyadic rates indicate that the dyad (or at least one individual within a dyad) engages more with this partner than he/she engages in this behavior usually. A high correlation between the A-to-B dyadic rate and the B-to-A dyadic rate indicates that when individuals A and B engage with each other, they either intensify or deescalate their general propensities as givers towards each other at about the same rate.

In grooming, both the empty and full model dyadic reciprocity estimates are $\rho_{Gdd} = 0.99$. This means that, once we account for base rate, group specific effects, and individual generalized effects, within a dyad, the actors intensify or de-escalate their grooming at about the same amount. The same is true for the null and full models of support in coalitionary aggression where the reciprocity estimate is $\rho_{Sdd} = 0.99$. To illustrate the dyadic effects, we plotted the dyad specific estimated effect for individual A against the dyad specific estimated effect for individual B in Figure 1.3 for the full groom model, and in Figure 1.4 for the full support model.

Figure 1.3. Dyadic relationship reciprocity in groom full model

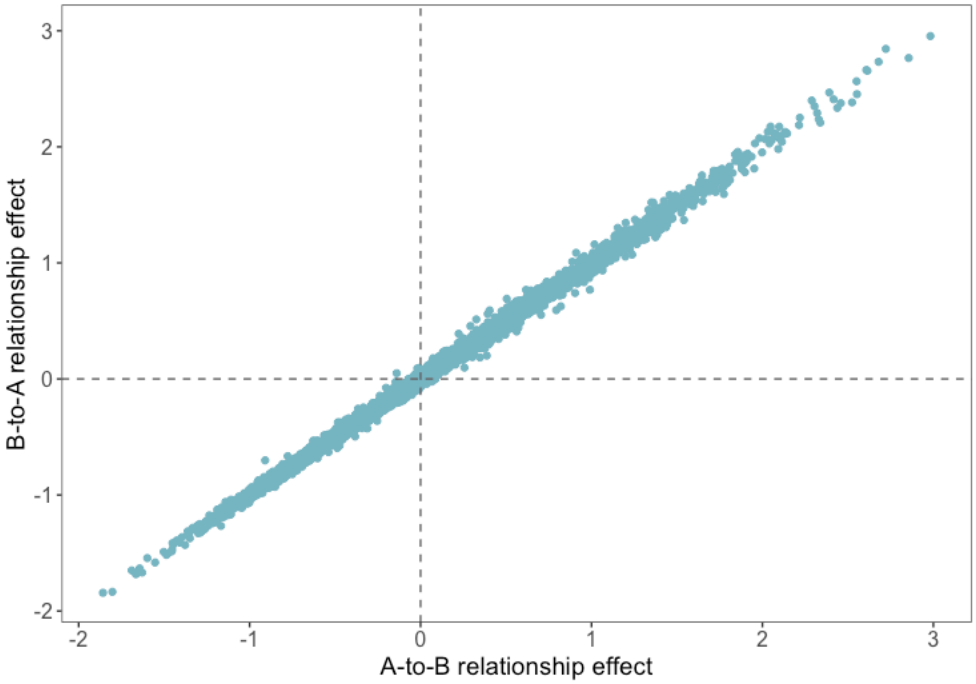
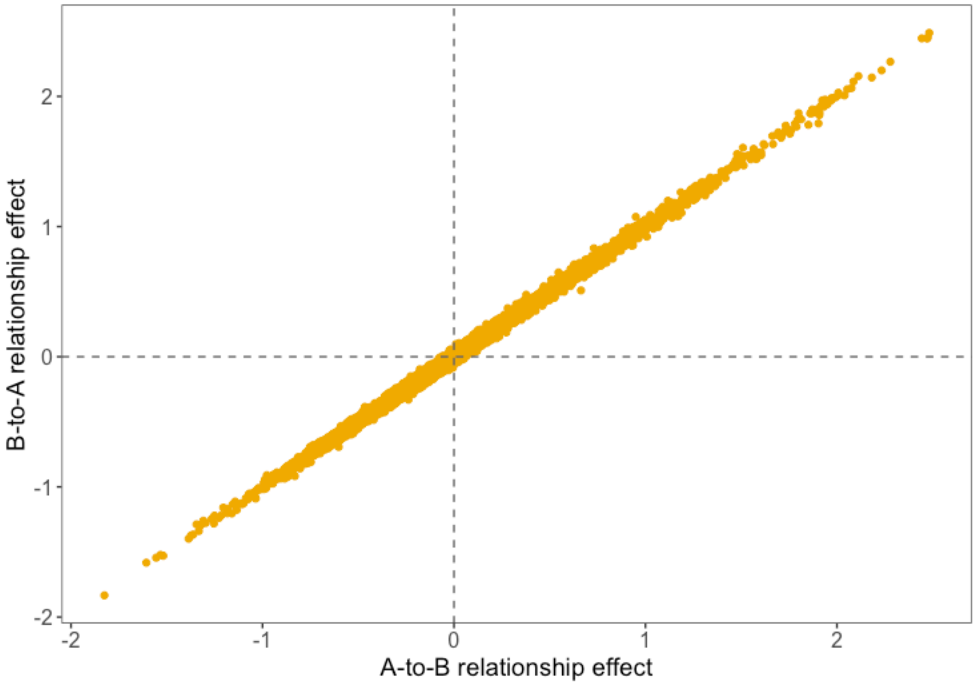


Figure 1.4. Dyadic relationship reciprocity in support in coalitionary aggression full model



Models with covariates

Three out of six models, one for each behavioral domain, had covariates in them related to sex, age, rank, group size, and kinship. We describe the results, grouped by type of covariate, for all three models.

<u>Sex</u>: For grooming and support in coalitionary aggression, both givers and receivers were less likely to be males than females (groom full model: $\beta_{G1} = -1.85, SD = 0.06,$ and $\beta_{G2} = -0.28, SD = 0.05$; support full model: $\beta_{S1} = -0.73, SD = 0.06,$ and $\beta_{S2} = -0.49, SD = 0.04)$, with the effects greater for givers, especially in the grooming model. This means that females are more likely to both groom and receive more grooming, and are also more likely to join a coalitionary conflict and to receive support during a coalitionary conflict.

For the "forage in close proximity" full model, the dyads that forage in close proximity are less likely to be a female-female dyad than a mixed-sex dyad ($\beta_{F1} = -0.26, SD = 0.04$), but more likely to be a male-male dyad than mixed-sex dyad ($\beta_{F2} = 0.73, SD = 0.05$).

<u>Age</u>: As individuals age, they provide less grooming ($\beta_{G3} = -0.34, SD = 0.02$) and less coalitionary support ($\beta_{G3} = -0.16, SD = 0.03$). However, age is not a strong predictor of being a recipient of grooming ($\beta_{G4} = -0.02, SD = 0.02$), and age had a small positive effect on the probability of receiving support in coalitionary aggression ($\beta_{S4} = 0.03, SD = 0.02$).

<u>Rank</u>: Rank had significant effects on interaction rates in all three models. Monkeys who are higher ranking are predicted both to give ($\beta_{G5} = 0.32, SD = 0.03$) and receive more grooming ($\beta_{G6} = 0.28, SD = 0.02$). In coalitionary support, the actors high rank had a greater impact on the rate of joining a coalition ($\beta_{S5} = 0.69, SD = 0.03$) than the receivers rank ($\beta_{S6} = 0.30, SD = 0.02$). Similarly ranked individuals are predicted to more likely forage in close proximity than distantly ranked individuals ($\beta_{F4} = -0.41, SD = 0.01$).

Group size: In all three models, as the number of adult males and females increases, the dyadic interaction rates decrease, with the greatest effect being for foraging in close proximity (groom full model: $\beta_{G7} = -0.16, SD = 0.04$; coalitionary support full model: $\beta_{S7} = -0.10, SD = 0.05$; forage full model: $\beta_{F5} = -1.62, SD = 0.16$).

Kinship: In the grooming full model, all kin categories, except maternal siblings, are predicted to have significantly higher rates of grooming than non-kin/distant kin dyads. Mother-offspring dyads are predicted to have the highest rates of grooming ($\beta_{G8} = 1.41, SD = 0.07$), followed by full sibling dyads ($\beta_{G9} = 0.92, SD = 0.09$), and paternal half-siblings ($\beta_{G10} = 0.80, SD = 0.08$). Co-migrant dyads are predicted to groom more than distant kin/non-kin male-male dyads ($\beta_{G14} = 0.68, SD = 0.22$). Father-offspring and other kin dyads are predicted to groom more than distant kin/non-kin, but have the smallest effect sizes from all kinship categories-although they do have large effect sizes in comparison to other covariates in the model (father-offspring: $\beta_{G9} = 0.44, SD = 0.12$); other kin: ($\beta_{G13} = 0.37, SD = 0.07$). Surprisingly, maternal half sibling dyads have a small and uncertain effect ($\beta_{G11} = 0.07, SD = 0.06$), suggesting that we should be skeptical about the predictions for this kin category.

In the support in coalitionary aggression full model, all kin categories, except father-offspring and co-migrant males, are predicted to have greater rates of coalitionary support than non-kin/distant kin. Mother-offspring ($\beta_{S8} = 0.52, SD = 0.05$), full siblings ($\beta_{S10} = 0.49, SD = 0.07$), and paternal half siblings ($\beta_{S12} = 0.39, SD = 0.07$) have the greatest effects. Other kin ($\beta_{S13} = 0.27, SD = 0.06$) and maternal half siblings have smaller ($\beta_{S11} = 0.12, SD = 0.05$), but significant effects. Father-offspring dyads had a small and uncertain negative effect ($\beta_{S9} = -0.02, SD = 0.08$), and co-migrants had a positive, but uncertain effect ($\beta_{S14} = 0.12, SD = 0.17$).

In the forage in close proximity full model, only mother-offspring dyads are more likely to forage in close proximity than non-kin/distant kin ($\beta_{F6} = 0.53, SD = 0.04$. Full siblings ($\beta_{F8} = -0.48, SD = 0.04,$ maternal half siblings ($\beta_{F9} = -0.74, SD = 0.05$), and other kin ($\beta_{F10} = -0.58, SD = 0.04$) are predicted to forage in close proximity less often than non-kin/distant kin. Father-offspring ($\beta_{F7} = -0.01, SD = 0.99$), paternal half sibs ($\beta_{F10} = 0.00, SD = 1.00$), and co-migrant ($\beta_{F12} = 0.00, SD = 1.00$) are very uncertain.

DISCUSSION

White-faced capuchin monkeys establish reciprocal social relationships. We investigated the rates of interactions in three different domains: grooming, support in coalitions, and tolerance during foraging. Our results suggest that even after accounting for kinship, age, sex, group size, dominance rank of the partners, the capuchin monkeys reciprocate in grooming and coalitionary support exchanges.

We find evidence for both generalized reciprocity (individuals that provide more of a service also receive more of it) and dyad-level reciprocity (if A increases their general tendency to provide service when their partner is B, then B increases their general tendency to provide service to A). The correlation between generalized individual giving and receiving indicates whether or not individuals who initiate one of these behaviors are also more likely to be the recipients of the behavior. This correlation is moderate in grooming, suggesting that those individuals who groom others more do tend to receive more grooming; but the lower variation in individual receiving versus giving of grooming suggests that grooming interactions are somewhat evenly distributed among social group members. The generalized reciprocity correlation between individual support provided and support received in coalitionary aggression is very strong, even after accounting for the covariates. Individuals that engage in a lot of coalitionary aggression tend to receive a lot of coalitionary support. This suggests that a subset of each social group tends, disproportionately, to carry out coalitional aggression.

After accounting for individual tendencies and covariates, we find very strong dyadic reciprocity in both grooming and support in coalitions. This adds to the evidence that long-term contingencies in exchanges are common in primates (Jaeggi et al. 2013). It is important to note that the model does not suggest that capuchin monkeys exchange equal amounts of grooming within dyads. The decomposition of the exchanges of interactions implies that after accounting for each individual's tendency to engage with others in general, when capuchins engage with a specific partner, both parties increase (or decrease) their rate of either grooming or providing coalitionary support by about the same amount. This means that two individuals who have very different individual base rates of grooming will both either increase or deescalate their rates when paired together by about the same amount. So, on an absolute level, they might provide each other with different amounts of grooming, but this grooming is reciprocal since their behavior is changed towards *one another* in approximately the same way.

Our methods for evaluating reciprocity were very different from the methods typically used in the primatological literature. We estimated the annual rates of interactions, which is methodologically more similar to estimating the *long-term statistical contingency* (Jaeggi et al. 2013) than to estimating the *short-term behavioral* reciprocity. We used the Social Relations Model to decompose the variation in grooming and coalitionary support given and received into individual generalized effects that describe an individual's general tendency to engage with anyone in their social group; and into dyadic relationship specific effects, which describe whether an individual engages more or less with a specific partner than their individual general tendency to engage with others. We estimated the reciprocity within grooming exchanges and coalitionary support exchanges separately, although there is some evidence that these different types of currencies may be exchanged (e.g. de Waal 1997; Gomes and Boesch 2009).

The patterns of individual giving and receiving of grooming, coalitional support and foraging tolerance suggest that a lot of variation in dyadic rates is explained by kinship, sex, age, rank, and group size. The estimates of variation in the model without the covariates, in comparison to the model with the covariates, show a decrease in individual variation in providing either grooming or coalitionary support, which suggests that the covariates are good predictors of which individuals are most likely to be either groomers or providers of coalitionary support.

The results of foraging in proximity model show different patterns in how kinship, age, sex, dominance rank, and group size explain the data. Specifically, all kin categories, except mother-offspring, are predicted to forage in close proximity less often than distant/non-kin dyads. This is surprising, since we expected foraging in close proximity to indicate tolerant relationships in feeding context and kinship is typically a good predictor of positive social interactions. What is different about the foraging in close proximity data? First, we used group scan data to extract information about foraging patterns. Group scan data does not contain information about who initiated an approach and who was the recipient of an approach, and this has possibly affected the inferences we can make about association patterns. Second, the model estimates contain a lot of uncertainty in the foraging model: there is huge variation among groups, with a large standard deviation, suggesting that patterns of variation within groups are great. This could be due to differences in habitats or seasonal differences in food availability (e.g. if some groups were more thoroughly observed during certain seasons than others). Third, it is possible that the patterns of association in foraging contexts differ from those in grooming and coalitionary support. Capuchins might be actively avoiding their kin to reduce feeding competition. If true, then this demonstrates that combining multiple behaviors into composite measures is problematic, because those measures implicitly assume the rates vary in similar way across behaviors.

We can detect strong reciprocity in dyadic grooming and coalitionary support relationships statistically, but this raises an intriguing question about how monkeys make decisions about how to modify their behavior when interacting with specific individuals. Do the standard mechanisms proposed for reciprocity in primates explain our findings? Brosnan and de Waal (2002) describe a possible taxonomy for the mechanisms for reciprocity: (1) symmetry-based reciprocity; (2) attitudinal reciprocity; and (3) calculated reciprocity. Symmetry-based reciprocity is mediated by dyadic characteristics, such as kinship, similarity in age, and similarity in rank. Some of the variation in dyadic reciprocity may be explained by these factors; however, even after accounting for them, the dyadic reciprocity measure remains strong. Calculated reciprocity is cognitively the most complex form of reciprocity and is based on mental score-keeping. It is similar to the classic *tit-for-tat* (Axelrod and Hamilton, 1981) behavioral contingency pattern. Attitudinal reciprocity is mediated through the perception of a partner's attitudes towards the subject; it does not require a precise calculation of cost and benefits, just an ability to perceive the other's social predisposition. Schino and Aureli (2008, 2010) propose emotional regulation mechanisms that combine attitudinal and calculated reciprocity mechanisms: i.e., the mediating role of social bonds with loose emotional book-keeping as a mechanism for partner choice.

Our results show that capuchin monkeys adjust their individual rate by about the same amount as their partners. Directly instantiated as a psychological mechanism, this would imply that monkey A knows whether monkey B treats her differently from monkey B's general tendencies, and also that monkey A can respond by matching her own behavior to this divergence. This suggests some sort of book-keeping mechanism, but it is not likely to be calculated reciprocity. There is little evidence that primates tally exchanges within dyadic sequences of interaction (Silk 2003), and the mechanisms necessary to explain our results would require that capuchins perform complex estimations of everyone's base rates from mere observations of exchanges. In humans, where we can access the process of decision making, there is plenty of evidence that in natural situations people do not actually perform calculations of costs and benefits (Collins 1993). A more plausible mechanism, consistent with our findings, would entail processes in which individuals do not retain detailed information about all their groupmates' social behavior, but instead know everyone's general attitudes toward others. Such a mechanism would resemble proposed reciprocity-promoting psychological processes such as emotional regulation (Schino and Aureli 2010a), attitudinal reciprocity (Brosnan and De Waal), and 'relationship score' (Jaeggi et al. 2010, 2013). Primates are good at keeping track of kinship, rank, and social relationships (reviewed in Cheney and Seyfarth 2003). They are likely to track attitudes and dispositions in order to make inferences about their relationships with others and the relationships of third parties.

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Chapter 2

Sociality is associated with longevity in female white-faced capuchins

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ABSTRACT

Across multiple species of social mammals evidence suggest that sociality is associated with fitness. In long-lived species, like primates, lifespan is one of the main fitness components. In this chapter, we investigated whether more social adult female capuchin monkeys live longer than less social females. We used 17 years of the long-term data from Lomas Barbudal Monkey project to quantify sociality in 11 capuchin social groups using three separate interaction types: grooming, support in coalitionary aggression, and foraging in close proximity. To estimate adult female interaction rates and to take into account the variation in observation time between individuals, we used the Social Relations Model. This approach enabled us to estimate individual rates of giving and receiving interactions and the uncertainty due to varying amounts of observations per each individual. We modeled adult females' survival as a function of their sociality, rank, age, group size, and maternal kin presence using a Bayesian Cox proportional hazard model. We found that females who give and receive more grooming and support in coalitionary conflicts tend to have higher survival rates, but rates of foraging in close proximity to others do not have a considerable effect on survival rates.

INTRODUCTION

Some evidence suggests that in social mammals individual sociality is linked to fitness. In humans, social relationships have been linked to health and longevity (reviewed in Holt-Lunstad 2018). Both the presence and the absence of social relationships have effects on lifespan: being socially connected is associated with a lower probability of dying (Holt-Lunstad et al. 2010, Shor and Roelfs 2015, Shor et al. 2013), while having few and poor social relationships is associated with a higher risk of death (Holt-Lunstad et al. 2015, Roelfs et al. 2011).

In non-human animals, the general pattern of positive association between sociality and fitness outcomes is also reported. Social relationships predict reproductive rates (female white-faced capuchins, *Cebus capucinus:* Fedigan et al. 2008; horses and zebras: Rubenstein and Nuñez 2009; male Assamese macaques, *Macaca assamensis*: Schülke et al. 2010; rhesus macaques, *Macaca mulatta*: Brent et al. 2013; male chimpanzees, *Pan troglodytes schweinfurthii*: Gilby et al. 2013) and infant survival (yellow baboons, *Papio cynocephalus ursinus*: Silk 2009; savannah baboons, *Papio cynocephalus*: Silk 2003; white-faced capuchins, *Cebus capucinus:* Kalbitzer et al. 2017).

In long-lived species like primates, lifespan is one of the main fitness components (Clutton-Brock 1998) and some evidence supports the hypothesis that sociality increases longevity. In chacma baboons (*Papio hamadryas ursinus*) females live longer if they maintain strong and stable social relationships with other females (Silk et al. 2010). A positive relationship between female association with both adult female and adult male partners affects longevity in baboons (Archie et al. 2014). Among the macaques of Cayo Santiago, the association between social integration and lifespan depends on age (Brent et al. 2017). For prime-aged females, but not for older females, number of living adult female relatives was positively associated with survival rate. A context dependent pattern was also reported in blue monkeys (*Cercopithecus mitis stuhlmanni),* where females who had a strong social relationship consistently with the same partner tended to live longer in comparison to females whose strong partnerships were inconsistent across multiple years (Thompson et al. 2018).

Besides primates, sociality is associated with longevity in some other animals (rats: Yee et al. 2008; free-ranging brown bears, *Ursus arctos*: Fagen & Fagen 2004; feral horses, *Equus caballus*: Nuñez et al. 2015), but we should be careful of assuming that there is always a positive association between sociality and fitness. In facultatively social yellow-bellied marmots (*Marmote flaviventer*), the relationship between sociality and longevity is negative: More social animals tend to live shorter lives (Blumstein et al. 2018).

We have very little information on how sociality shapes fitness in neotropical primates. One study reported the differential survival of white-faced capuchin offspring as a function of the mother's sociality and the group's stability (Kalbitzer et al. 2017). The nature and magnitudes of the costs and benefits that individuals can confer on social partners vary across species, and possibly even among populations of the same species. In this chapter, we investigate whether female white-faced capuchins who are more social live longer than less social females.

White-faced capuchins have a similar social structure to cercopithecine monkeys (Perry 2012). These monkeys live in multimale, multifemale social groups (Perry et al. 2012). Females are philopatric – they stay in their natal groups for their entire lives – which allows researchers to collect data about the social interactions from large portions of their lives (Fragaszy et el. 2004; Perry et al. 2008). As a result, females' demographic and behavioral records are more complete than males' records, because males transfer to different groups multiple times in their lives and often leave the study area. This makes female capuchins more suitable subjects for the investigation of the relationships between individual sociality and survival.

In this chapter, we analyze seventeen years of interactions of white-faced capuchin monkeys. To quantify individual sociality, we selected interactions from three domains in order to take into account the variety of social behaviors that capuchin monkeys engage in: grooming, coalitionary aggression, and foraging in proximity to others.

Allogrooming, or social grooming, is a common behavior in capuchin monkeys (Perry 1996). Grooming serves a hygienic and social bonding function. It also thought to impose costs on groomers - of loss of time and increased vigilance. Therefore, grooming is thought of as a form of altruism (Manson et al. 2004) and is possibly shaped by reciprocity (Trivers 1971). These features of grooming behavior make it a good candidate for providing information regarding an individual's sociality.

Coalitionary aggression is frequent in capuchin monkeys (Perry 2012). Engaging in aggressive behavior when joining an existing conflict can be very costly since there is a high rate of coalitionary lethal aggression in capuchins (Gros-Louis et al. 2003). Individuals might be more willing to join coalitionary conflicts on the side of individuals with whom they cultivate strong social bonds.

Foraging is one of the main activities that capuchins engage in. Although foraging is a seemingly asocial behavior, the way individuals distribute themselves across space can be indicative of their social relationships. Greater social tolerance, possibly indicative of stronger social bonds, may characterized dyads that forage in close proximity more frequently. While it is costly (more competition for food), foraging in proximity might also strengthen existing social bonds.

Lomas Barbudal Monkey dataset provides a great opportunity to test for an association between female sociality and survival. The dataset has longitudinal records on individuals living in 11 capuchin social groups. It contains detailed records including demographic information, pedigree information, and data regarding social interactions that are necessary for quantifying individual sociality.

METHODS

Study subjects and the dataset

We studied members of the wild white-faced capuchin population at the Lomas Barbudal Biological Reserve and surrounding private lands in Guanacaste, Costa Rica (Perry et al. 2012). The records on capuchin behavior were collected between January 2002 and May 2018. The subjects were 125 adult females, living in eleven different social groups over 140 group years (average years per group = 12.7; range = 7 – 17 years). The females were considered adults once they reached the age of 5 years. The behavioral and demographic data on each group were collected by experienced observers during censuses lasting at least 6 hours/day.

Measuring Sociality

To measure female sociality, we chose three behavioral domains: grooming, coalitional aggression, and foraging. Grooming and coalition formation were treated as directional behaviors, and we used observations of individuals as both initiators and recipients of the behavior. Foraging in proximity was treated as a non-directional behavior, i.e. we did not incorporate information about which individual had initiated the proximity. In calculating the frequency with which adult females engaged in these interactions, we used behavioral records from all the individuals who resided in the eleven groups during the study period. There were a total of 511 monkeys, residing in 11 social groups, comprising 11798 dyads. We chose not to use "composite" indices of sociality (e.g. Silk 2006 a,b; Archie et al. 2014; Kalbitzer et al. 2017) and instead treated each of the three interaction types as a separate measure of sociality. Composite sociality measures (Silk et al. 2013) implicitly assume that the behaviors included in the index are weighted equally. We had no reason to assume that grooming, joining a coalitionary conflict, and foraging in the proximity of others occur at the same rates and would contribute equally to an individual's sociality. Furthermore, due to the differences between each type of behavior, various data collection protocols were required for the collection of data. This makes composite measure even more problematic (Farine 2015).

Grooming (groom give and groom receive)

Grooming rates were estimated using data collected during 10-min. focal follows. To estimate individual grooming rates, we calculated dyadic counts of grooming and dyadic opportunities for grooming. The opportunity for a dyad, A-B, to engage in grooming, was calculated as the sum of the focal follows of A and the focal follows of B at times when A and B were residents of the same social group. The dyadic counts of giving and receiving grooming were assigned as follows: a count of 1 was assigned if A groomed B during a focal follow; a count of 1 was also assigned if B groomed A during a focal follow, otherwise 0 was assigned for either direction. Only one count per direction in one focal follow was scored.

Joining a coalitionary conflict (support give and support receive)

The behavior of joining a coalitionary conflict was defined as an individual intervening on one side during an ongoing aggressive conflict. This definition only indicates the functional aspect of joining a side; it entails no inferences about internal psychological states such as the intent to help a specific individual. Since aggressive interactions are salient and harder to miss than quiet activities like grooming or foraging in proximity, aggressive interactions were collected both *ad libitum* and during focal follows. The chronological stream of aggressive behaviors was divided into 5 min. segments. In order to identify instances of joining a coalitionary conflict, monkey A is identified as joining monkey B, if A performed an aggressive behavior toward either monkey B's opponent or victim within the context of the 5-minute segment. Even if multiple instances of A joining monkey B were observed during the 5 min segment, we scored only one instance of A joining B. To calculate the opportunities to join a coalitionary conflict, all individuals who were co-resident during the aggressive conflict were counted as having had an opportunity to join on either side during the conflict.

Foraging in proximity

Foraging in close proximity was estimated from group scans that occurred in the context of foraging. In group scans, the identity of the scanned individuals, their activity and their proximity to other individuals within 10 body lengths (~2 m) was noted. We considered individuals to be foraging in close proximity if they were scanned within 5 body lengths (~1m) of each other. For each dyad, we scored whether they were observed foraging within close proximity in 10 min. segments (i.e. if they were observed doing this more than once within 10 min., only one instance was counted). The number of opportunities that the dyad had to forage within close proximity is a sum of group scans in the foraging context that are 10 min. apart, where one of the individuals is a subject of a group scan.

The Social Relations Model and Individual Relative Rates

Typically, counts of observed interactions divided by the opportunities to engage are used as a raw frequency of interactions (e.g. Silk 2006a, b). We found a great deal of variation among dyads in their opportunities to engage. In order to take this variation into account, we used observed counts and opportunities to model the interaction rates using the Social Relation Model. These model estimates were then used as predictor variables, with survival as the outcome variable (see below).

The Social Relations Model (Kenny 1994, Snijders and Kenny 1999) decomposes the variance in giving and receiving behaviors into separate giving, receiving, and dyadic relationship components. To account for the variation in exposure for dyads we entered the natural logarithm of the opportunities to engage in behavior as an offset in the model. We fitted a Bayesian multilevel Social Relations Model with the following parameters: the intercept parameter (base rate), social group-level, individual giving, individual receiving, dyadic symmetric, and dyadic asymmetric random effects parameters. We used data collected on the entire population (i.e. adult males, females, and immatures) since Social Relations Model is a multi-level model and can take advantage of pooling and shrinkage in estimating the average rates of interactions in the population (McElreath 2015). Although we estimated the random effects for all the individuals in the population, we used the adult female individual random effects estimates of groom giving, groom receiving, support giving, support receiving, and non-directional foraging in proximity rate estimates as our five individual estimates of sociality.

The posterior estimates of mean and SD of female giving and receiving random effects capture the extent to which an individual female deviates from the estimated average rate of engaging in this behavior in the population. The estimates are centered on zero, which represents the population mean. Each behavior domain has its own base rate estimate. For example, the mean estimates of groom giving ranges from -2.9 to 3.5 across the entire population. For a particular individual, a posterior mean estimate closer to the minimum indicates that this individual grooms others much less than the average monkey grooms her partners in the population. The reverse is true for a posterior mean estimate close to the maximum of the range. We will refer to these posterior estimate means and distributions as relative estimates.

The Social Relations Model estimates resulted in five individual-based, age specific relative estimates for adult females: the relative estimate of grooming others (groom give); the relative estimate of receiving grooming from others (groom receive); the relative estimate of joining a coalitionary aggression (support give); the relative estimate of others joining coalitionary aggression on the same side as the focal (support receive), and a non-directional relative estimate of foraging within close proximity of others (forage in proximity).

Testing relative estimates of social behaviors as predictors of survival

To test whether sociality affected female survival, we used Baysian Cox proportional hazards models. In separate models, each of the five relative behavioral rate estimates described above (groom giving estimate, groom receiving estimate, support giving estimate, support receiving estimate, and foraging in proximity of others estimate) was modeled as a predictor of survival probability over one-year periods. These models included the following time-varying (calendar year-specific) covariates: the female's age, her dominance index, the average number of individuals in her group, the proportion of time during that year that her mother was alive, and the number of adult daughters that she had.

Age: The age of focal females was estimated from demographic records on births and deaths collected from 1990 – 2018. The age of females who were born before 1990 was estimated in part by retroactively comparing photos taken then with photos of known-aged females collected later in the study. In addition, we inferred reproductive histories via genetic maternity data, and assuming that, given two-year interbirth interval and an age of first birth of six years (Fedigan et al. 1995, Perry 2012), that a female with one offspring had to be at least six years old, a female with at least two offspring had to be at least eight, etc.

Age is not likely to have a linear relationship to survival across a female's lifespan. We included linear and quadratic functions of *age* to account for expected non-linearity in the effects of age on survival probability.

Average number of individuals in her group: This is the mean number of adult females, adult males and immatures that resided in the female's group during the days when researchers spent at least six hours of observation with the group, averaged for the year.

Mother's presence: The proportion of the year that the female's mother was alive and co-resided with her. The measure varies from 0 to 1, where 1 indicates that the mother was alive and co-resident with the focal female for the entire year, and 0 indicates that the mother died in some previous year.

Number of daughters: The number of daughters that a focal female had was very highly correlated with her age (0.72). To control for the effect of age on the number of daughters, we grouped all of the females that were the same age together, and centered the number of daughters for each age group. For every age group we subtracted the mean number of daughters for that age group to reduce the confounding between age and number of daughters. The resulting variable was not correlated with age (~0).

Annual dominance index: The annual dominance index represents the proportion of group members that the female dominated, on average, that year. For each observation day that the female (the focal) resided in a social group, we identified all of the other co-resident individuals (alters). To assess whether the female was dominant to an alter on a particular day, we identified the two most recent dominance interactions for each focal-alter dyad: one immediately before and one immediately after the day. The total number of these interaction across all focal-alter dyads represents the number of opportunities for the focal to dominate someone. For each interaction, we identified that the focal individual was dominant if she was either the animal performing the supplanting, or being cowered at, or being avoided, or fled from. The daily dominance index, DDI_i, of a focal individual, i, is a sum of dominance interactions where focal was dominant to their alters, $w_{i\text{-}a}$, divided by the total number of dominance interactions that the focal had with her alters, $s_{i\text{-a}}$:

$$DDI_i = \frac{\sum w_{i-a}}{\sum s_{i-a}} \, . \qquad (5)$$

Then, the average annual dominance index, ADI_i, is an average of daily dominance indices:

$$ADI_i = \frac{1}{n} \sum_{i=1}^{n} DDI_i \, . \qquad (6)$$

In some cases, either one or no dominance interactions were available for a focal-alter dyad. As a result, the individuals who did not have dominance interactions with the focal did not contribute to the calculation of the daily dominance index.

Modeling approach

To take into account that some females contributed different numbers of years to the analysis, we modeled individual differences using a random effect term. Models were run using the *rethinking* package (v. 1.82: McElreath 2019) in *R* (v. 3.5.2; R Core Team 2018).

More formally, we specified the following model for D_i, the number of days before death. The probability for number of days before death come from cumulative probability distribution:

$$\Pr\,(D_i \mid \lambda_i) = \lambda_i \exp(-\lambda_i D_i)\,. \tag{1}$$

For females who did not die during the observation period, the probability of waiting D_i without dying comes from the complementary cumulative probability distribution:

$$\Pr\,(D_i \mid \lambda_i) = \exp\,(-\lambda_i D_i)\,. \tag{2}$$

We model the rate of dying, λ_i, as follows

$$\lambda_i = 1/\mu_i\,. \tag{3}$$

where μ_i is the number of days till death

$$\begin{aligned}\log(\mu_i) = \alpha + a[id] + b_{sociality} * true\ sociality\ estimate[id] + b_{rank} * rank_s \\ + b_{age} * age_s + b_{age2} * age_s^2 + b_{daughters} * daughters_c \\ + b_{daughters} * mother_s + b_{grsize} * group\ size_s\,.\end{aligned} \tag{4}$$

α denotes intercept or the base rate of number of days survived, $\alpha[id]$ denotes individual female random effects. The model coefficients $b_{sociality}$, b_{rank}, b_{age}, b_{age2}, $b_{daughters}$, b_{mother}, b_{grsize} describe the impact of sociality, rank, age, number of daughters, mother's presence, and group size. We took a latent variable approach to model the sociality estimates, since sociality estimates are not point estimates, but rather posterior distributions with mean and SD reflecting uncertainty about the true rate. Under this approach, we assumed that each female had some true underlying sociality measure, $true\ sociality\ estimate[id]$, which was normally distributed with mean and SD equal to the mean and SD of the sociality estimate drawn from Social Relations Model results.

We used Bayesian approach to fit Cox proportional hazard model (McElreath, forthcoming). We assumed Normal (3.81, 0.5) prior for base rate, α, and Normal (0,1) prior for all the rest of the mixed effects. All of the covariates, except for the sociality relative estimates and the number of daughters, were standardized by subtracting the mean and diving it by the standard deviation.

Calculating Relative Effects

To calculate the proportional changes in the odds of dying between low and high sociality individuals, we multiplied the sociality coefficient, $b_{sociality}$, by the 25th percentile and separately by the 75th percentile of the relative sociality estimate. The exponentiated difference between these two values represents the relative effects of proportional changes in the odds of dying in a given year between a female who is at the 25th percentile of the sociality distribution and 75th percentile of sociality distribution.

RESULTS

(1) Measures of sociality

Figure 2.1 illustrates how the estimates of the relative frequencies of grooming, coalitional support, and foraging in proximity by adult females compared to the estimates for other age-sex classes. Adult females gave more grooming than individuals of other age-sex classes. With respect to receiving grooming, and giving and receiving coalitional support, adult females’ estimated frequencies were slightly higher than those of other age-sex classes. Adult females had slightly lower estimated frequencies of foraging in close proximity to others, compared to individuals of other age-sex classes.

Figure 2.1 also shows the ranges of variation among females in these measures of sociality. Females varied much more in how much grooming and support they provided than in how often they were recipients of those interactions. Despite this variation, in the domains of grooming and coalitional support, there were strong positive correlations between the estimates of giving and receiving (Figure 2.2), i.e. females who gave more grooming also received more grooming (r = 0.68), and females who gave more support also received more support (r = 0.98). Correlations between the relative rates of other pairs of sociality behaviors were positive, but moderate.

Figure 2.1. Posterior mean distributions of annual relative rates for each type of behavior. Orange represents adult females, blue represents the rest of the population. Population base rate is at zero.

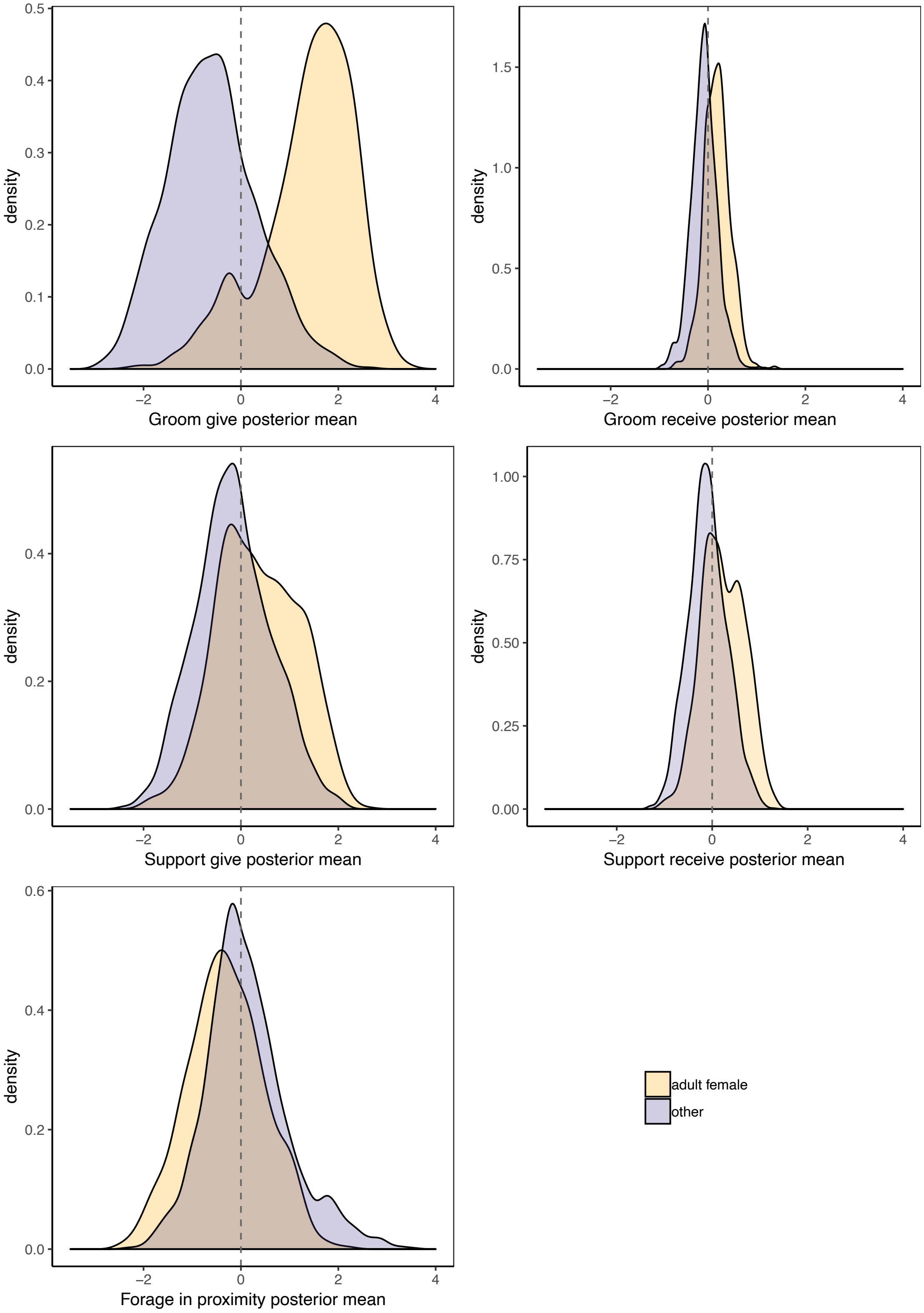
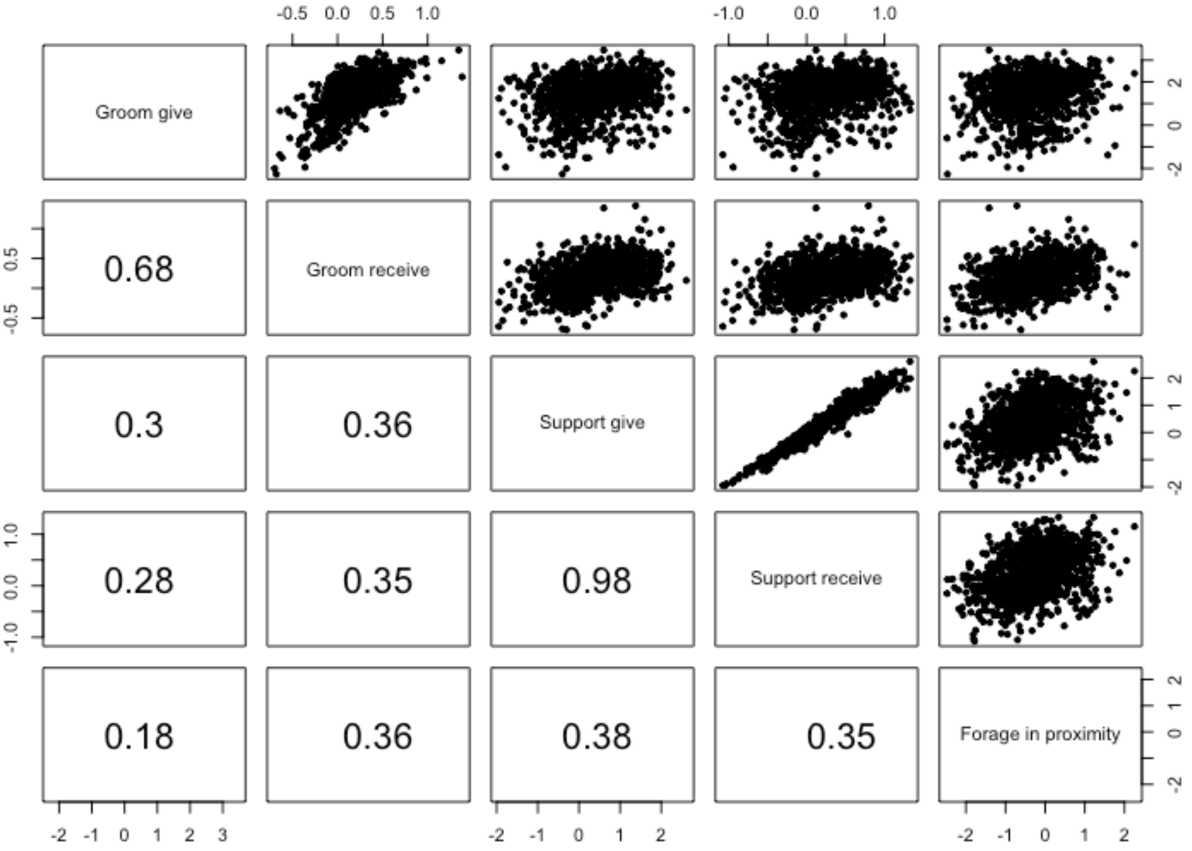


Figure 2.2. Bi-variate correlations of sociality measures.



(2) Adult female sociality has an effect on survival

Independent of the effects of covariates (age, dominance rank, group size, number of adult daughters, co-residence with mother), more social females survived at higher rates than less social females. Table 2.1 presents Cox proportional hazards model posterior mean estimates and 95% Highest Posterior Density Interval (HPDI), representing the narrowest interval containing the 95% probability mass. The relative effects of sociality were highest in the grooming domain. Figure 2.3 provides a comparison of the posterior means and their standard errors across five Cox proportional hazard models.

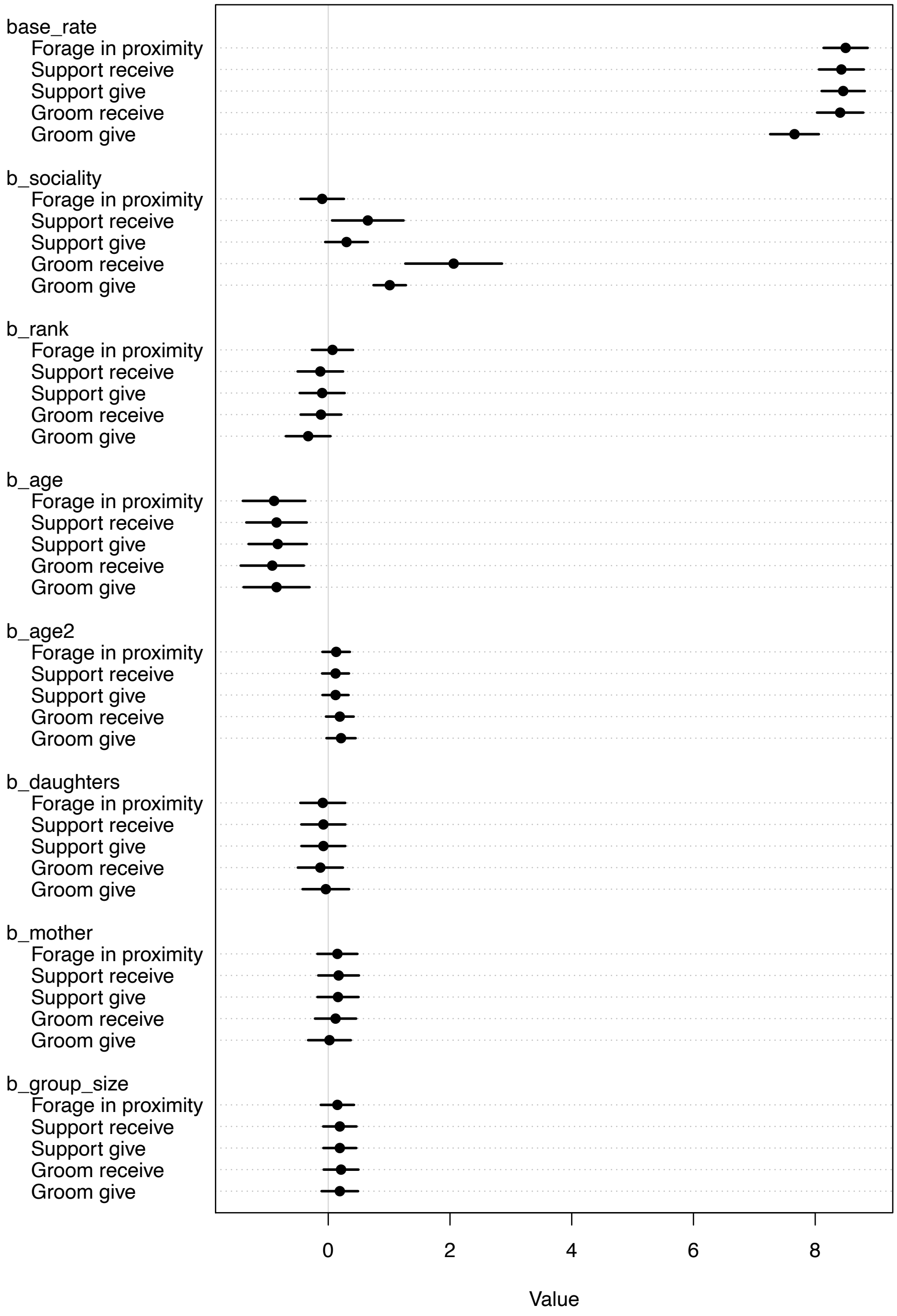
On average, females who were in the lower 25th percentile of groom giving experienced 230% increase in odds of dying in a given year, compared to females in the upper 75th percentile of groom giving. Females that were in the lower 25th percentile as receivers of grooming had 107% increase in odds of dying in a given year than the females in the upper 75th percentile of groom receiving. Females who were in the lower 25th percentile of providing support in coalitional conflicts had 149 % increase in odds of dying in a given year than the females in the upper 75th percentile. Females who were in the lower 25th percentile as the recipients of support during coalitional conflicts had 158% increase in odds of dying in a given year than the females in the upper 75th percentile.

Females who spent more time foraging in close proximity to others actually had an increased probability of dying, but this effect was small, and the estimates were more uncertain than those for the effects of grooming and coalitional support (Table 2.1 and Figure 2.3). Females who were in the upper 75th percentile of foraging in close proximity rates had 8 % increase in odds of dying than the females in the lower 25th percentile.

Table 2.1. Estimates of fixed effects of each of the Cox proportional hazards models: posterior means and 95% HPDI.

	Sociality measure				
Parameter	Groom give	Groom receive	Support give	Support receive	Forage in proximity
Intercept	7.66 [7.33,8]	8.41 [8.11,8.73]	8.46 [8.18,8.75]	8.43 [8.14,8.74]	8.5 [8.21,8.79]
β sociality	1.01 [0.8,1.24]	2.06 [1.43,2.7]	0.3 [0.01,0.58]	0.65 [0.17,1.13]	-0.1 [-0.39,0.19]
β rank	-0.33 [-0.62,-0.04]	-0.12 [-0.37,0.16]	-0.1 [-0.41,0.18]	-0.13 [-0.43,0.18]	0.07 [-0.21,0.34]
β age	-0.85 [-1.3,-0.42]	-0.92 [-1.36,-0.5]	-0.83 [-1.22,-0.45]	-0.85 [-1.26,-0.44]	-0.89 [-1.31,-0.47]
β age^2	0.21 [0.02,0.42]	0.19 [0,0.38]	0.12 [-0.06,0.3]	0.12 [-0.06,0.3]	0.13 [-0.05,0.32]
β daughters	-0.04 [-0.35,0.27]	-0.13 [-0.44,0.18]	-0.08 [-0.38,0.21]	-0.08 [-0.38,0.21]	-0.09 [-0.39,0.22]
β mother	0.02 [-0.27,0.31]	0.12 [-0.16,0.39]	0.16 [-0.12,0.44]	0.17 [-0.11,0.44]	0.15 [-0.12,0.43]
β group size	0.19 [-0.06,0.43]	0.21 [-0.02,0.44]	0.19 [-0.02,0.41]	0.19 [-0.02,0.42]	0.15 [-0.07,0.38]

Figure 2.3. Posterior means and standard errors of Cox proportional hazards model.

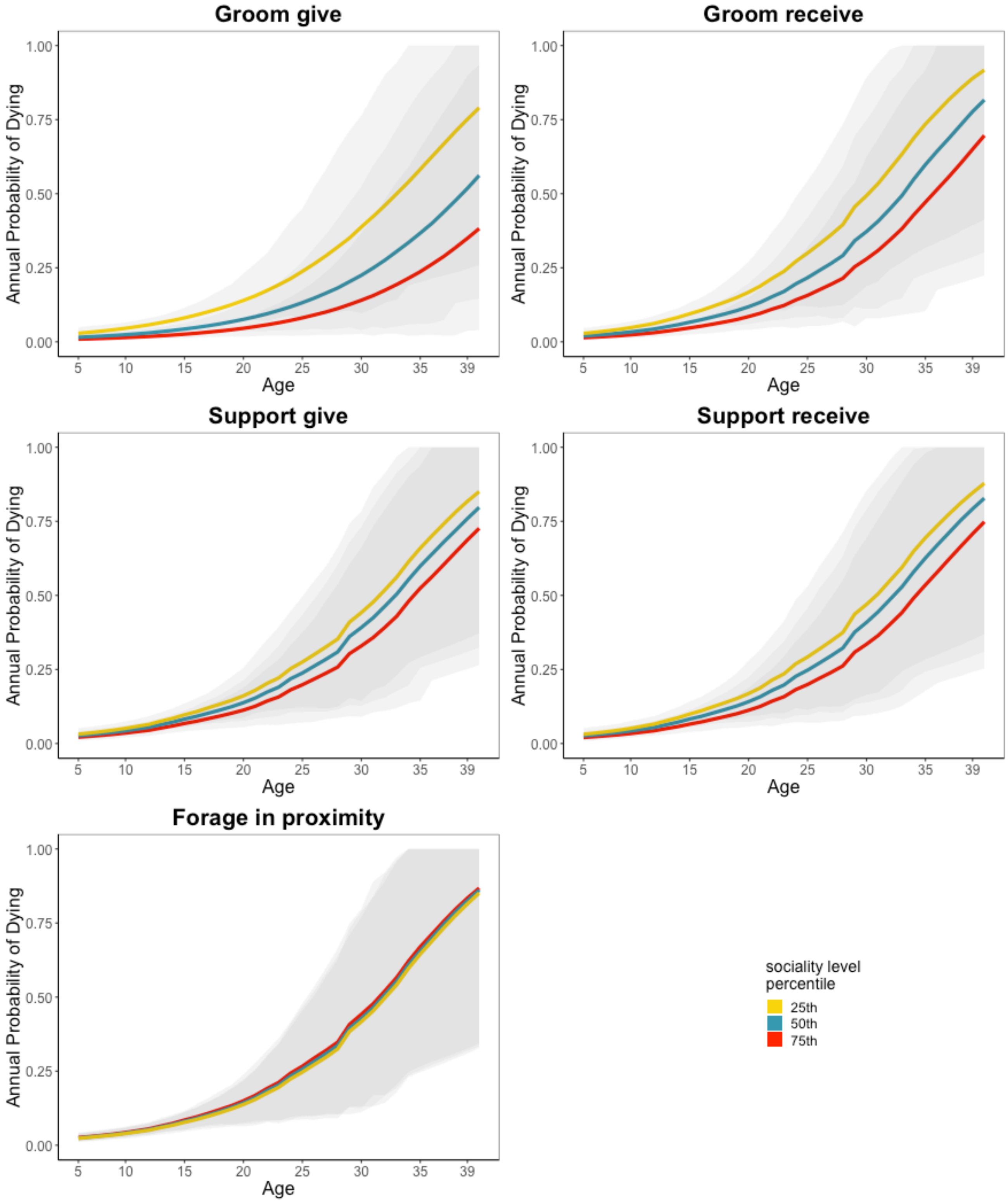


To facilitate the interpretation of Cox proportional hazard model coefficients, we plotted model predicted annual probabilities of dying (Figure 2.4). We computed annual probability of dying for females who live in a median size group (22.6 individuals on average), are in the middle of the hierarchy, have an average number of daughters for their age, and who are co-resident with their mothers for an average proportion of the year for their age. We have varied females' age and their sociality level to compute the predictions. Figure 2.4 illustrates the annual probability of dying as a function of female's age and her sociality level, holding all other covariates fixed. Unsurprisingly, probability of death increased with age. Females at the 25th percentile of the grooming and coalitional support distributions had a higher probability of dying than females who engaged in more grooming and coalitional support. Females at the 25th percentile of the distribution of foraging in proximity to others had a slightly lower probability of dying than females who spent more time foraging in proximity to others.

(3) Other predictors of survival

Besides sociality measures, we also modeled how age, rank, average group size, mother's presence and number of daughters affects survival. All of these effects had very similar estimates across five models (Table 2.1 and Figure 2.3). With the exception of age, the predictors had small and uncertain effects, especially rank and number of daughters posterior mean estimates were close to zero. The base rate of groom give model was lower than other base rate estimates. This is due to female groom give estimates being very different from the rest of the population, with majority of the females providing more than average rates of grooming.

Figure 2.4. Cox proportional hazard model predicted annual probabilities of dying as a function of female's age and her sociality level.



DISCUSSION

In female white-faced capuchin monkeys, greater sociality is associated with higher survival rates. Females who provided, and received, more grooming and coalitional support died at lower rates than females who engaged in these behaviors less often. These results are consistent with findings that various measures of sociality are positively associated with survival in baboons (Silk et al. 2010; Archie et al. 2014), macaques (Brent et al. 2017), humans (Holt-Lunstad et al. 2010), rats (Yee et al. 2008), horses (Nuñez et al. 2015) and bears (Fagen & Fagen 2004).

Importantly, survivorship is just one of several fitness components (Clutton-Brock 1998). Other research indicates that offspring survival is not always enhanced by higher levels of a mother's social engagement. Kalbitzer et al. (2017) reported that in white-faced capuchins, the offspring of highly social females suffered greater death rates, compared to the offspring of less social females, during periods of an alpha male takeover. The more social females and the alpha male tend to be central in the social group (Perry 2012; Kalbitzer et al. 2017). During periods of social stability, spatial centrality provides benefits to females such as better access to food, alloparental care, and protection from predation, but these benefits may be outweighed by an increased risk of infanticide when a new alpha male takes over. Both infant survival and longevity are important components of variation in fitness in long-lived species, but individual fitness benefits of survival, provided by stronger social bonds, might outweigh the cost of higher infant mortality during periods of instability.

The analytical methods that we used distinguish our study from others in several respects. First, we chose to not use composite sociality measures that are typically used in primatology (e.g. Silk et al. 2006 a,b). We chose three behavioral domains, each of which represent different type of social engagement in capuchins: grooming, coalitionary conflicts, and foraging. Composite measures implicitly assume that interaction rates contribute equally to capturing an individual's sociality. We had no reason to assume that the three types of behaviors we chose should be weighted equally, because the rate at which capuchins engage in these behaviors differs, and their potential impacts on social relationships and fitness are likely to be different as well. For example, joining coalitionary aggression occurs less frequently than grooming, but these interactions can have a greater impact on the social relationships and fitness of those involved. Moreover, different observation protocols were used to collect data for each of these behavioral domains: grooming exchanges were recorded through focal follows, aggressive interactions were documented *ad libitum,* and foraging in close proximity observations were collected using scan sampling techniques. Constructing a single composite measure from these three types of behavior, while ignoring the differences in the processes that generated the data, could distort statistical inferences regarding the relationship of sociality to survivorship.

Instead, we ran separate models of the relationships between five forms of social behavior (predictors) and survival rate (the outcome variable). In other words, our goal was to see if we could detect relationships between sociality and longevity across multiple types of interactions (Farine 2015). Our results show that, in female capuchins, different forms of social behavior had different relationships with survival – in particular, rates of foraging within close proximity of others was not positively associated, and may even have been weakly negatively associated, with longevity. Thus, combining these behaviors into a composite measure would not have been appropriate.

As in previous studies, we did not focus on adult female interactions with other adult females only (Silk et al. 2010, Kalbitzer et al. 2017; Archie et al. 2014) or with adult males only (Archie et al. 2014). The consideration of sample size in estimating rates was a priority in our analysis (Farine 2015). There are few datasets that contain detailed longitudinal information about the social interactions of primates. Records of social history are particularly valuable for estimating the variation in sociality among individuals. However, interaction data is typically more sparse than proximity data, because it is harder to collect. Analysts therefore face a high risk of false negatives, i.e. some dyads are inferred to have no social relationship at all, whereas if behavior sampling were sufficiently dense, they would be observed to interact, although rarely (Farine 2015). We prioritized higher resolution of the data, and therefore we chose to use each female's entire observation history with her group members to ensure as accurate as possible a picture of a female's true sociality (Farine & Whitehead 2015).

In addition to overall sample size, we also attempted to address the variation between and within dyads of females based on how much information we had annually (Farine & Strandburg-Peshkin 2015). There was a lot of variation in the amounts of data we collected for each dyad in terms of opportunities they had to engage, and this varied between the social groups, and within dyads across years. To estimate the uncertainty about the rates of interaction we used the Social Relations Model (Kenny 1994; Snijders and Kenny 1999). This approach enabled us to estimate individual rates of giving and receiving interactions and the uncertainty associated with varying number of observations. As a multi-level model, the Social Relations Model takes advantage of shrinking and pooling across the population (McElreath 2016), which underscores the importance of using the entire interaction network to estimate females' individual rates.

A biologically interesting question deals with the mechanisms that facilitate the relationship between sociality and longevity. Although our study does not directly address this question, there are some implications that may be drawn from our findings. A key question is whether the tested behaviors themselves have a direct effect on survival, or whether these behaviors serve as proxies of other processes that affect survival. If we assume the former, then we should address how providing and receiving grooming and coalitional support translate into increased rates of survival. Receiving grooming can serve a hygienic function (Akinyi et al. 2013), thermoregulatory function (McFarland et al. 2016), and can reduce stress (Wittig et al. 2008), while receiving coalitional support might result in fewer injuries and the acquisition of higher rank (Shülke et al. 2010). It is difficult to imagine how providing these behaviors could increase an individual's chances for survival.

Perhaps thinking in terms of isolated interactions is not very useful, because individual sociality is likely to be composed of the many types of relationships that an animal has: affiliative, agonistic and others. Genetic and dominance relationships are bound to play a role too. The lifespans that we observe are a result of many decisions and resulting interactions and there is arguably more than one pathway composed of multiple mechanisms in how sociality can affect survival in a particular species (Ostner & Shülke 2018; Thompson 2019). Behaviors such as grooming and coalitional support indicate social relationships that individuals cultivate, but are probably not the sole indicators of those relationships.

Recently there has been a call for an increased focus on understanding how sociality is associated with fitness in primates (Ostner & Shülke 2018; Thompson 2019). A satisfying investigation would entail collecting data in order to address one or more of the proposed pathways. Our study was not designed with this purpose in mind, but the way we measured sociality excludes some of the possible pathways linking sociality to longevity. For example, we estimated annual rates of interactions, which excludes any pathway associated with chronic stress induced by low sociality (Uchino 2006; Holt-Lunstad et al. 2010). There is a possibility that acute stress experienced as a result of reduced sociality has effects on longevity. Acute stressors such as predators (van Noordwijk & van Schaik 1986), harassment from conspecifics (Stanton et al. 2012), or extreme cold (McFarland & Mojolo 2013), can have an impact on survival.

A more direct way social interactions might influence fitness is proposed by the main effects model (Cohen and Gottlieb 2001). The social partners influence an individual's cognition, emotions, behavior, and biology through interactions that are not explicitly intended to help or support (Cohen and Gottlieb 2001). For example, in humans, feelings of increased self-worth, belonging, and conformity can affect behavior and eventually health (Holt-Lunstad et al. 2010). Social integration may also confer psychological benefits through the reduced perception of risk in capuchin females (Thompson 2019). More social females might enjoy the benefits of both the reduction in exposure to actual stressors and the moderation of their perception of stressors by their sociality level; these in turn could affect their longevity positively. Taken together, these data suggest that capuchin monkeys may provide another datapoint suggesting that natural selection might have favored the formation of social bonds in the primate lineage.

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Chapter 3

White-faced capuchin monkeys use both rank and relationship quality to recruit allies

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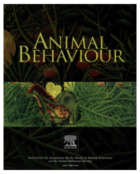

White-faced capuchin monkeys use both rank and relationship quality to recruit allies

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Coalitionary recruitment offers a window into animal social cognition. However, naturally observed coalitionary conflicts are challenging to analyse because the researcher has no control over the context in which they occurred, and observed behaviour patterns are typically consistent with multiple explanations. In this paper we analyse observational data of coalitionary solicitations during conflicts in wild capuchin monkeys, *Cebus capucinus*. We build upon previous work that focuses on identifying the cues that animals use to solicit allies in agonistic encounters. In contrast to previous studies, we applied a statistical technique that allows us to simultaneously compare different hypotheses regarding which cues animals use and how these cues interact. Our analysis shows that capuchin monkeys use information about both relationship quality and dominance when recruiting allies during conflicts. Monkeys primarily use rank when recruiting an ally, but will also use relationship quality, particularly when the potential ally has low rank. This study provides evidence that nonhuman primates are able to classify other group members using multiple criteria simultaneously. In addition, this paper presents a statistical technique that animal researchers can use to infer decision rules from observational data.

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Many animals, including humans, use social information to navigate the world around them. The cognitive demands of social living may well have shaped the minds of social species (Whiten & Byrne, 1997). If so, studying social abilities may offer insights into the link between sociality and intelligence (Byrne, 2018; Humphrey, 1976; Jolly, 1966; Whiten & Byrne, 1997). A key question is how animals use information about their social environment to negotiate relationships. Coalitionary behaviour offers particularly good insights into how individuals use social information. Participants in conflicts must decide whom to solicit for help, while onlookers must decide whether to join a conflict if solicited. This requires that individuals both know their own relationships with others and know the relationships among others.

Coalitions typically occur in an aggressive context in which two animals join together against a third party, or one individual intervenes in an ongoing dyadic conflict in support of one of the parties (Harcourt & de Waal, 1992). Although extensively documented in primates (reviewed in Bissonnette et al., 2015), coalitionary behaviour occurs in other taxa as well (reviewed in Smith et al., 2010). Third-party intervention in dyadic conflicts and coalition formation have been reported in a variety of mammals (e.g. spotted hyaenas, *Crocuta crocuta*: Engh, Siebert, Greenberg, & Holekamp, 2005; bottlenose dolphins, *Tursiops* sp.: Parsons et al., 2003; African wild dogs, *Lycaon pictus*: De Villiers, Richardson, & Van Jaarsveld, 2003) and birds (greylag geese, *Anser anser*: Scheiber, Weiß, Frigerio, & Kotrschal, 2005; jackdaws, *Corvus monedula*: Wechsler, 1988; rooks, *Corvus frugilegus*: Emery, Seed, Von Bayern, & Clayton, 2007; Seed, Clayton, & Emery, 2007).

Coalitionary behaviour represents a continuum (Olson & Blumstein, 2009), ranging from mutual tolerance (e.g. refraining from fighting in raccoons, *Proycyon lotor*: Gehrt & Fox, 2004) to the recruitment of coalition partners using evolved and formal recruitment signals (e.g. white-faced capuchin monkeys, *Cebus capucinus*; Perry, 2012), with many intermediate forms including the active collaboration between two or more individuals (e.g. males collaborate when taking over groups with reproductive females in banded mongoose, *Mungos mungo*: Waser, Keane, Creel, Elliott, & Minchella, 1994). Animals soliciting help often have a choice between multiple bystanders present in the vicinity. This

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offers an opportunity to investigate what animals know about their fellow group members and whether they strategically use that information.

Research on soliciting behaviour mostly comes from primate studies. Silk's (1999) pioneering study examined observational data to assess whether bonnet macaques, *Macaca radiata*, use information about third-party relationships while recruiting allies. She showed that male macaques consistently choose allies that outrank both themselves and their opponents. Similar patterns have been observed in juvenile sooty mangabeys, *Cercocebus torquatus atys* (Range & Noë, 2005) and white-faced capuchin monkeys (Perry, Barrett, & Manson, 2004). Some evidence suggests that animals classify others using more than one individual attribute or relationship (e.g. combining rank and kinship information). For example, Bergman, Beehner, Cheney, and Seyfarth (2003) experimentally demonstrated that baboons respond more strongly to call sequences that indicate rank reversal between families than within families, showing that baboons recognize that the dominance hierarchy is subdivided into family groups.

Although informative regarding how primates use social knowledge, observational data present inferential challenges. We cannot directly study social cognition. Instead, we must observe which individuals are recruited as allies and which are not, and from these observations make inferences about social cognition. The task is made even more difficult because the pattern of choices animals make when recruiting allies are typically consistent with multiple explanations (Kummer, Dasser, & Hoyningen-Huene, 1990; Silk, 1999). As we will discuss, previous statistical approaches forced the research to test each possible explanation against a null hypothesis, not against each other. With observational data, our goal should be to compare models against each other and assign relative plausibilities to them.

Some previous studies (Perry et al., 2004; Silk, 1999; but see ; Schino, Tiddi, & Di Sorrentino, 2006) have been able to evaluate whether a single facet of social cognition is used for determining coalitionary behaviour (e.g. 'solicit the highest-ranking individual' or 'solicit someone with whom you have the highest relationship quality'), but could not address hypotheses that combine two types of information (e.g. 'solicit someone who has high rank and good relationship quality with you'). The exception is one captive observational study (Schino et al., 2006) that investigated whether animals combine cues in a coalitionary recruitment context. These authors provided evidence that Japanese macaques, *Macaca fuscata,* prefer allies who outrank their opponents but will avoid recruiting such individuals when they are the opponent's kin. Although the rule in which macaques combine information about rank and kin was plausible when tested against the null model, the methods employed in the analyses were not sufficient to decide whether such a rule is more likely than rules employing a single facet of social cognition.

Wild white-faced capuchins engage in exceptionally high rates of coalitionary aggression (Perry, 2012). The rate of lethal coalitionary aggression in this species is comparable to rates in eastern chimpanzees, *Pan troglodytes schweinfurthii* (Gros-Louis, Perry, & Manson, 2003). The frequent formation of coalitions means that monkeys have to decide whom to recruit as allies on a daily basis. Coalitionary behaviour provides a window into how capuchin monkeys use and integrate social cues (e.g. whether or not capuchins use information about third-party relationships). Perry et al. (2004) investigated whether capuchins understand rank relationships and relationship quality among other group members and whether they use this knowledge in the solicitation of coalitionary partners. The authors used a Monte Carlo simulation to produce a distribution of coalitionary partner choices assuming monkeys choose at random. The plausibility of each hypothesized decision rule was assessed by comparing it against the null distribution. A rule was considered plausible if the observed patterns were not likely to have arisen by chance. This kind of statistical approach does not allow for the direct comparison of different hypothesized decision rules against each other. All the analyst can do is state whether the choices predicted by any particular decision rule would have been likely given the null model (Hillborn & Mangel, 1997). In Perry et al. (2004), four different decision rules were found to be plausible. However, their methods did not allow them to determine which particular decision rule, if any, was most plausible.

Here, we reanalyse the data set on capuchin coalitionary behaviour published in Perry et al. (2004) using a conditional logistic regression model. Our goal is to pit the different decision rules identified by Perry et al. (2004) against each other. Some of these rules use a single cue, while others combine cues. Based on previous findings about coalitionary recruitment patterns in capuchins (Perry, 1996, 1997, 1998a, 2003; Perry et al., 2004), we focus on rank relationships and the quality of social relationships among the individuals present during the conflicts as predictors of solicitation decisions.

METHODS

The Data Set

The records on capuchin solicitation during conflicts were collected between May 1991 and May 1993 at Lomas Barbudal Biological Reserve and surrounding private lands in Guanacaste, Costa Rica (Perry, 1995, 1996, 1997, 1998a, 1998b). The conflict data set, identical to the data presented in Perry et al. (2004), was recorded in a single capuchin group, Abby's group, which consisted of 21 individuals: 4 adult males, 6 adult females and 11 immatures. The data include observations from 10 min focal follows and ad libitum observations. To identify the audience members for each conflict, a scan sample was taken every 2.5 min in which the identities of all individuals in the view of the focal animal were recorded. Monkeys within a 10–20 m radius were considered to be available for solicitation. To be included in the data set, the conflict had to include a response from the target of the initial aggressive action, and the recruitment signals from either the aggressor or the target had to be obviously directed towards a particular individual. Recruitment signals include the headflag (the head is jerked quickly towards the solicitee and then back towards the opponent), the aggressive embrace, cheek-to-cheek posture (the monkeys in coalition touch their cheeks together while threatening a common opponent) and the overlord posture (the monkeys align themselves on top of one another, with heads stacked like a totem pole while jointly threatening their opponent; Perry et al., 2004).

Of the 21 group members, 18 were decision makers who solicited help from the audience members and 17 were opponents of the decision makers. The four individuals who never participated as either decision makers and/or opponents were young juveniles (age 1–2 years). Of the 21 group members, 14 individuals from the group were solicited as audience members.

Rank

White-faced capuchin societies are characterized by an alpha male at the top of the dominance hierarchy (Fragaszy, Visalberghi, & Fedigan, 2004; Jack, 2010; Perry, 2012). The linear ranks of adult subordinate males are hard to distinguish because interactions are rare and often interrupted by the alpha male, whose decisions about whom to support in male–male conflicts are inconsistent (Perry, 1998a). Female capuchins rank below adult males (Perry, 1997). In contrast to adult males, female–female dominance relationships tend to be linear (Bergstrom & Fedigan, 2010; Perry, 1996). A female's position in the dominance hierarchy is not only a function of her kin ties within the group, but also dependent on her individual competitive ability (Perry, 2012; Perry & Manson, 2008). Females are usually able to change their dominance rank upon reaching physical maturation by frequently fighting and winning against other females (Perry, 2012). Female dominance ranks are stable later in life (Bergstrom & Fedigan, 2010; Manson, Rose, Perry, & Gros-Louis, 1999).

Dominance ranks were determined using individuals' submissive behaviours (avoidance and cowering) in dyadic interactions (Perry et al., 2004). Ranks were assigned on a scale ranging from 0 (the lowest-ranked individual) to 1 (the highest rank). There were six dyads for which we assigned tied ranks, because it was impossible to determine their relative ranks. Additionally, there was an alpha male rank reversal during the data collection period (Perry, 1998b), which resulted in a change in the dominance hierarchy. Following Perry et al. (2004), we used two dominance hierarchies: one for the conflicts that occurred prior to the rank reversal and the other for conflicts that occurred after the rank reversal.

Relationship Quality Index

The relationship quality index was constructed based on the interaction history for each dyad (Perry et al., 2004). All interactions between two individuals for each 10 min focal follow were coded as being affiliative (e.g. grooming, resting in contact), cooperative (e.g. supporting each other in a conflict), agonistic (e.g. aggressive or submissive behaviours) or neutral. The relationship quality index between the decision maker and an audience member, $Q_{i\text{-}a}$, is defined as a proportion,

$$Q_{i-a} = \frac{I_+}{I_+ + I_-} \tag{1}$$

where I_+ is the number of 10 min samples with affiliative/cooperative interactions, and I_- is the numbers of 10 min samples with agonistic interactions. A 10 min sample could have been coded as having both affiliative/cooperative behaviours and agonistic interactions. The relationship quality index could range from 0 (indicating that a dyad relationship quality was completely characterized by agonistic interactions) to 1 (indicating only affiliative/cooperative interactions within a dyad). In the data set, the majority of the relationship quality indices were above 0.5 (84%), with the range between 0.2 and 1.0. Following Perry et al. (2004), separate relationship quality indices were calculated for the periods before and after the alpha male rank reversal.

Statistical Approach

We modelled each decision rule using a multilevel conditional logistic regression model. The goal of this model was to consider the attributes of each audience member when predicting the likelihood that a specific individual was solicited. The dependence on other individuals is natural: if we consider a group with the first, second and fifth top-ranking individuals, we expect the probability of soliciting the fifth-ranking individual to be low. In contrast, if we consider a group with the fifth-, 15th- and 20th-ranking individuals, we expect the probability of soliciting the fifth-ranking individual to be high. Thus, the likelihood of soliciting an audience member should depend not only on the audience member's own rank, but also on the ranks of other audience members. More traditional modelling frameworks, such as a binomial generalized linear model, fail to capture the dependence on a solicitation choice with the other audience members, particularly if the size of the audience is not constant. Conditional logistic regression is a natural extension of logistic regression that allows selecting a choice based on the other choices available.

Conditional logistic regression is a two-step process. First, the model uses a function (equation (2)) to score each audience member based on their rank and their relationship quality. Then the model uses a choice function (equation (4)) that takes the scores of all audience members into account to determine the likelihood of soliciting a particular audience member. This model is linear in that we assume that the scoring function will be a linear function of the audience member's rank and relationship quality, and potentially the product of those two values (i.e. an interaction term).

More formally, we assume that each decision maker (i) assigns a score (S_a) to each audience member (a), which is a linear combination of the potential coalition partner's rank (R), relationship quality to the decision maker (Q_i), and the sum of rank and relationship quality ($R \times Q_i$):

$$S_a = \beta_{R,i}\, R + \beta_{Q,i}\, Q_i + \beta_{RQ,i}\, R \times Q_i \tag{2}$$

The model coefficients, $\beta_{R,i}$, $\beta_{Q,i}$ and $\beta_{RQ,i}$, determine the impact that dominance rank, relationship quality index and the interaction between the two variables have on the audience member's score. The subscript '*i*' for each of the model coefficients denotes the fact that these coefficients might be different for each decision maker. We model individual differences using a random effect model assuming that the coefficient for each individual is the product of a fixed effect term (shared between all individuals in the population) and an individual deviation term, for example,

$$\beta_{R,i} = \beta_R + \beta'_{R,i} \tag{3}$$

If rank, relationship quality or the interaction term is not included in the model, then the respective parameter may be set to zero.

To convert the audience members' scores to choice probabilities, we constructed a choice function based on the softmax decision rule, a widely used model of animal and human behaviour (Luce, 1963; Racey, Young, Garlick, Pham, & Blaisdell, 2011),

$$P(a) = \frac{e^{S_a}}{\sum_{a'} e^{S_{a'}}} \tag{4}$$

In equation (4), the exponential of the particular audience member's score is divided by the sum of the exponentials of all audience members' scores. This ensures that each audience member is assigned a probability ranging from 0 to 1 that is based on his or her score relative to the scores of other audience members, and that the probabilities of all audience members sum to 1. The exponential link function ensures that the scores are evaluated relative to each other. For example, the probability that each audience member is solicited is the same for a group in which the scores are 1, 20 and 100 as for a group in which the scores are 101, 120 and 200.

Under this choice function, individuals with the highest score will be chosen more often than those with the lowest score. However, the highest-scoring audience member will not always be chosen, only more likely to be chosen. If the scores among audience members are fairly close, we expect that individuals will be chosen with roughly equal probability.

Before fitting the model, we standardized all predictor variables by subtracting the mean and dividing by the standard deviation.

Model Fitting

We used a Bayesian approach to fit the conditional logistic regression model. We included uninformative Normal (0,100) priors on each of the fixed effects, β_R, β_Q and β_{RQ}, and Normal $(0,\sigma^2)$ priors on each of the individual-level random effects. We used three different approaches to model the variance of the random effects, σ^2: (1) fitting the model without random effects; (2) setting the value of σ^2 to 1 and using a Normal (0,1) prior for each of the random effects; (3) inferring the value of σ^2 as another model parameter by using an InvGamma (0.001, 0.001) prior and allowing the value of σ^2 to differ between fixed effects (i.e. between rank, relationship, or the interaction). The choice of a wide inverse gamma-distributed prior for a variance term is thought to be relatively uninformative (Lunn, Jackson, Best, Spiegelhalter, & Thomas, 2012; but see ; Gelman, 2006). All three approaches for modelling the variance of the random effects produced similar results. We present the results from approaches (1) and (2) in the Supplementary Material, and focus on the results of approach (3) in the main text.

To perform a model comparison, we evaluated the WAIC values for each model (Watanabe, 2010). WAIC is an estimate of out-of-sample predictive validity taking into account the number of parameters (McElreath, 2016). Unlike AIC, which includes a fixed penalty for the number of parameters in the model (Akaike, 1973), in WAIC, the effective number of parameters is based on the diversity of the posterior distribution. This produces estimates for the effective number of parameters that tend to be much smaller than the total number of parameters if many of the parameters have small effects, or only contribute to fitting a subset of the data. This is particularly important for evaluating models where there are a large number of random effects (one for each fixed effect per individual), but where each parameter may only influence a small number of observations. We present the WAIC for each model, the standard error of the WAIC, the difference between the WAIC of each model and the top model, and the standard error of that difference.

In addition to reporting the WAIC statistics, we also report the median posterior estimate for each fixed effect term and its 95% highest posterior density interval (HPDI), representing the narrowest interval containing the 95% probability mass (McElreath, 2016).

We fitted the models using Stan (v.2.18.0) via its R interface, RStan (v.2.18.2; Stan Development Team, 2018). We used R (v.3.5.2; R Core Team, 2018), and used the package ‘loo’ (v.2.0.0; Vehtari, Gabry, Yao, & Gelman, 2018) to calculate WAIC values and the package ‘rethinking’ (v.2.18.2; McElreath, 2019) to calculate model comparison statistics. An example R script using simulated data and the Stan model files are available in the Supplementary Material.

Relative, Absolute or Threshold Rules

We assume that rank, R, and relationship quality index, Q, can be measured in one of three ways. The decision to investigate each rule was based on Perry et al. (2004), who suggest capuchin monkeys might be paying attention to either absolute or relative criteria of relationship quality and rank relationships.

Absolute rules

For absolute rules, the values of R and Q are equal to the audience member's rank (R_a) and the relationship between the individual and the audience member ($Q_{i\text{-}a}$): $R_{absolute} = R_a$; $Q_{absolute} = Q_{i\text{-}a}$.

Relative rules

For relative rules, R (or Q) is based on the difference between the solicited target's rank (or relationship quality index) and the opponent's rank (or relationship quality index). If the rank of the opponent is R_o and the rank of the target audience member is R_a, then $R_{relative} = R_a - R_o$.

Since the rank of the opponent is constant and the model depends only on the relative score of individuals, $R_{relative}$ and $R_{absolute}$ are identical.

In the case of relationship quality index, the relationship depends on the difference between the relationship of the individual with the audience member, $Q_{i\text{-}a}$, and the relationship of the opponent and the audience member, $Q_{o\text{-}a}$: $Q_{relative} = Q_{i\text{-}a} - Q_{o\text{-}a}$.

Threshold rules

For threshold rules, R and Q are assigned a value of 0 or 1, based on whether the opponent has a higher rank than the audience member, or whether the decision maker has a higher relationship quality index with the audience member compared to its opponent: $R_{threshold} = 1$ if $R_a > R_o$ and 0 otherwise; $Q_{threshol} = 1$ if $Q_{i\text{-}a} > Q_{o\text{-}a}$ and 0 otherwise.

Full Model Set

We evaluated 12 models. First, we fitted a model with just an intercept and no predictor variables, which represents a null model in which choices are determined at random. Then we fitted five models with a single predictor each (3 relationship quality models and 2 rank models; as we discussed, absolute and relative ranks are equivalent). We followed this with three models containing both rank and relationship quality predictors from each rule (absolute, relative, threshold). We also assumed that either the influence of rank or relationship quality might depend on the other, particularly when deciding between low-ranking individuals. If one has a strong preference for high-ranking individuals, then maybe she is less concerned with her relationship quality with those individuals. On the other hand, if someone is deciding between low-ranking individuals, then relationship quality might play a larger role in the decision. We modelled this assumption including an interaction term and fitted the three models with both predictors and an interaction term between them. All of the models used the same type of rule, i.e. both rank and relationship quality predictors were operationalized using the absolute, relative or threshold rule.

The single-variable models are similar to the decision rules tested in Perry et al. (2004). The two-predictor models allow us to evaluate whether models that combine rank and relationship quality explain the data better than any of the decision rules that are based on just one variable.

Ethical Note

This was a strictly observational study of wild animals, involving no manipulation on the part of the observers, aside from the application of a small amount dye to a few of the small juveniles to assist in recognizing individuals during quick action. These individuals were squirted with Clairol Born Blonde hair dye (Procter & Gamble Co., Cincinnati, OH, U.S.A.), dispensed from a 100 cc syringe from which the needle had been removed. The dye was squirted onto their backs from a 1–2 m distance and never produced noticeable distress. The protocols for this study were approved by the University of Michigan Committee on Use and Care of Animals, IUCUC number 3081, and permission was obtained from the Servicio de Parques Naciónales de Costa Rica and the regional division (Area de Conservacion Tempisque).

RESULTS

We found that an interaction model using both absolute rank and absolute relationship quality (absolute interaction model) provided the best fit to the data. Table 1 presents model comparison statistics for the 12 models. The absolute interaction model garnered 63% of the WAIC weight, and the majority of the remaining weight (24%) was placed on the absolute rank and relationship quality model without an interaction (absolute additive model). The two relative criteria models received much of the remaining weight (11%). The threshold models, the single-variable models (except the absolute rank model, which received 2% of the weight) and the random choice model received almost no weight and had low-ranking WAIC scores. Table 2 presents the posterior mean estimates and 95% HPDI of the parameters across the 12 models presented in Table 1.

Best-fitting Model

Figure 1 illustrates how the best-fitting model, the absolute interaction model, predicts the interaction between the dominance rank and relationship quality by marginalizing over the model parameters for all of the samples in the posterior distribution. This model predicts that the audience member's score, a linear combination of their rank, relationship quality and their product, will be highest for an audience member who has the top rank and greatest relationship quality index with the decision maker. However, Fig. 1 shows that if the audience member is at the top of the hierarchy, the predicted effect of the relationship quality on their score is very small. As the rank of the audience member decreases, the influence of relationship quality on the value of the audience member becomes increasingly important.

Observed Choices

One of the main objectives of our statistical approach was to evaluate the likelihood of an audience member being solicited while considering the other available options. Below we present the observed audience members in each conflict and highlight which individual was solicited. Figure 2 illustrates all of the audience members available in the 38 conflicts where a single audience member was both highest ranking and had the highest relationship quality with the decision maker. Figure 3 illustrates the remaining 72 conflicts in which the decision maker had a choice between the highest-ranking member and another member with the highest relationship quality.

DISCUSSION

In this paper we reanalysed the data set on capuchin coalitionary behaviour published in Perry et al. (2004) using a conditional logistic regression model. We found that both high rank

Table 1
Model comparison

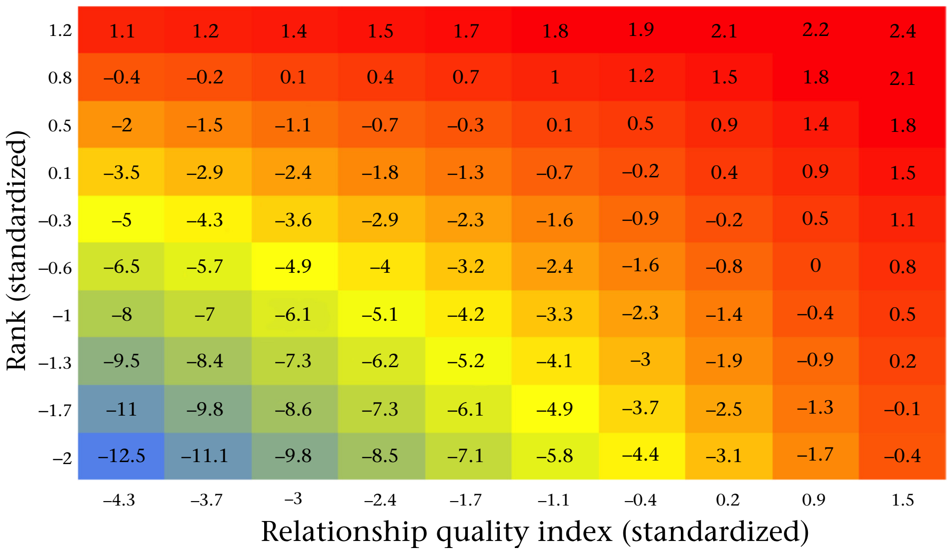
Model	pWAIC	WAIC	SE	dWAIC	dSE	Weight
Absolute rank × relationship quality (absolute interaction model)	9.2	174.96	17.27	0.00	NA	0.63
Absolute rank + relationship quality (absolute additive model)	9.7	176.87	17.59	1.90	2.86	0.24
Relative rank + relationship quality	10.9	179.15	17.26	4.18	4.63	0.08
Relative rank × relationship quality	12.5	181.16	17.46	6.20	4.83	0.03
Absolute rank	7.1	181.93	16.63	6.97	6.09	0.02
Threshold rank + relationship quality	10.9	198.65	15.89	23.68	11.32	0.00
Threshold rank × relationship quality	13.4	199.46	16.38	24.49	12.06	0.00
Threshold rank	5.0	204.52	15.94	29.55	11.75	0.00
Threshold relationship quality	6.2	224.25	12.98	49.28	16.42	0.00
Relative relationship quality	3.8	232.71	12.98	57.75	15.99	0.00
Random choice	0.0	236.60	12.10	61.64	16.05	0.00
Absolute relationship quality	2.6	238.98	12.21	64.02	15.88	0.00

The table reports the effective number of parameters (pWAIC), the information criterion WAIC, standard error of the WAIC estimate (SE), the difference between each WAIC and the smallest WAIC (dWAIC), and standard error of the difference in WAIC between each model and the top-ranked model (dSE), and the approximate WAIC weight. Additive models are indicated with +, interaction models are indicated with ×.

Table 2
Parameter estimates

Model	Fixed effects			Random effects		
	Rank	Rel. quality	Interaction	σ^2_{Rank}	$\sigma^2_{\text{Rel. quality}}$	$\sigma^2_{\text{Interaction}}$
Absolute rank × relationship quality (absolute interaction model)	1.74 [1.15, 2.44]	0.90 [0.32, 1.52]	−0.57 [−1.29, 0.14]	0.05 [2×10^{-4}, 0.59]	0.02 [1×10^{-4}, 0.22]	0.04 [2×10^{-4}, 0.59]
Absolute rank + relationship quality (absolute additive model)	1.53 [0.96, 2.25]	0.58 [0.12, 1.07]	–	0.22 [2×10^{-4}, 1.35]	0.02 [2×10^{-4}, 0.25]	–
Relative rank + relationship quality	1.39 [0.81, 2.15]	0.42 [−0.01, 0.88]	–	0.28 [2×10^{-4}, 1.45]	0.06 [2×10^{-4}, 0.48]	–
Relative rank × relationship quality	1.41 [0.83, 2.21]	0.45 [0.01, 0.93]	−0.05 [−0.33, 0.28]	0.30 [2×10^{-4}, 1.59]	0.07 [2×10^{-4}, 0.50]	0.01 [2×10^{-4}, 0.11]
Absolute rank	1.33 [0.77, 2.05]	–	–	0.22 [2×10^{-4}, 1.27]	–	–
Threshold rank + relationship quality	1.81 [0.87, 2.76]	0.74 [−0.69, 2.21]	–	0.19 [2×10^{-4}, 3.66]	1.74 [3×10^{-4}, 6.89]	–
Threshold rank × relationship quality	2.79 [1.18, 4.71]	1.75 [−0.08, 4.26]	−1.45 [−3.51, 0.36]	0.13 [3×10^{-4}, 2.98]	2.51 [2×10^{-4}, 9.72]	0.07 [2×10^{-4}, 1.39]
Threshold rank	1.83 [0.95, 2.71]	–	–	0.11 [2×10^{-4}, 2.41]	–	–
Threshold relationship quality	–	0.93 [−0.45, 2.57]	–	–	2.34 [4×10^{-4}, 8.77]	–
Relative relationship quality	–	0.35 [−0.04, 0.77]	–	–	0.07 [2×10^{-4}, 0.48]	–
Random choice	–	–	–	–	–	–
Absolute relationship quality	–	0.03 [−0.34, 0.40]	–	–	0.02 [2×10^{-4}, 0.24]	–

The table reports fixed effect parameter estimates including the median and 95% HDPI (in brackets) for each model and the variance for random effects. Additive models are indicated with +, interaction models are indicated with ×.



	−4.3	−3.7	−3	−2.4	−1.7	−1.1	−0.4	0.2	0.9	1.5
1.2	1.1	1.2	1.4	1.5	1.7	1.8	1.9	2.1	2.2	2.4
0.8	−0.4	−0.2	0.1	0.4	0.7	1	1.2	1.5	1.8	2.1
0.5	−2	−1.5	−1.1	−0.7	−0.3	0.1	0.5	0.9	1.4	1.8
0.1	−3.5	−2.9	−2.4	−1.8	−1.3	−0.7	−0.2	0.4	0.9	1.5
−0.3	−5	−4.3	−3.6	−2.9	−2.3	−1.6	−0.9	−0.2	0.5	1.1
−0.6	−6.5	−5.7	−4.9	−4	−3.2	−2.4	−1.6	−0.8	0	0.8
−1	−8	−7	−6.1	−5.1	−4.2	−3.3	−2.3	−1.4	−0.4	0.5
−1.3	−9.5	−8.4	−7.3	−6.2	−5.2	−4.1	−3	−1.9	−0.9	0.2
−1.7	−11	−9.8	−8.6	−7.3	−6.1	−4.9	−3.7	−2.5	−1.3	−0.1
−2	−12.5	−11.1	−9.8	−8.5	−7.1	−5.8	−4.4	−3.1	−1.7	−0.4

Figure 1. A heat map of audience member scores for the absolute interaction model. The values in the heat map represent audience member scores (S_a , equation (2)) computed using the estimated parameters of the absolute interaction model (Table 1).

and having a high relationship quality with the focal individual increased the probability that an audience member was solicited. This is consistent with findings that primates classify their group members using multiple criteria simultaneously (Bergman et al., 2003) and that they use this information in making decisions during conflicts (Perry et al., 2004; Schino et al., 2006; Silk, 1999). Unlike the original analysis of these data (Perry et al., 2004), we do not find that triadic awareness is required to explain the solicitation behaviours of the capuchin monkeys. Here we discuss

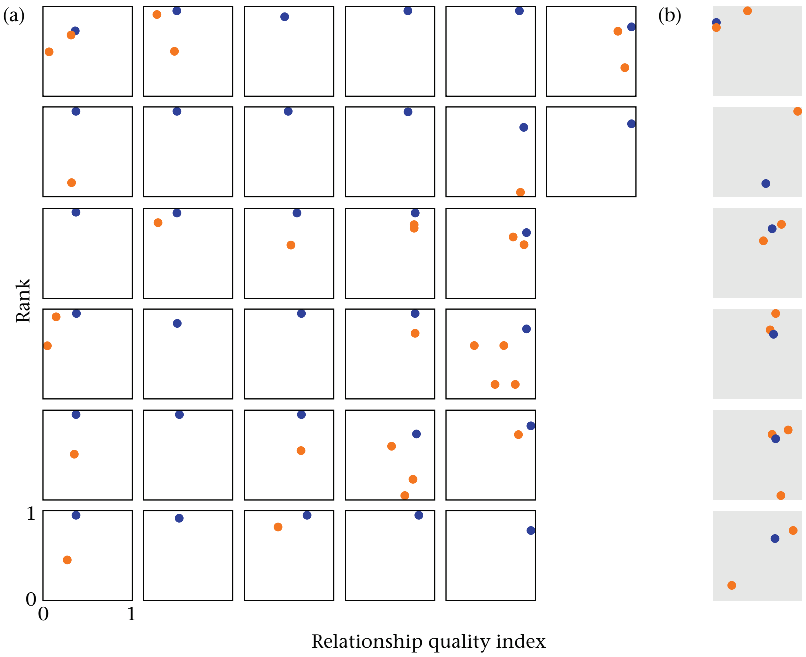


Figure 2. The choice of allies in conflicts when there is a single audience member who is both highest ranking and has the highest relationship quality with the decision maker. Each square represents the audience available in a particular conflict. The blue dots represent the audience member who was solicited, while the orange dots represent all of the other audience members who were available during that conflict. The *X* axis represents the audience member's relationship quality with the decision maker (range 0–1, where the highest relationship quality is 1) and the *Y* axis represents the audience member's rank (range 0–1, where the highest rank is 1). (a) In 32 of 38 conflicts (84%) in which the decision maker could choose an audience member who had the highest value on both dimensions, he or she did so. (b) In the remaining six conflicts (16%), the decision maker chose to recruit someone else.

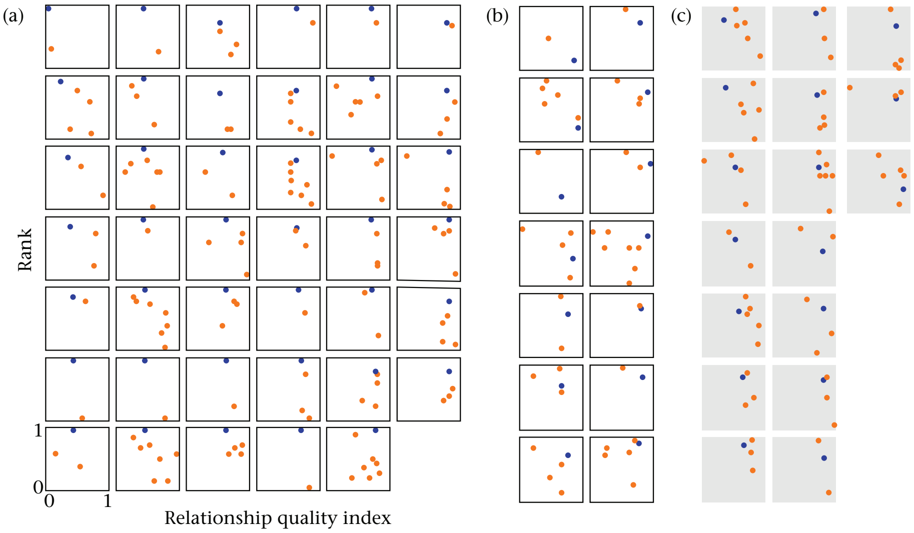


Figure 3. The choice of allies in conflicts in which one audience member is highest ranking and another has the highest relationship quality with the decision maker. Each square represents the audience available in a particular conflict. The blue dots represent the audience member who was solicited, while the orange dots represent all the other audience members who were available during that conflict. (a) In 42 of 72 conflicts (58%), the decision maker chose the highest-ranking individual, not the one with the highest relationship quality. Plots are arranged (starting at the top left and going down) from the lowest relationship quality of the solicited member to the highest. (b) In 14 of 72 conflicts (19%), the decision maker solicited the audience member with whom he had the highest relationship quality, not the one with the highest rank. Plots are arranged (starting at the top left and going down) from the lowest rank of the solicited audience member to the highest. (c) In the remaining 17 of 72 conflicts (24%), the decision maker chose an audience member that was neither highest ranking nor had the greatest relationship quality with the decision maker.

the methodological contribution of our study and the substantive contribution regarding coalitionary behaviour and cognition.

Conditional Logistic Regression as a General Framework for Studying Partner Choice

The use of conditional logistic regression to model solicitation behaviour in conflicts represents a methodological advance compared to previous studies (Perry et al., 2004; Schino et al., 2006; Silk, 1999). Conditional logistic regression was used for two reasons. First, previous analyses were limited in that they could not simultaneously consider multiple competing hypotheses and determine which, if any, are most plausible given the data. In addition, previous analyses could not model decision rules in which individuals combine different kinds of social information. Conditional logistic regression solves these limitations by allowing multiple cues to be combined in an additive model. In addition, using conditional logistic regression instead of simulation techniques allows the comparison of different decision rules using an information-theoretic approach. The richer modelling framework used here allows us to learn more with the same data, providing more nuanced insights into the capuchins' behaviours.

Second, conditional logistic regression was also chosen to solve the problem of how to model solicitation decisions when individuals have to choose from a subset of possible audience members. The problem of partner choice features prominently in the literature on biological markets (Noë & Hammerstein, 1994). Previous analyses that relied on simple binomial regression models (or GLMMs) are insufficient because they do not consider which animals are available to choose from. In contrast, conditional logistic regression explicitly takes into account which audience members are available and allows inferences to be made that more closely resemble the individual's actual decision making. We believe this modelling framework—using conditional logistic regression in combination with an information-theoretic approach—represents a powerful approach for similarly structured coalitionary behaviour data (and could be applied in, e.g. olive baboons, *Papio anubis*: Packer, 1977; brown capuchin monkeys, *Sapajus apella*: Ferreira, Izar, & Lee, 2006; African wild dogs, *L. pictus*: De Villiers et al., 2003; spotted hyenas: Smith et al., 2007). More broadly, it can be applied to decision-making problems in which individuals choose from multiple potential partners, such as grooming (e.g. sooty mangabeys: Mielke et al., 2018*;* western chimpanzees, *P. t. verus*: Mielke et al., 2018), food sharing (e.g. western chimpanzees: Samuni, 2018; humans: Koster & Leckie, 2014), group foraging (e.g. bluegill sunfish, *Lepomis macrichirus*: Dugatkin & Wilson, 1992), antipredator inspection (e.g. guppies, *Poecilia reticulata*: Dugatkin & Alfieri, 1991) and mate choice (e.g. sage grouse, *Centrocercus urophasian*: Gibson, Bradbury, & Vehrencamp, 1991).

The Importance of Relationship Quality and Rank in Partner Solicitation in Capuchins

Our findings are consistent with previous findings on joining ongoing conflicts in capuchins. When intervening in a conflict, capuchins tend to join with either higher-ranking individuals or individuals with whom they have better social relationship (Perry, 1996, 1997; 1998a; 1998b, 2003). In other species, rank and relationship quality have also been shown to be important in soliciting help (bonnet macaques: Silk, 1999; sooty mangabeys: Range & Noë, 2005; Japanese macaques: Schino et al., 2006), joining a conflict (hyaenas: Engh et al., 2005; sooty mangabeys: Range & Noë, 2005), or predicting competitor's supporter (chimpanzees: Wittig et al., 2014). In addition, our analyses show that, in capuchins, rank is more important than relationship quality when soliciting allies. The importance of rank in capuchin monkeys is not surprising given that high-ranking individuals are more likely to participate in coalitions (Perry, 1996) and are almost never challenged in a conflict (Perry, 2012), and that the alpha male enjoys a central position with other group members seeking his help and readily offering their own support (Perry, 1996, 1998, 2012). Taken together, this suggests that capuchins form coalitions primarily to reinforce existing hierarchy rather than to challenge it ('all-down' coalitions in Bissonnette et al., 2015).

Do Capuchin Monkeys Exhibit Triadic Awareness?

Triadic awareness is the ability to have some knowledge of the relationships between other individuals (de Waal, 1982; Tomasello & Call, 1997). Being able to know something about third-party relationships might be very useful in soliciting help during conflicts, because a decision maker might prefer a potential ally who has better relationship with him or her than with the opponent. Perry et al. (2004) reported that such a decision rule is plausible for these data.

Our analyses included 12 hypotheses about possible decision rules that ranged from the assumption that monkeys are making random choices, to hypotheses in which monkeys take into account multiple types of information simultaneously when assessing a potential ally. Each of these rules assumes a certain level of cognitive ability. To use relative and threshold decision rules, the monkeys must have knowledge of third-party relationships: The decision maker must assess the difference between his relationship quality to the audience member and the opponent's relationship quality to the audience member. Absolute decision rules do not require triadic awareness, because the decision maker only uses information about the audience member's rank or his relationship quality with the audience member. Our model comparison shows that the rules that do not require triadic awareness have the best model fit, suggesting that triadic awareness is not required to explain the solicitation patterns in this data set.

The differences between the results of Perry et al. (2004) and our results come down to differences in the analytical approach. Consistent with previous findings, we found that decision rules requiring triadic awareness are more plausible than the random choice model. However, we showed that these rules are far less plausible than the rules that do not require triadic awareness. Although we do not find strong support for triadic awareness, this does not rule out the possibility that capuchins may have this ability. Experimental studies may be a better way to establish whether species have a particular cognitive ability.

In addition, we aimed to make inferences based on the entire set of models rather than selecting the best model (Burnham & Anderson, 2004; McElreath, 2016). This enabled us to infer that the decision rules in which animals assess only one attribute of a potential ally are far less plausible than decision rules where the decision maker combines information about rank and relationship quality. This provides more evidence that monkeys evaluate potential allies by combining multiple types of information about them.

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Supplementary Material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.anbehav.2019.06.008.

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