Fitness benefits of providing services to others: Sociality predicts survival in a neotropical primate

Supplemental material

KAJOKAITE ET AL.

1. INTRODUCTION

This supplemental file contains five sections. First, we provide a description of the adaptations of the Social Relations Model that were used to estimate the sociality measures. Second, we describe covariates used in the models. Third, we include a Directed Acyclic Graph (DAG) showing the purported causal relationships between variables. Fourth, we plot the posterior means and their standard errors across five Cox proportional hazards models to illustrate how estimates compare across the models. Fifth, we present model results from Cox proportional hazards models with alternative specifications and priors.

2. SOCIALITY ESTIMATES

A central challenge to estimating sociality is the heterogeneous sampling that characterizes ethological research [1]. Because some animals and their dyadic interactions are observed more than others, there is heterogeneous uncertainty about the underlying sociality of the individuals in the population. As an alternative to point estimates of sociality, our approach was designed to obtain measures of sociality that reflect that uncertainty, which subsequently carries forward into the proportional hazards models.

To model sociality, we adapt the multilevel Social Relations Model, or SRM [2, 3]. Originally formulated as an ANOVA model, the SRM partitions the variance of a directed dyadic outcome from actor i to partner j into (1) actor-level variation reflecting individual-level heterogeneity of directing or sending ties to others, (2) partner-level variation reflecting individual-level heterogeneity of receiving ties from others, and (3) dyadic variation, which reflects the extent to which the i to j relationship is similar, or reciprocal, to the j to i relationship. The multilevel parameterization of the SRM advantageously allows this variation to be modeled with random effects, or varying intercepts, which accommodates imbalanced sampling relatively easily. Originally designed for continuous responses, the SRM can be adapted for binary, count, and ordered outcomes [4–7]. Implementations of these models have become common among researchers studying cooperative behavior in humans [8–10].

In this case, the dyadic behavior of the capuchin monkeys is a binomial outcome, where the numerator is the number of times that the behavior was observed and the denominator is the maximum number of times it could have been observed given the sampling of the individuals and dyads. Using a "snapshot" approach that is common to behavioral ecology [11], we aggregated the observations by calendar year. Thus, an effect for each individual and dyad was estimated on an annual basis.[1] This timeframe was chosen primarily because the Cox proportional hazards models employed a similar annual timeframe. Each of the behaviors (grooming, coalitional support, and foraging proximity) was estimated separately, though we note that a multivariate SRM can be used to model multiple discrete behavioral outcomes [12].

A. Directed Behaviors

Grooming and coalitional support are directed behaviors, where the behavior originates from individual i and is directed toward individual j. The models assume that both individuals are members of group k in year t. These models can be notated:

---

[1]Although individuals and dyads may appear in multiple group-year datasets, the random effects for each group-year were modeled separately. That is, we did not attempt to model correlations between individuals and dyads when they appear in multiple group-years.

$$y_{ijkt} \sim \text{binomial}(n_{ijkt}, p_{ijkt})$$

$$\text{logit}(p_{ijkt}) = \alpha + m_k + a_{ikt} + b_{jkt} + u_{|ijkt|} + d_{ijkt}$$

where α represents the intercept, m_k is a group-level random intercept for the group, a_{ikt} is a node-level random intercept for the sending node i in group k in year t, b_{jkt} is an analogous random intercept for incoming events to j in group k in year t, $u_{|ijkt|}$ is a symmetric random intercept for dyad ij in group k in year t, and d_{ijkt} is a parameter that reflects the extent to which the directed i to j effect is distinguished from the symmetric effect. This latter parameter also serves to reflect possible overdispersion beyond the conditional expectation for the binomial distribution [13].

The effects for the group effects are assumed to be normally distributed:

$$m_k \sim \text{Normal}(0, \sigma_m^2)$$

The variance of these effects is interpretable as the extent to which the groups tend to differ from each other in their overall propensities for the behaviors.

The random effects for sending and recipient nodes are assumed bivariate normally distributed with zero means and homogeneous covariance matrix:

$$\begin{pmatrix} a_{ikt} \\ b_{ikt} \end{pmatrix} \sim \text{Normal} \left\{ \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma_a^2 & \\ \sigma_{ab} & \sigma_b^2 \end{pmatrix} \right\}$$

As in other applications of the SRM [6], the correlation between the respective effects is known as the "generalized reciprocity correlation." Conceptually, this correlation is similar to the correlation between the nodes' out-degree and in-degree centrality, but note that even in the case of balanced sampling the node-level random effects do not necessarily correspond monotonically to the calculated degree centrality of the nodes [5]. As noted below, this difference is because the random effects are estimated jointly with other parameters in the model.

The use of symmetric dyadic effects in this analysis parallels their use by Koster et al. [14]. That is, within each dyad, the relationship from ikt to jkt and the relationship from jkt to ikt share the same index, which is distinguished by vertical pipes $|ijkt|$. The effects are assumed to be normally distributed:

$$u_{|ijkt|} \sim \text{Normal}(0, \sigma_u^2)$$

The effects for the directed dyadic effects are likewise assumed to be normally distributed:

$$d_{ijkt} \sim \text{Normal}(0, \sigma_d^2)$$

Note that binomial models lack the constant residual variance of Gaussian regression models. As an alternative, latent parameterizations of binomial models may assume that the corresponding variance is $\pi^2/3$, or 3.29 [13].

The dyadic reciprocity correlation, ρ_{ijkt}, can then be calculated by dividing the symmetric dyadic variance by the sum of the dyadic variances and the latent residual variance:

$$\rho_{ijkt} = \frac{\sigma_u^2}{\sigma_u^2 + \sigma_d^2 + 3.29}$$

This parameterization of ρ_{ijkt} assumes that dyadic reciprocity must be positive, which we believe to be a reasonable assumption for the cooperative behaviors in this analysis.[2]

The inclusion of the dyadic effects in the model pertains to our goal of partitioning the effects of reciprocity from the estimation of the individual-level giving and receiving effects. For instance, when a monkey has a high giving effect for grooming, it is generally because the monkey was observed to groom others above the model's expectation for reciprocal grooming. Similar logic applies to the inclusion of both giving and receiving effects. That is, assume that two monkeys spend equivalent amounts of time grooming others. If the first monkey directs its grooming toward the individuals that receive grooming from many others in the group, it will have a lower giving effect than the second monkey that directs grooming toward individuals who receive relatively little grooming from others.

---

[2]Agonistic behaviors, by contrast, would potentially need to be modeled in ways that permit negative dyadic reciprocity[14].

B. Symmetric Behavior

Unlike grooming and coalitional support, foraging in proximity to others is regarded as an undirected, or symmetric, behavior. For symmetric behavior, it is not appropriate to fit a Social Relations Model because the assignment of individuals to the respective i and j indices is arbitrary. The random effects for these individual should have a common variance, not the respective actor-level and partner-level variances that are estimated by the SRM [3, 5, 15, 16]. [3] Individual-level variation may still be pronounced with symmetric behaviors, however, so we fit our model with individual-level random effects.

The binomial model examines the number of times that individuals i and j were observed in proximity in year t, denoted y_{ijkt}, as a proportion of the number of times that they could have been observed, n_{ijkt}. The model is notated as:

$$y_{ijkt} \sim \text{binomial}(n_{ijkt}, p_{ijkt})$$
$$\text{logit}(p_{ijkt}) = \alpha + m_k + v_{ikt} + v_{jkt}$$
$$m_k \sim \text{Normal}(0, \sigma_m^2)$$
$$v_{ikt} \sim \text{Normal}(0, \sigma_v^2)$$
$$v_{jkt} \sim \text{Normal}(0, \sigma_v^2)$$

where α represents the intercept, m_k is a group-level random intercept for the group, v_{ikt} is a node-level random intercept for the individual who has been assigned index i, and v_{jkt} is a node-level random intercept for the individual who has been assigned index j. Note that the group effects are again assumed to be normally distributed with variance σ_m^2. A similar assumption applies to the individual-level effects, v_{ikt} and v_{jkt}. Importantly, note that they share the same variance, σ_v^2.

As noted, we implemented these models in part to reflect the measurement uncertainty of heterogeneously sampled individuals. This uncertainty is evident in the individual-level estimates from the models, as seen in Figure S3. This figure, which depicts foraging proximity, represents the individuals from a single group in a single year of observation. Similar results are evident for other domains and other annualized observations of groups.

---

[3] Dyadic models for symmetric data lack the nomenclature of the "Social Relations Model." Because the model we fit draws on the principles of multiple membership models [17], the approach might be described as a "Multiple Membership Relations Model."
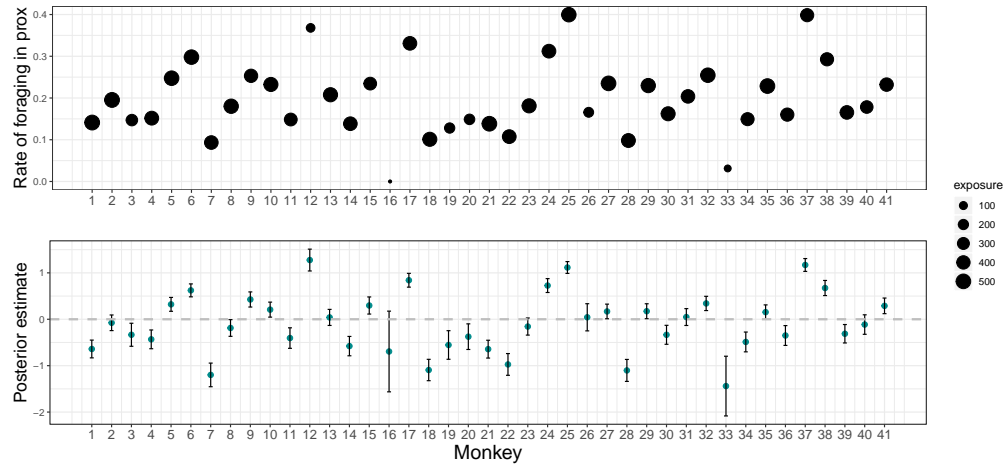
Fig. S1. Comparison of the empirical data to model estimates for the domain of foraging proximity for a representative group of monkeys. Points correspond to individual monkeys who were present in the group during a calendar year. The top panel shows the empirical data, represented as the rate at which individuals were observed to be foraging in proximity to others in the group. The points are sized proportional to the number of observations of that individual in that year, per the legend. The bottom panel shows the model estimates for the same monkeys, as represented by the posterior means (i.e., the points) and standard deviations (i.e., the confidence bands, which represent 1 standard deviation). Note in particular that the model estimates show greater uncertainty (larger standard deviations) as the empirical sample size decreases for a given monkey. Owing to the partial pooling, the posterior means for these individuals have also been "shrunk" toward the population average.

3. COVARIATES

A. Age

Focal female ages were assigned based on demographic records of births and deaths collected from 1990 – 2019. The ages of females who were born before 1990 were 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. We assumed that the age of first birth for each mother was six years, and that interbirth intervals were 2 years [18, 19].

B. 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.

C. 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.

D. 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). This is equivalent to modeling an interaction between age and number of daughters, with age treated as a categorical variable.

E. 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 first identified the dominance interaction immediately preceding and following the day of interest for each focal-alter dyad. The total number of these interactions 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, $w_{i\tilde{\ }a}$, divided by the total number of dominance interactions that the focal had with her alters, $s_{i\tilde{\ }a}$:

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

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

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

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.

We included the covariates, because each of them is likely to influence females' probability of survival. An adult female's probability of dying in a given year is expected to increase with age [20, 21]. Females who live in larger groups might experience greater survival rates due to reduced predation risks [22]. Higher-ranking females possibly enjoy reduced mortality in comparison to lower-ranking females due to their central position in the group [23], which also reduces risks of predation. The presence of a mother and/or adult daughters approximate female's close kin

network benefits: Females who have a more extensive kin network might experience reduced mortality [21].

4. DIRECTED ACYCLIC GRAPH

Having many covariates in the model can result in "included variable bias" [24] where predictors are not only causally influencing the outcome, but also influencing each other. This can result in predictor induced statistical selection within the model and manifest itself through misleading statistical, but not causal, associations between the variables we are interested in [24]. A female's rank and age are likely to influence how much the female participates in social interactions. Females who reside in larger groups are likely to have different interaction networks in comparison to females in smaller social groups due to a larger number of social partners available [20]. To check if the above assumed relationships justify the inclusion of all of the predictor variables in the model, we drew a directed acyclical graph (DAG) using the package daggity (v.3.0) and analyzed implied functional relationships.
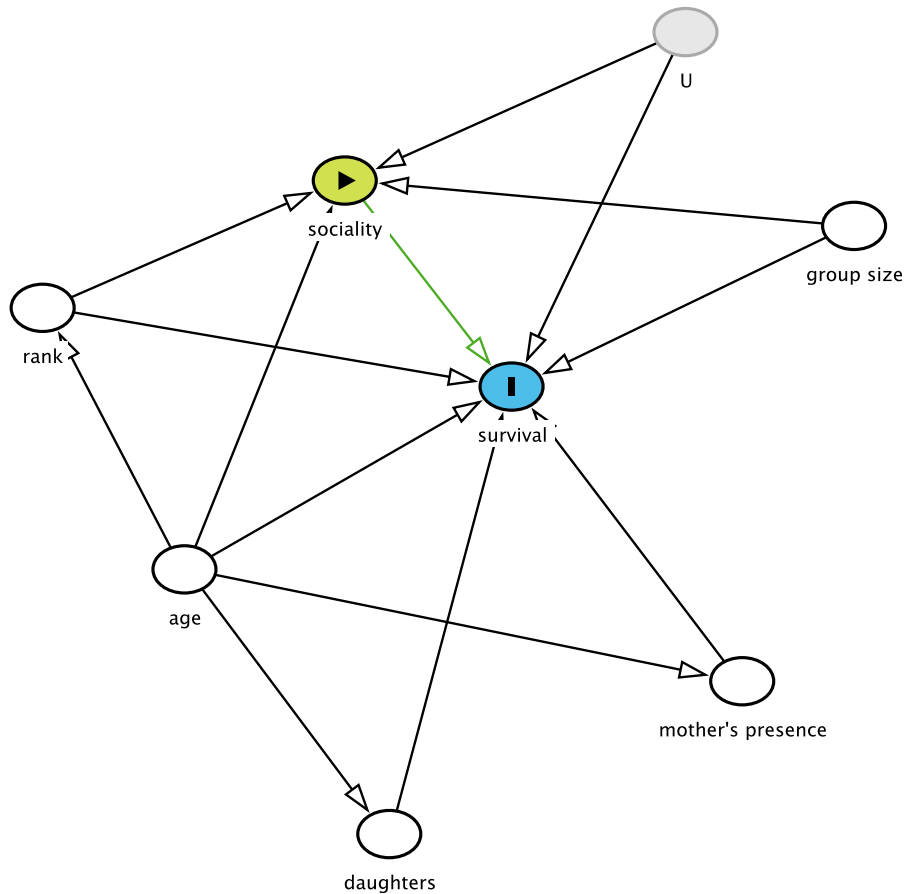
Fig. S2. The assumed causal relationships between the variables represented as a DAG (Directed Acyclic Graph). We assumed that sociality, rank, age, group size, number of daughters (daughters), and whether or not the female's mother is alive (mother's presence) directly influence a female's longevity. In addition, rank, age, and group size influence a female's sociality. Age influences a female's rank, the number of daughters she has, and whether her mother is alive. U represents the possible confounds that are unobserved.

5. POSTERIOR MEANS AND STANDARD DEVIATIONS OF 5 COX PROPORTIONAL HAZARDS MODELS
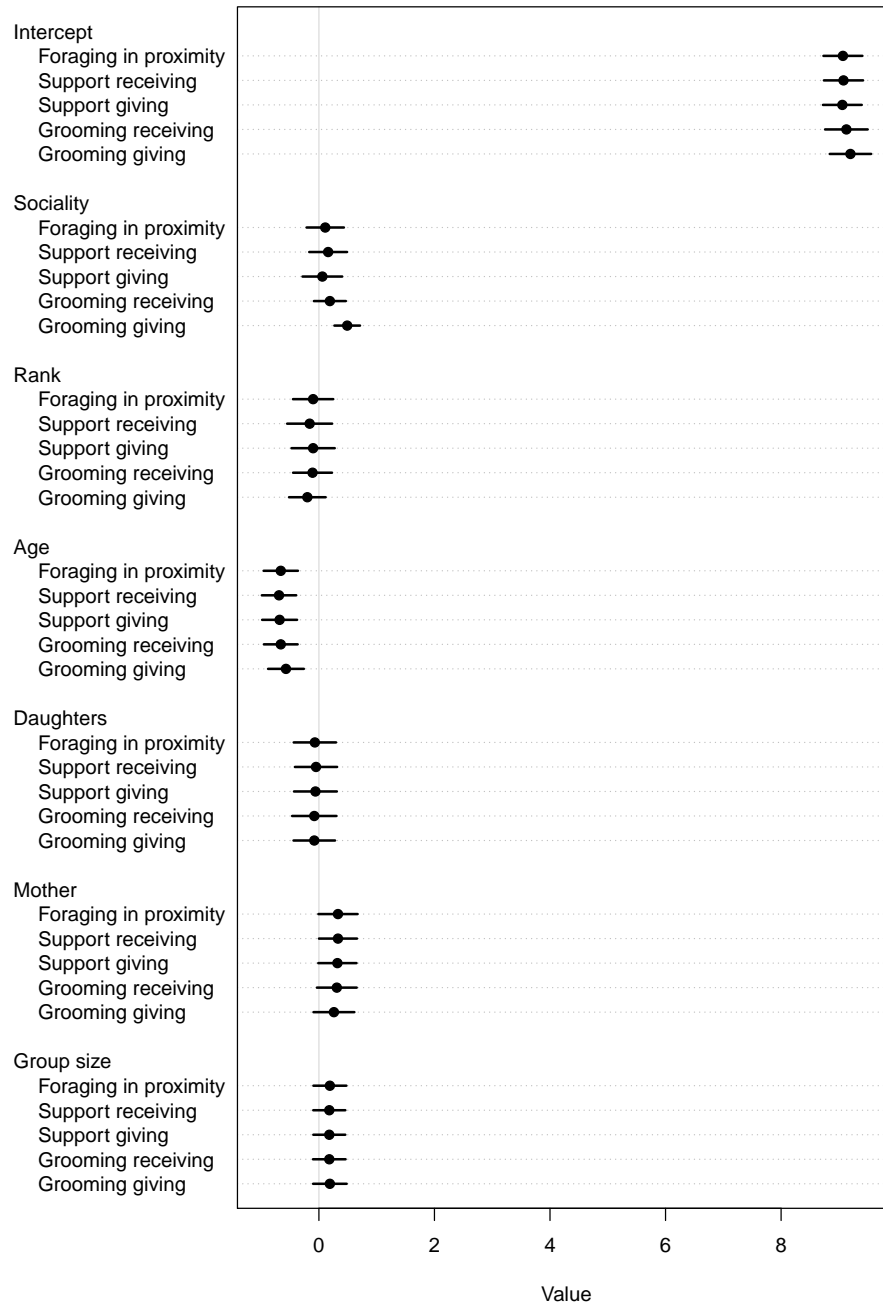
Fig. S3. Posterior means and standard deviations of 5 Cox proportional hazards models (Table 1 in the main text) in which annual survivorship varied as a function of sociality (a different measure for each model), but all models had the same covariates. The five measures of sociality were *foraging in proximity*, *support receiving*, *support giving*, *grooming receiving*, and *grooming giving*.

6. ALTERNATIVE SPECIFICATIONS OF THE PROPORTIONAL HAZARDS MODELS

In this section, we present model results when we alter the parameterizations of the Cox proportional hazards models.

We compared three types of models: one with no random effects and two with individual-level random effect priors assumed as Normal (0, 0.2) or Normal (0, 1). All three model types resulted in similar estimates; therefore here we are reporting the results with individual-level random effect prior Normal (0, 1) in the main text, while the results of the other two types of models are reported here (Table S1 and Table S2).

Table S1. Model without random effects. Estimates of fixed effects of each of the Cox proportional hazards models: posterior means and 95% HPDI.

Parameter	Groom give	Groom receive	Support give	Support receive	Forage in proximity
Intercept	9.01 [8.71,9.33]	8.95 [8.65,9.28]	8.88 [8.62,9.18]	8.88 [8.62,9.17]	8.89 [8.59,9.21]
β Sociality	0.44 [0.22,0.64]	0.18 [-0.08,0.43]	0.07 [-0.23,0.38]	0.05 [-0.29,0.36]	0.15 [-0.17,0.44]
β Rank	-0.17 [-0.41,0.08]	-0.1 [-0.37,0.16]	-0.08 [-0.37,0.2]	-0.08 [-0.41,0.24]	-0.15 [-0.48,0.17]
β Age	-0.38 [-0.6,-0.17]	-0.43 [-0.66,-0.19]	-0.44 [-0.66,-0.21]	-0.45 [-0.67,-0.23]	-0.45 [-0.67,-0.23]
β Daughters	-0.07 [-0.36,0.21]	-0.08 [-0.38,0.22]	-0.06 [-0.37,0.24]	-0.06 [-0.35,0.24]	-0.06 [-0.35,0.24]
β Mother	0.22 [-0.07,0.52]	0.27 [-0.03,0.59]	0.28 [-0.02,0.57]	0.28 [-0.02,0.59]	0.28 [-0.02,0.58]
β Group Size	0.15 [-0.11,0.42]	0.15 [-0.11,0.41]	0.16 [-0.1,0.40]	0.14 [-0.1,0.39]	0.14 [-0.11,0.40]

Table S2. Model with random effects prior Normal(0, 0.2). Estimates of fixed effects of each of the Cox proportional hazards models: posterior means and 95% HPDI.

Parameter	Groom Give	Groom Receive	Support Give	Support Receive	Forage in proximity
Intercept	9.01 [8.72,9.33]	8.95 [8.65,9.3]	8.90 [8.63,9.2]	8.90 [8.62,9.19]	8.90 [8.62,9.21]
β Sociality	0.43 [0.23,0.62]	0.19 [-0.08,0.44]	0.07 [-0.22,0.37]	0.05 [-0.26,0.37]	0.15 [-0.15,0.45]
β Rank	-0.17 [-0.42,0.09]	-0.10 [-0.35,0.16]	-0.08 [-0.37,0.20]	-0.08 [-0.42,0.24]	-0.14 [-0.46,0.19]
β Age	-0.39 [-0.61,-0.16]	-0.44 [-0.67,-0.2]	-0.46 [-0.69,-0.22]	-0.46 [-0.67,-0.24]	-0.46 [-0.69,-0.23]
β Daughters	-0.07 [-0.36,0.22]	-0.08 [-0.38,0.23]	-0.06 [-0.36,0.24]	-0.06 [-0.33,0.24]	-0.06 [-0.36,0.26]
β Mother	0.22 [-0.07,0.54]	0.27 [-0.03,0.58]	0.28 [-0.01,0.56]	0.28 [-0.02,0.58]	0.28 [-0.01,0.58]
β Group Size	0.16 [-0.12,0.43]	0.15 [-0.11,0.40]	0.15 [-0.09,0.41]	0.15 [-0.11,0.41]	0.15 [-0.11,0.40]

REFERENCES

1. D. Lusseau, H. Whitehead, and S. Gero, "Incorporating uncertainty into the study of animal social networks," arXiv preprint arXiv:0903.1519 (2009).
2. T. A. Snijders and D. A. Kenny, "The social relations model for family data: A multilevel approach," Pers. Relationships **6**, 471–486 (1999).
3. J. Koster, G. Leckie, and B. Aven, "Statistical methods and software for the multilevel social relations model," Field Methods **32**, 339—345 (2020).
4. J. M. Koster and G. Leckie, "Food sharing networks in lowland Nicaragua: an application of the social relations model to count data," Soc. Networks **38**, 100–110 (2014).
5. P. D. Hoff, "Dyadic data analysis with amen," arXiv preprint arXiv:1506.08237 (2015).
6. J. Koster and B. Aven, "The effects of individual status and group performance on network ties among teammates in the National Basketball Association," PloS One **13**, e0196013 (2018).
7. J. Loncke, W. L. Cook, J. M. Neiderhiser, and T. Loeys, "The social relations model for count data," Methodology (2019).
8. M. G. Thomas, B.-J. Bårdsen, and M. W. Næss, "The narrow gap between norms and cooperative behaviour in a reindeer herding community," Royal Soc. Open Sci. **5**, 171221 (2018).
9. A. C. Pisor, M. M. Gervais, B. G. Purzycki, and C. T. Ross, "Preferences and constraints: the value of economic games for studying human behaviour," Royal Soc. Open Sci. **7**, 192090 (2019).
10. S. Lew-Levy, S. M. Kissler, A. H. Boyette, A. N. Crittenden, I. A. Mabulla, and B. S. Hewlett, "Who teaches children to forage? exploring the primacy of child-to-child teaching among hadza and bayaka hunter-gatherers of tanzania and congo," Evol. Hum. Behav. **41**, 12–22 (2020).
11. N. Pinter-Wollman, E. A. Hobson, J. E. Smith, A. J. Edelman, D. Shizuka, S. De Silva, J. S. Waters, S. D. Prager, T. Sasaki, G. Wittemyer *et al.*, "The dynamics of animal social networks: analytical, conceptual, and theoretical advances," Behav. Ecol. **25**, 242–255 (2014).
12. S. Nestler, "Likelihood estimation of the multivariate social relations model," J. Educ. Behav. Stat. **43**, 387–406 (2018).
13. W. J. Browne, S. V. Subramanian, K. Jones, and H. Goldstein, "Variance partitioning in multilevel logistic models that exhibit overdispersion," J. Royal Stat. Soc. Ser. A (Statistics Soc. **168**, 599–613 (2005).
14. J. Koster, G. Leckie, A. Miller, and R. Hames, "Multilevel modeling analysis of dyadic network data with an application to ye'kwana food sharing," Am. J. Phys. Anthropol. **157**, 507–512 (2015).
15. J. B. Silk, E. R. Roberts, B. J. Barrett, S. K. Patterson, and S. C. Strum, "Female–male relationships influence the form of female–female relationships in olive baboons, *Papio anubis*," Animal Behav. **131**, 89–98 (2017).
16. J. Bray and I. C. Gilby, "Social relationships among adult male chimpanzees (*Pan troglodytes schweinfurthii*): variation in the strength and quality of social bonds," Behavioral Ecology and Sociobiology **74**, 1–19 (2020).
17. G. Leckie, "Multiple membership multilevel models," arXiv preprint arXiv:1907.04148 (2019).
18. L. M. Fedigan and L. M. Rose, "Interbirth interval variation in three sympatric species of neotropical monkey," Am. J. Primatol. **37**, 9–24 (1995).
19. S. Perry, "The behavior of wild white-faced capuchins: demography, life history, social relationships, and communication," in *Advances in the Study of Behavior,* vol. 44 (Elsevier, 2012), pp. 135–181.
20. E. A. Archie, J. Tung, M. Clark, J. Altmann, and S. C. Alberts, "Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons," Proc. Royal Soc. B: Biol. Sci. **281**, 20141261 (2014).
21. L. J. Brent, A. Ruiz-Lambides, and M. L. Platt, "Family network size and survival across the lifespan of female macaques," Proc. Royal Soc. B: Biol. Sci. **284**, 20170515 (2017).
22. E. H. Sterck, D. P. Watts, and C. P. Van Schaik, "The evolution of female social relationships in nonhuman primates," Behav. ecology sociobiology **41**, 291–309 (1997).
23. U. Kalbitzer, M. L. Bergstrom, S. D. Carnegie, E. C. Wikberg, S. Kawamura, F. A. Campos, K. M. Jack, and L. M. Fedigan, "Female sociality and sexual conflict shape offspring survival in a neotropical primate," Proc. Natl. Acad. Sci. **114**, 1892–1897 (2017).
24. R. McElreath, *Statistical rethinking: A Bayesian course with examples in R and Stan* (CRC press,

2020).