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Publication Date
2019-08-01

DOI
10.1016/j.anbehav.2019.06.008

Peer reviewed

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 analyze because the researcher has no control over the context in which they occurred, and observed behavior patterns are typically consistent with multiple explanations. In this paper we analyze 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.

Keywords

Cebus capucinus, coalitions, decision making, conditional logistic regression, observational data

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 and Byrne 1997). If so, studying social abilities may offer insights into the link between sociality and intelligence (Jolly 1966; Humphrey 1976; Whiten and Byrne 1997; Byrne 2018). A key question is how animals use information about their social environment to negotiate relationships. Coalitionary behavior 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 relatioships 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 and De Waal 1992). Though extensively documented in primates (reviewed in Bissonnette et al. 2015), coalitionary behavior 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. Hyenas, *Crocuta crocuta:* Engh et al. 2005; bottlenose dolphins, *Tursiops sp.:* Parsons et al. 2003; African wild dogs, *Lycaon pictus:* de Villiers et al. 2003;) and birds (Graylag geese, *Anser anser:* Scheiber et al. 2005; Jackdaws, *Corvus monedula:* Wechsler 1988; rooks, *Corvus frugilegus:* Emery et al. 2007, Seed et al. 2007).

Coalitionary behavior represents a continuum (Olson and Blumstein 2009), ranging from mutual tolerance (e.g. refraining from fighting in raccoons, *Proycyon lotor*: Gehrt and 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 et al. 1994). Animals soliciting help often have a choice between multiple bystanders present in the vicinity. This offers an opportunity to investigate what animals know about their fellow group members and whether they strategically use that information.

Research on soliciting behavior 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 (Range and Noë, 2005) and white-faced capuchin monkeys (Perry et al. 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 et al. (2003) experimentally demonstrated that baboons responded 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.

Though 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 et al. 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 (Silk 1999; Perry et al. 2004; but see Schino et al. 2006) have been able to evaluate whether a single facet of social cognition is used for determining coalitionary behavior (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. They provided evidence that that Japanese macaques 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 (Gros-Louis et al. 2003). The frequent formation of coalitions means that monkeys have to decide whom to recruit as allies on a daily basis. Coalitionary behavior 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. Each hypothesized decision rule's plausibility was assessed by comparing it against the null distribution. A rule was considered plausible if the observed patterns are 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 (Mangel and Hillborn, 2005). 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 reanalyze the dataset on capuchin coalitionary behavior published in Perry et al. (2014) 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; Perry 1997; Perry 1998a; Perry 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 dataset

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,b). 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: four adult males, six adult females and eleven immatures. The data include observations from 10-minute focal follows and *ad libitum* observations. To identify the audience members for each conflict, a scan sample was taken every 2.5 minutes 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. In order 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 toward a particular individual. Recruitment signals include the headflag (the head is jerked quickly towards the solicitee and then back toward 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 et al. 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 (Perry 1996; Bergstrom and Fedigan

2010). 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 and Manson 2008; Perry 2012). 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 (Manson et al. 1999; Bergstrom and Fedigan 2010).

Dominance ranks were determined using individuals' submissive behaviors (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-minute focal follow were coded as being either affiliative (e.g. grooming, resting in contact), cooperative (e.g. supporting each other in a conflict), agonistic (e.g. aggressive or submissive behaviors), or neutral. The relationship quality index between the decision maker and an audience member, Q_{i-a}, is defined as a proportion,

$$Q_{i-a}=\frac{I_{+}}{I_{+}+I_{-}} \qquad (1)$$

where I_+ is the number of 10-minute samples with affiliative/cooperative interactions, and I_- is the numbers of 10-minute samples with agonistic interactions. A 10-minute sample could have been coded as both having affiliative/cooperative behaviors and agonistic interactions. The relationship quality index could range from 0 (indicating that a dyad relationship quality is completely characterized by agonistic interactions) to 1 (indicating only affiliative/cooperative interactions within a dyad). In the dataset, 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 the alpha male rank reversal and after.

Statistical approach

We modeled each decision rule using a multi-level 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 1st, 2nd, and 5th top ranking individuals, we expect the probability of soliciting the 5th ranking individual to be low. In contrast if we consider a group with the 5th, 15th and 20th ranking individuals, we expect the probability of soliciting the 5th 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 modeling 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, 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 ($R * Q_i$):

$$S_a = \beta_{R,i} R + \beta_{Q,i} Q_i + \beta_{RQ,i} R * Q_i \qquad (2)$$

The model coefficients, $\beta_{R,i}$, $\beta_{Q,i}$, and $\beta_{RQ,i}$ determine the impact 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, e.g.,

$$\beta_{R,i} = \beta_R + \beta'_{R,i}. \qquad (3)$$

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 behavior (Luce 1963; Racey et al. 2011),

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

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 a 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,σ^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 et al. 2012; but see Gelman 2006). All three approaches for modeling 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 fit the models using Stan v.2.18.0 via its R-interface, RStan v.2.18.2. We used R v.3.5.2, and used the packages *loo* v.2.0.0 to calculate WAIC values and *rethinking* v.2.18.2 to calculate model comparison statistics. An example R script using simulated data and the Stan model files are available in the Supplementary Materials.

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 to 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 if the decision maker has a higher relationship quality index with the audience member compared to their opponent.

$R_{threshold} = 1$ if $R_a > R_o$ and 0 otherwise.

$Q_{threshold} = 1$ 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 modeled 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 either 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, dispensed from a 100-cc syringe from which the needle had been removed. The dye was squirted onto their backs from a 1-2 meter 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 #3081, and permission was obtained from the Servicio de Parques Naciónales de Costa Rica and the regional division (Area de Conservacion Tempisque).

RESULTS

We find that an interaction model using both absolute rank and absolute relationship quality (Absolute Interaction Model) provides the best fit to the data. Table 1 presents model comparison statistics for the twelve 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 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 twelve models presented in Table 1.

Table 1. Model comparison. 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 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 x.

Model	pWAIC	WAIC	SE	dWAIC	dSE	weight
Absolute rank x 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 x 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 x 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

Table 2. Parameter estimates. 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 x.

	Fixed Effects			Random Effects		
Model	Rank	Rel. quality	Interaction	σ^2_{Rank}	$\sigma^2_{Rel.\ quality}$	$\sigma^2_{Interaction}$
Absolute rank x 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 x 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 x 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]	-

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, Figure 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.

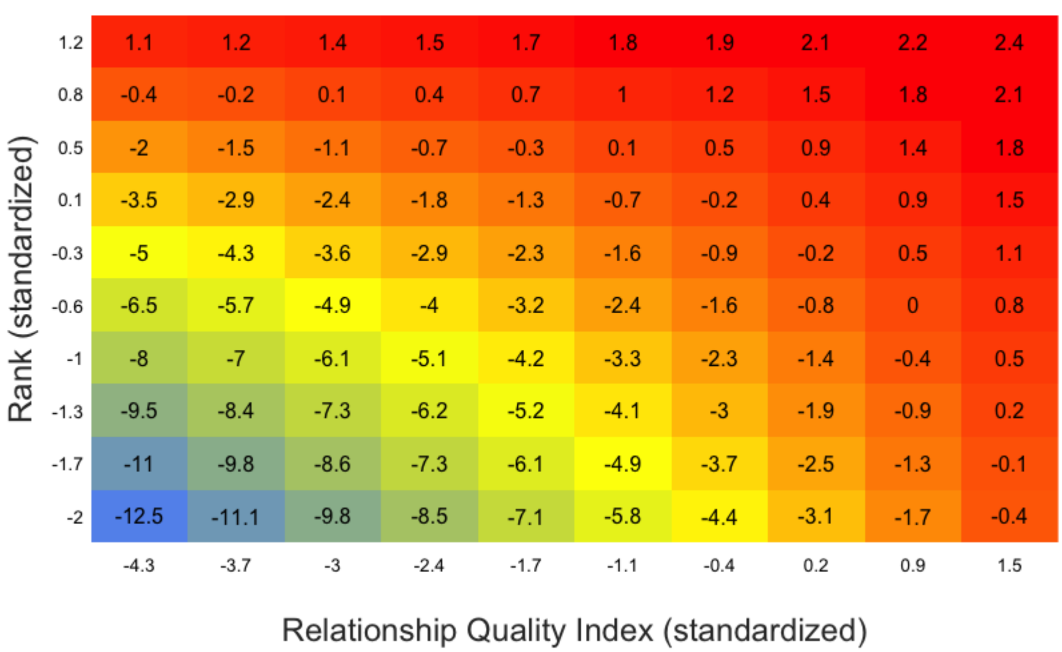

Figure 1. A heat map of audience member scores for the Absolute Interaction model. The values in the heat map represent audience member scores (S_a, Equation 2) computed using the estimated parameters of the Absolute Interaction model (Table 1).

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 of the 72 conflicts in which the decision maker had a choice between the highest-ranking member and another member with the highest relationship quality.

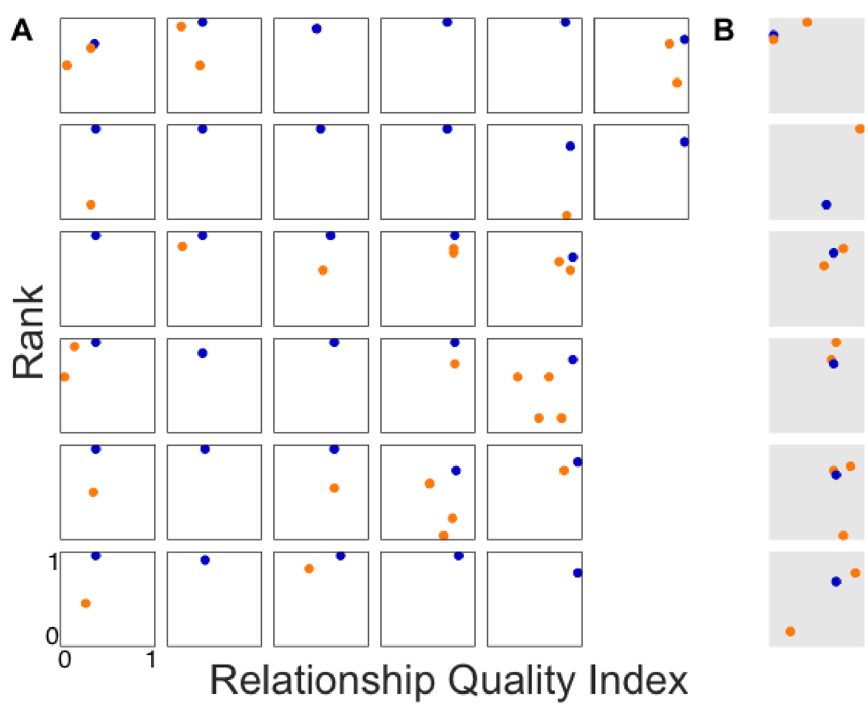

Figure 2. The choice of allies in conflicts when there is a single audience member who is both highest ranking and has the highest relationship quality with the decision maker. Each square represents the audience available in a particular conflict. The blue dots represent the audience member who was 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 (ranges 0-1, where the highest relationship quality is 1) and the y-axis represents the audience member's rank (ranges from 0-1, where the highest rank is 1). 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 (Panel A). Panel B depicts the remaining 6 conflicts (16%) in which the decision maker chose to recruit someone else.

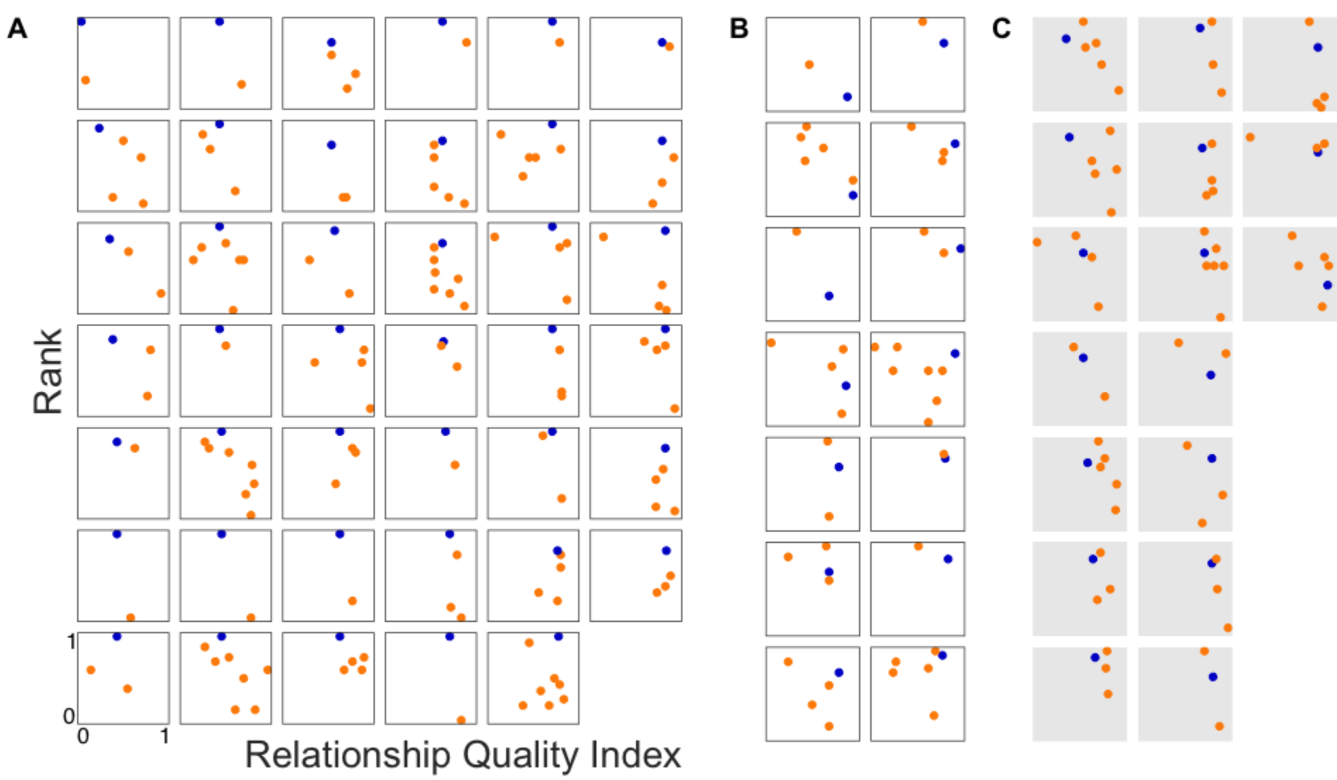

Figure 4. The choice of allies in conflicts in which one audience member is highest ranking and another has the highest relationship quality with the decision maker. Each square represents the audience available in a particular conflict. The blue dots represent the audience member who was solicited, while the orange dots represent all the other audience members who were available during that conflict. In 42 of 72 conflicts (58%), the decision maker chose the highest-ranking individual, not the one with the highest relationship quality (Panel A). The plots in Panel A are arranged (starting at the top left and going down) from the lowest relationship quality of the solicited member to the highest. 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 (Panel B). The plots in Panel B are arranged (starting at the top left and going down) from the lowest rank of the solicited audience member to the highest. And in the remaining 17 of 72 conflicts (24%), the decision maker chose an audience member was neither highest ranking nor had the greatest relationship quality with the decision maker (Panel C).

DISCUSSION

In this paper we reanalyzed the dataset on capuchin coalitionary behavior published in Perry et al. (2004) using a conditional logistic regression model. We find that both high rank 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 (Silk 1999; Perry et al. 2004; Schino et al. 2006). Unlike the original analysis of these data (Perry et al. 2004), we do not find that triadic awareness is required to explain the solicitation behaviors of the capuchin monkeys. Here we discuss the methodological contribution of our study and the substantive contribution regarding coalitionary behavior and cognition.

Conditional logistic regression as a general framework for studying partner choice

The use of conditional logistic regression to model solicitation behavior in conflicts represents a methodological advance compared to previous studies (Silk 1999; Perry et al. 2004; Schino et al. 2006). 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 modeling framework used here allows us to learn more with the same data, providing more nuanced insights into the capuchins' behaviors.

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 and 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 modeling framework—using conditional logistic regression in combination with an information theoretic approach—

represents a powerful approach for similarly structured coalitionary behavior data (and could be applied in, e.g. olive baboons, *Papio anubis:* Packer 1977; brown capuchin monkeys, *Sapajus apella:* Ferreira et al. 2006; African wild dogs, *Lycaon pictus*: de Villiers et al. 2003; spotted hyenas, *Crocuta crocuta:* Smith et al. 2010). 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, *Cercocebus atys atys: Mielke et al. 2018;* chimpanzees, *Pan troglodytes verus*: Mielke et al. 2018), food sharing (e.g. chimpanzees, *Pan trogolodytes verus* : Samuni 2018; humans: Koster and Leckie 2014), group foraging (e.g. bluegill sunfish, *Lepomis macrichirus:* Dugatkin and Wilson 1992), antipredator inspection (e.g. guppies, *Poecilia reticulata*: Dugatkin and Alfieri 1991), and mate choice (e.g. sage grouse, *Centrocercus urophasian*: Gibson et al. 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,b; 2003). In other species, rank and relationship quality have also been shown to be important in soliciting help (bonnet macaques, *Macaca radiata*: Silk 1999; sooty mangabeys, *Cercocebus torquatus atys:* Range and Noë 2005; Japanese macaques, *Macaca fuscata*: Schino et al. 2006), joining a conflict (hyenas, *Crocuta crocuta:* Engh et al. 2005; sooty mangabeys, *Cercocebus torquatus atys:* Range and 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), high-ranking individuals 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; Perry 1998; Perry 2012). Taken together, this suggests that capuchins form coalitions primarily to reinforce existing hierarchy rather than 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 and 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 decision rule is plausible for these data.

Our analyses included twelve 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 which do not require triadic awareness have the best model fit, suggesting that triadic awareness is not required to explain the solicitation patterns in this dataset.

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 that 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 and 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 provided more evidence that monkeys evaluate potential allies by combining multiple types of information about them.

ANIMAL WELFARE 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, dispensed from a 100-cc syringe from which the needle had been removed. The dye was squirted onto their backs from a 1-2 meter 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 #3081, and permission was obtained from the Servicio de Parques Naciónales de Costa Rica and the regional division (Area de Conservacion Tempisque).

ACKNOWLEDGEMENTS

We thank J. Manson, J. Gros-Louis and L. Sirot for their invaluable assistance in data collection. L. Sirot, M. Tomaszycki, M. Landys and S. Newman assisted in data processing. This paper has benefited from helpful discussions with H. C. Barrett, J. Manson, T. Scott-Phillips, B. Scelza, E. S. Gillen, members of UCLA's Biological Anthropology subfield, the Behavior, Evolution and Culture group, members of the Healey Lab who provided valuable feedback; the editor J. Higham and an anonymous reviewer who suggested individual level analysis. We thank the Costa Rican Servicio de Parques Naciónales and the Area de Conservación Tempisque for permission to work in Lomas Barbudal Biological Reserve, and the community of San Ramón de Bagaces and Rancho Jojoba for permission to work on private lands near the reserve. G. Frankie and J. Frankie, the Rosales family and M. Cedillos provided logistical assistance in the field. K.K. was supported by NSF Graduate Research Fellowship Grant DGE-1650604. S.E.P. was supported by the L.S.B. Leakey Foundation (two grants), the National Science Foundation (graduate fellowship to S.E.P., and grants to B. Smuts and J. Mitani), the National Geographic Society, Sigma Xi, the Rackham Graduate School, the Evolution and Human Behavior Program and the University of Michigan Alumnae Society.

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