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

Kotrina Kajokaite*[a], Andrew Whalen[b], Jeremy Koster[a,c], and Susan Perry[d,e]

a. Department of Human Behavior, Ecology and Culture, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany

b. The Roslin Institute and Royal (Dick) School of Veterinary Studies, The University of Edinburgh, Easter Bush Campus, Midlothian EH25 9RG, UK

c. Department of Anthropology, University of Cincinnati, PO BOX 210380 481 Braunstein Hall, Cincinnati, OH 45221-0380, USA

d. Department of Anthropology, University of California, 375 Portola Plaza, Los Angeles, CA 90095, USA

e. Behavior, Evolution and Culture Program, Department of Anthropology, University of California, 375 Portola Plaza, Los Angeles, CA 90095, USA

* Corresponding author: Kotrina Kajokaite, Department of Human Behavior, Ecology and Culture, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6 04103 Leipzig, Germany

ABSTRACT

Across multiple species of social mammals, evidence is accumulating that sociality is associated with fitness. In long-lived species, like primates, lifespan is one of the main fitness components. Here, we provide the first direct evidence that females who provide more in social services live longer. We used 18 years of data from the Lomas Barbudal Monkey project to quantify sociality in 11 capuchin (*Cebus capucinus*) social groups using three interaction types: grooming, support in coalitionary aggression, and foraging in close proximity. We analyzed each domain separately to understand how giving and receiving social favors predict survivorship. To estimate female sociality in each of these domains, we implemented an adaptation of the Social Relations Model. This approach enabled us to estimate individual rates of giving and receiving interactions while accounting for the inherent measurement uncertainty in these estimates due to varying amounts of observations of each individual. Subsequently, we modeled adult females' survival as a function of their sociality estimates, rank, age, group size, and maternal kin presence using a Bayesian Cox proportional hazards model. We found that females who provide more grooming to other group members survive longer, but other social interaction types had little effect on survivorship.

Keywords: capuchins, C*ebus*, sociality, social relationships, survival, fitness

INTRODUCTION

A key question for understanding the evolution of animal sociality is: Do animals that are more social enjoy greater fitness benefits? A number of studies link components of reproductive success, such as fecundity (Fedigan et al., 2008; Schülke et al., 2010; Gilby et al., 2013) and offspring survival (Silk, 2009; Silk et al., 2003; Kalbitzer et al., 2017), to differences in the social behavior of individuals.

In long-lived, iteroparous species, lifespan is also an important component of reproductive success contributing to fitness variation (Clutton-Brock, 1998). In human populations, 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 (Roelfs et al., 2011). In nonhuman species there is similar evidence that various aspects of individual sociality are associated with lifespan (e.g., Silk et al. 2010).

Detailed longitudinal behavioral records are necessary for relating an individual's social behavior patterns to longevity (Clutton-Brock, 1988). Because these data are logistically difficult to collect in many habitats, the data are often challenging to analyze given heterogeneous sampling across time periods, social groups, and individuals. Although research on sociality often ignores this sampling variability (reviewed in Silk et al. 2013), the measurement uncertainty can be substantial, complicating inferences.

The primary objective of this paper in an investigation of the effects of sociality on survivorship among female white-faced capuchins (*Cebus capucinus*). We test this relationship using data spanning 18 years of capuchin monkeys' social interactions and demography from the Lomas Barbudal Monkey dataset. To quantify individual sociality, we selected interactions from three domains to represent the variety of social behaviors that capuchin monkeys engage in: grooming, coalitionary aggression, and foraging in proximity to others. A secondary goal of the paper is to develop analytical approaches for the measurement uncertainty stemming from heterogenous sampling, which we address by adapting the multilevel Social Relations Model (Snijders and Kenny, 1999; Koster et al. 2020). We generate individuals' sociality estimates that reflect the measurement uncertainty, which are subsequently used to test the hypothesis that social behavior predicts longevity.

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 dataset has longitudinal records including demographic information, pedigree information, and social interactions on individuals living in 11 capuchin social groups. The data on capuchin behavior were collected between January 2002 and December 2019. All groups in this study were observed in at least 7 calendar years (mean = 13.27). The primary subjects of this analysis were 132 adult females, where adulthood is assumed to begin at the age of 5 years. The behavioral and demographic data on each group were collected by experienced observers during visits lasting at least 6 hours/day.

Measuring Sociality

As measures of female sociality, we focused on three behavioral domains: grooming, coalitionary aggression, and foraging. We treated grooming and coalition formation as directed behaviors, and we used observations of individuals as both initiators and recipients of the behavior. We did not have information about which individual had initiated the proximity when foraging, and therefore foraging in proximity was treated as an undirected behavior. In calculating the frequency with which adult females engaged in these interactions, we used behavioral records from all the individuals who resided in the 11 respective groups during the study period. There were a total of 563 monkeys and 13,770 unique dyads. We treated each of the five interaction types (*grooming giving, grooming receiving, support giving, support receiving, forage in proximity*) as a separate measure of sociality.

Grooming (groom giving and groom receiving)

Grooming rates were estimated using data collected during 10-minute 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 co-resident. A count of 1 was assigned if A groomed B at least once during a focal follow, otherwise 0 was assigned. The same was done when evaluating if B groomed A.

Joining a coalitionary conflict (support giving and support receiving)

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, aggressive interactions were collected both *ad libitum* and during focal follows. The chronological stream of aggressive behaviors was divided into 5-

minute intervals. 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 intervals. The measure is dichotomous, and a single instance was recorded for the occasions when there were multiple observations of monkey A joining monkey B during the interval. To calculate the opportunities to join a coalitionary conflict, all individuals who were co-resident during the aggressive conflict were regarded as having the 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-minute intervals. 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 minutes apart, where one of the individuals is a subject of a group scan.

Individual sociality measures

The data for these analyses were collected across eighteen years and the number of observed social groups and individuals generally increased over time. As a result, the density of data is uneven across time periods, social groups, and individuals. We incorporated uneven distributions of the data by aggregating the data annually and using adaptations of the multilevel Social Relations Model (Snijders and Kenny, 1999; Koster et al. 2020) to estimate individual annual rates of grooming, coalitionary support, and foraging (see supplemental material). This method provided estimates of individual sociality that reflect the measurement uncertainty, with the uncertainty increasing for infrequently observed individuals.

Modeling survival as a function of individual sociality measure

To investigate whether sociality is associated with adult female longevity, we used Bayesian Cox proportional hazards models. In separate models, each of the five individual sociality measures was modeled as a predictor of survival probability over one-year periods. In addition to the respective sociality measures, these models included the following time-varying (calendar year-specific) covariates: the female's age, her dominance rank (ranges from 0 to 1, where 1 represents the highest rank), 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 (see supplemental material for further details on covariates).

Modeling approach

We specified the following model for the number of days before death, D_i,. The probability for the number of days before death comes from the cumulative probability distribution:

$$\Pr\left(D_i \mid \lambda_i\right) = \lambda_i \exp(-\lambda_i D_i) \; . \tag{3}$$

For females who did not die during the observation period, the probability of surviving D_i comes from the complementary cumulative probability distribution:

$$\Pr\,(D_i \mid \lambda_i) = \exp\,(-\lambda_i D_i)\ . \tag{4}$$

We model the rate of dying, λ_i, as follows:

$$\lambda_i = 1/\mu_i\ . \tag{5}$$

where μ_i is the expected number of days till death

$$\begin{aligned}\log(\mu_i) = \alpha + a[\,id\,] + b_{sociality} * true\ sociality\ estimate[id] + b_{rank} * rank \\ + b_{age} * age + b_{daughters} * daughters \\ +\ b_{mother} * mother + b_{grsize} * group\ size\ .\end{aligned} \tag{6}$$

where α denotes the intercept or the base rate of number of days survived, $\alpha[id]$ denotes individual female random effects corresponding to the observation period. The model coefficients $b_{sociality}$, b_{rank}, b_{age}, $b_{daughters}$, b_{mother}, and b_{grsize} describe the impact of sociality, rank, age, number of daughters, mother's presence, and group size, respectively. We adopted a latent variable approach to model the sociality estimates given that the individuals' sociality estimates are not point estimates, but rather posterior distributions with means and standard deviations that reflect the measurement uncertainty.

We used the Bayesian approach to fit Cox proportional hazards models (Singer and Willett 2003). We assumed a Normal (8, 0.5) prior for a base rate of survival, α, which places most of the prior mass between 0 to 20 years with the mean of 8 years and a long tail allowing more extreme values. For fixed effects, we assumed Normal (0, 1) priors. For individual-level random effects, $\alpha[id]$, we use a Normal (0, 1) prior (see supplemental material). All of the covariates, except the number of daughters, were standardized by subtracting the mean and dividing it by the standard deviation. The number of daughters was centered by subtracting the mean number of daughters for each age.

Models were run using Stan (v.2.19.1) and the *rethinking* package (v. 1.93: McElreath, 2020) in *R* (v. 3.6.2; R Core Team 2019).

RESULTS

For perspective on the individual sociality measures, Figure 1 illustrates how the estimates of *grooming, coalitionary support,* and *foraging in proximity* by adult females compare to the estimates for other age-sex classes. Females differ the most from the other age-sex classes in their distribution of *grooming giving* measures. A majority of the females (80%) groom more than an average monkey in the population (Figure 1, panel A). The female distributions for the rest of the behavioral domains are comparatively similar to the other age-sex distributions, indicating that females behave similarly to adult males and immatures in those domains.

We plotted the pairwise correlations between each of the sociality measures in Figure 2 in order to investigate if female profiles are similar across all five measures, e.g. is a frequent groomer also a frequent recipient of grooming and coalitional support? Within the coalitionary aggression domain, estimates of female giving and receiving coalitionary support were highly correlated (r=0.97). In the grooming domain, the correlation between giving and receiving estimates was moderate (r=0.57). The correlations across behavioral domains are smaller than within a domain, between 0.15 and 0.37.

Our primary objective was to test the effects of sociality on survivorship. Table 1 presents the Cox proportional hazards model posterior mean estimates and the 95% Highest

Posterior Density Interval (HPDI), representing the narrowest interval containing the 95% probability mass. Independent of the effects of covariates, females who groomed others more survived at higher rates than other females. The other sociality measures had mean estimates consistent with sociality predicting greater survival, but their HPDI intervals were wide and included zero, suggesting uncertainty about the effects of these estimates.

To facilitate the interpretation of the Cox proportional hazards model coefficients, we plotted model predictions showing the probability of dying in a given year (Figure 3). Across all five sociality measures, the less social females have a greater probability of dying than more social females, but only the slopes for *groom giving* confidently suggest a beneficial effect on survivorship (Figure 3, panel A).

Figure 1. Posterior mean distributions of annual individual sociality measures for each type of behavior. The orange density represents adult females whereas the white density represents the rest of the population. The population base rate is normalized at approximately zero.

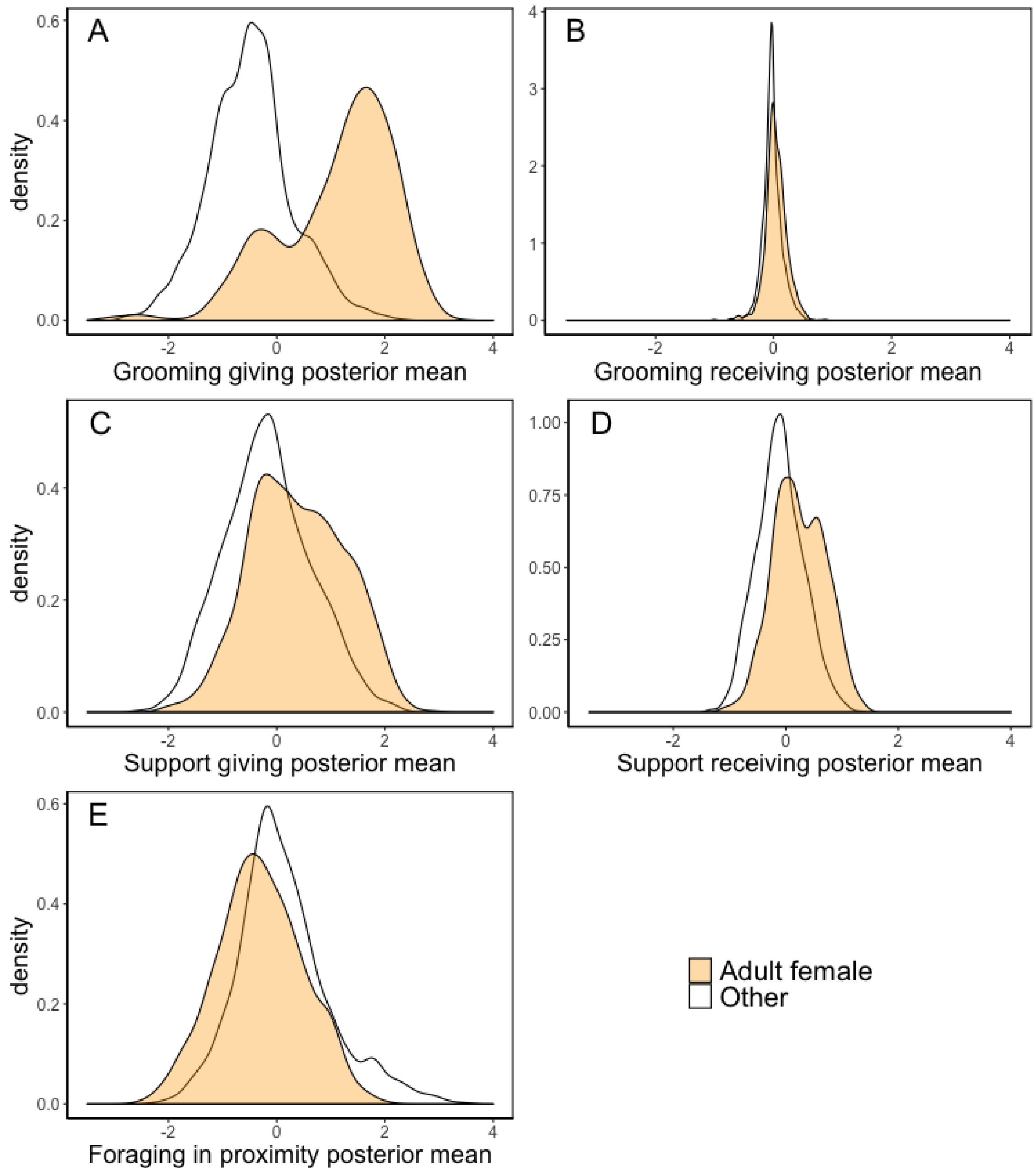


Figure 2. Bivariate correlations of individual sociality measures. Each point represents the posterior mean of an annual estimate for an individual female in the sample.

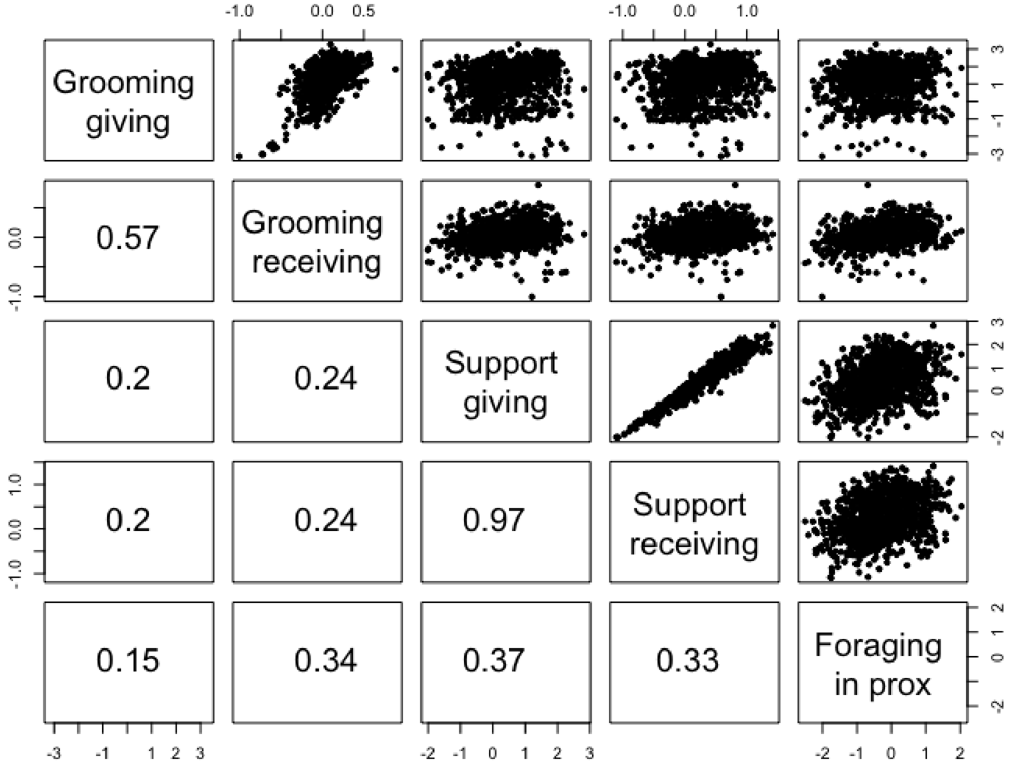
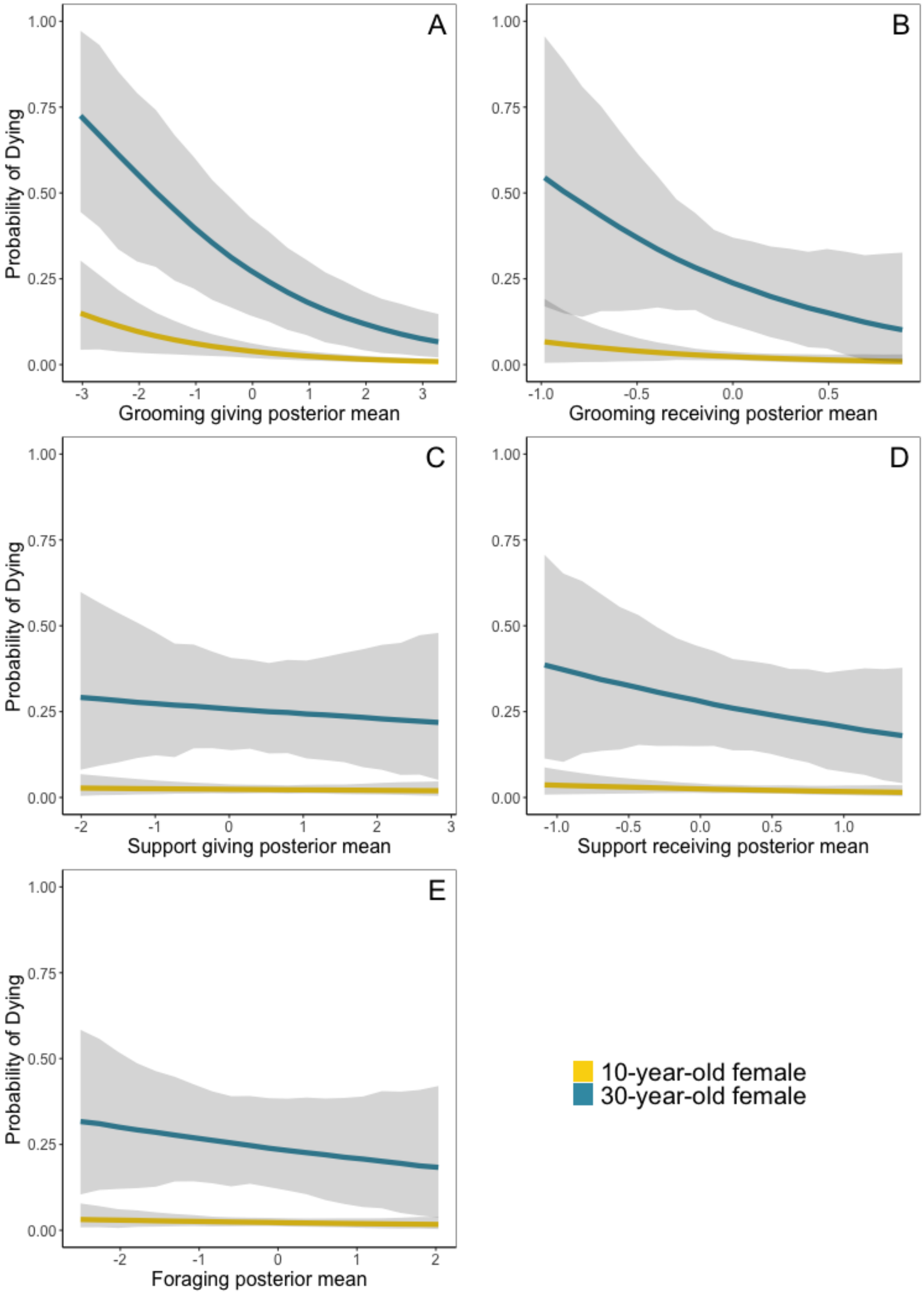


Table 1. Estimates of fixed effects of each of the Cox proportional hazards models: posterior means and 95% HPDI (see supplemental material for graphical representation of this table).

Parameter	Sociality measure Grooming giving	Grooming receiving	Support giving	Support receiving	Foraging in proximity
Intercept	9.20 [8.86,9.56]	9.13 [8.78,9.52]	9.07 [8.74,9.42]	9.06 [8.73,9.41]	9.08 [8.74,9.42]
β sociality	0.49 [0.26,0.70]	0.19 [–0.09,0.45]	0.11 [–0.21,0.45]	0.06 [–0.28,0.40]	0.16 [–0.18,0.47]
β rank	–0.20 [–0.51,0.11]	–0.11 [–0.45,0.24]	–0.10 [–0.45,0.24]	–0.10 [–0.47,0.28]	–0.16 [–0.54,0.23]
β age	–0.57 [–0.88,–0.25]	–0.66 [–0.96,–0.37]	–0.66 [–0.96,–0.37]	–0.68 [–0.99,–0.38]	–0.69 [–0.98,–0.39]
β daughters	–0.08 [–0.45,0.28]	–0.08 [–0.45,0.31]	–0.07 [–0.44,0.31]	–0.06 [–0.43,0.30]	–0.05 [–0.43,0.32]
β mother	0.26 [–0.09,0.63]	0.31 [–0.02,0.66]	0.33 [–0.01,0.67]	0.32 [–0.01,0.65]	0.33 [–0.01,0.66]
β group size	0.19 [–0.1,0.49]	0.18 [–0.10,0.46]	0.19 [–0.10,0.48]	0.18 [–0.1,0.46]	0.18 [–0.09,0.46]

Figure 3. The predicted annual probabilities of dying at two representative ages (10 and 30) as a function of the sociality levels in five behavioral domains, as calculated from the Cox proportional hazards models. For both ages, we assumed median group size, median rank, and average number of daughters for the age. For 10-year-old females, we assumed a co-resident mother, while predictions for the 30-year-old assume the mother is deceased.



DISCUSSSION

In female white-faced capuchin monkeys, providing grooming to others is associated with greater survival rates. Females who provide more grooming die at lower rates than females who engage in this behavior less often. By contrast, there was no strong evidence that females who receive more grooming, participate more often in coalitionary aggression, and forage more often in close proximity of others also have higher survivorship. Our results in the grooming domain are consistent with findings that social integration is associated with longevity in humans (Holt-Lunstad et al., 2010) and adds a neotropical primate species to the list of mammalian species where a similar association between sociality and longevity has been demonstrated (Fagen and Fagen, 2004; Yee et al. 2008; Cameron et al. 2009; Silk et al., 2010; Archie et al., 2014; Brent, 2017; Thompson and Cords, 2018).

A biologically interesting question deals with the mechanisms that facilitate the relationship between sociality and longevity. In the human literature, two general models have been proposed for the influence of social relationships on health (Holt-Lunstad et al. 2010). First, the stress buffering model assumes that social relationships provide resources that affect either behavioral or neuroendocrine responses which buffer the influence of stress on health. Second, the main effects model assumes that participating in social relationships itself encourages healthy behaviors.

In the primate literature, recently there has been discussion of the specific pathways that connect social behavior to fitness (Ostner and Schülke 2018; Thompson, 2019). Consistent with the stress buffering model, providing grooming can have either direct effects on longevity or influence other behaviors that in turn influence survival.

Directly, females might derive benefits when grooming others, such as social bonding through the release of hormones (Dunbar 2010). Both providing and receiving grooming seemingly influence oxytocin and glucocorticoid levels in primates (reviewed in Crockford et al. 2017), but our analysis reveals a stronger effect of providing grooming on survival in comparison to receiving grooming. The variation in engaging in these behaviors among individuals helps to explain this pattern: Adult females do not vary greatly in how much grooming they receive; therefore, the neuroendocrine benefits they receive from it are less likely to differentiate the stress buffering among individuals. However, females vary considerably in how much they are likely to groom others, and those who are the most avid groomers are likely to derive the greatest benefits related to stress reduction.

Indirectly, grooming interactions potentially shape females' participation in coalitionary behavior via the effects of mediating variables. Notably, the females who groom others the most are usually not the same females who participate in coalitionary aggression the most frequently. It is possible that avid groomers receive less aggression and, as a result, fewer of the detrimental consequences that directly reduce survival.

In this study, confidence in the statistical findings is enhanced by a methodological approach that incorporates the measurement uncertainty that typifies observational data. Data from the natural habitats are notoriously difficult to gather. Inevitably, the records for social interactions are sparse (Farine, 2015) and some individuals are observed more often than others (Silk et al., 2013). Based on limited observational data, some dyads may appear to have no social relationship, whereas if behavioral sampling were sufficiently dense, they would be observed to interact, albeit rarely (Farine, 2015).

To address the uneven sampling effort of individuals and social groups in our dataset, we adapted the Social Relations Model. Based on multilevel partial pooling (McElreath 2002), the resulting estimates of sociality reflect the latent uncertainty of observational data. We generated these estimates from dyadic observations of adult females with all other group members rather than demographic subsets of peers as in previous studies (e.g. Silk et al., 2010; Archie et al., 2014; Kalbitzer et al., 2017). The methods used in this study, however, offer similar benefits for research on subgroups of dyads and more generally provide an alternative that is suited to the imbalanced data structures of observational research.

CONCLUSION

Across taxa, research on sociality has revealed diverse effects on components of fitness. This study examines sociality in detail, showing that grooming others is the social behavior that most prominently distinguishes individuals, and this aspect of sociality concomitantly predicts the survivorship of adult female capuchins. These results accentuate the need for greater attention to the mechanistic pathways that connect sociality to fitness (Ostner and Schülke, 2018). As longitudinal data become increasingly common in studies of animal behavior, careful analyses can better elucidate the evolutionary consequences of variation in sociality among individuals.

ETHICS

The study was strictly observational, all protocols were approved by UCLA's Animal Care Committee (protocol 2016-022). All necessary permits were obtained from SINAC and MINAE (the Costa Rican government bodies responsible for research on wildlife) and renewed every 6 months over the course of the study; the most recent scientific passport number being #117-

2019-ACAT and the most recent permit being Resolución # M-P-SINAC-PNI-ACAT-072-2019. This research is in compliance with the Animal Behavior Society's Guidelines for the Use of Animals in Research.

DATA AND CODE ACCESSIBILITY

The data and code used to produce the analyses in this paper are available at: www.doi.org/10.5281/zenodo.3961479

AUTHOR CONTRIBUTIONS

K.K. and S.E.P. designed the study, wrote the queries to assembled the data set. K.K. collected some of the data. S.E.P. runs the long-term study, wrote the grants funding data collection, was the primary data collector and data cleaner, supervised the data collection and cleaning done by others, and manages the database. K.K. and J.K. developed SRM analyses and K.K. set up and carried out the implementation. K.K. and A.W. developed and analyzed Bayesian Cox proportional hazards model. K.K. took the lead in writing the manuscript. All authors provided critical feedback and helped to write the manuscript.

COMPETING INTERESTS

We declare we have no competing interests.

FUNDING

K.K. was supported by a University of California-Los Angeles (UCLA) Pauley Fellowship, a UCLA Dissertation Year Fellowship, and by the Max Planck Institute for Evolutionary Anthropology. This material is based on data collection supported by funding provided to S.E.P. by the National Science Foundation (under grant numbers 1638428, 0613226, 0848360, and 1232371), the Max Planck Institute for Evolutionary Anthropology, the L.S.B. Leakey Foundation (5 grants), the National Geographic Society (5 grants), the Templeton World Charity Foundation (grant #0208), the Wild Capuchin Foundation, and multiple Committee on Research grants from UCLA.

ACKNOWLEDGEMENTS

The following field assistants contributed significant amounts of data to the Lomas Barbudal Monkey Project dataset: C. Angyal, A. Autor, B. Barrett, L. Beaudrot, M. Bergstrom, R. Berl, A. Bjorkman, L. Blankenship, T. Borcuch, J. Broesch, D. Bush, J. Butler, F. Campos, C. Carlson, A. Cobden, M. Corrales, J. Damm, B. Davis, C. deRango, N. Donati, C. Dillis, G. Dower, R. Dower, A. Duchesneau, K. Feilen, J. Fenton, S. Fiello, K. Fisher, A. Fuentes J., M. Fuentes A., T. Fuentes, C. Gault, H. Gilkenson, I. Godoy, I. Gottlieb, J. Griciute, L.M. Guevara R., L. Hack, R. Hammond, S. Herbert, C. Hirsch, M. Hoffman, A. Hofner, C. Holman, J. Hubbard, S. Hyde, M. Jackson, O. Jacobson, E. Johnson, L. Johnson, S. Lee, S. Leinwand, T. Lord, M. Kay, E. Kennedy, D. Kerhoas-Essens, E. Johnson, S. Kessler, B. Krimmel, W. Lammers, S. Lopez, S. MacCarter, J. Mackenzie, M. Mayer, F. McKibben, W. Meno, A. Mensing, M. Milstein, C. Mitchell, Y. Namba, A. Neyer, C. O'Connell, J. C. Ordoñez, J., N. Parker, B. Pav, R. Popa, K. Potter, K. Ratliff, K. Reinhardt, N. Roberts Buceta, E. Rothwell, J. Rottman, H. Ruffler, S. Sanford, M. Saul, E. Seabright, I. Schamberg, S. Schembari, N. Schleissman, C. Schmitt, S. Schulze, A. Scott, S. Sita, J. Shih, K. Stewart, W. Tucker, E. Urquhart, K. van Atta, J. Vandermeer, L. van Zuidam, J. Verge, V. Vonau, A. Walker-Bolton, E. Wikberg, E. Williams, L. Wolf, and D. Wood. We thank H. Gilkenson and W. Lammers for long-term management of the field site during 2002-2013. We thank the Costa Rican park service (Sistema Nacional de Áreas de Conservación and Área de Conservación Tempisque), Hacienda Pelon de la Bajura, Hacienda Brin D'Amor, and the residents of San Ramon de Bagaces for permission to work on their land. D. Cohen assisted with database management and queries. This paper has benefited from helpful discussions with H. Clark Barrett, Donald Cohen, Joseph Manson, Mary Brooke McElreath, Oliver Schülke, and Julia Ostner.

REFERENCES

Archie, E. A., Tung, J., Clark, M., Altmann, J., & Alberts, S. C. (2014). Social affiliation matters: Both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1793), 20141261.

Brent, L. J. N., Ruiz-Lambides, A., & Platt, M. L. (2017). Family network size and survival across the lifespan of female macaques. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1854), 20170515.

Cameron, EZ, Setsaas, TH, & Linklater, WL (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences* , *106* (33), 13850-13853.

Clutton-Brock, T. H. (1988). *Reproductive success: Studies of individual variation in contrasting breeding systems*. University of Chicago Press.

Crockford, C., Deschner, T., & Wittig, R. M. (2017). The role of oxytocin in social buffering: What do primate studies add? In *Behavioral Pharmacology of Neuropeptides: Oxytocin* (pp. 155-173). Springer, Cham.

Dunbar, R. I. M. (2010). The social role of touch in humans and primates: Behavioural function and neurobiological mechanisms. *Neuroscience & Biobehavioral Reviews*, *34*(2), 260–268. https://doi.org/10.1016/j.neubiorev.2008.07.001

Fagen, R., & Fagen, J. (2004). Juvenile survival and benefits of play behaviour in brown bears, Ursus arctos. *Evolutionary Ecology Research*, *6*(1), 89–102.

Farine, D. R. (2015). Proximity as a proxy for interactions: Issues of scale in social network analysis. *Animal Behaviour*, *104*, e1–e5.

Fedigan, L. M., Carnegie, S. D., & Jack, K. M. (2008). Predictors of reproductive success in female white-faced capuchins (Cebus capucinus). *American Journal of Physical Anthropology, 137*(1), 82–90.

Fragaszy, D. M., Visalberghi, E., & Fedigan, L. M. (2004). *The complete capuchin: The biology of the genus Cebus*. Cambridge University Press.

Gilby, I. C., Brent, L. J., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., & Pusey, A. E. (2013). Fitness benefits of coalitionary aggression in male chimpanzees. *Behavioral Ecology and Sociobiology*, *67*(3), 373–381.

Gros-Louis, J., Perry, S., & Manson, J. H. (2003). Violent coalitionary attacks and intraspecific killing in wild white–faced capuchin monkeys (Cebus capucinus). *Primates*, *44*(4), 341–346.

Hinde, R. A. (1976). Interactions, relationships and social structure. *Man*, 1–17.

Holt-Lunstad, J., Smith, T. B., & Layton, J. B. (2010). Social relationships and mortality risk: A meta-analytic review. *PLoS Medicine*, *7*(7), e1000316.

Kalbitzer, U., Bergstrom, M. L., Carnegie, S. D., Wikberg, E. C., Kawamura, S., Campos, F. A., Jack, K. M., & Fedigan, L. M. (2017). Female sociality and sexual conflict shape offspring survival in a Neotropical primate. *Proceedings of the National Academy of Sciences*, *114*(8), 1892–1897.

Koster, J., Leckie, G., Miller, A., & Hames, R. (2015). Multilevel modeling analysis of dyadic network data with an application to Ye’kwana food sharing. *American Journal of Physical Anthropology*, *157*(3), 507–512.

Koster, J., Leckie, G., & Aven, B. (2020). Statistical methods and software for the Multilevel

Social Relations Model. *Field Methods*, *32*(4), 339–345.

Manson, J. H., Navarrete, C. D., Silk, J. B., & Perry, S. (2004). Time-matched grooming in female primates? New analyses from two species. *Animal Behaviour*, *67*(3), 493–500.

McElreath, R. (2020). *Statistical rethinking: A Bayesian course with examples in R and Stan*. CRC press.

McElreath, R. (2020). rethinking: Statistical rethinking book package (R package Version 1.93). https://github.com/rmcelreath/rethinking.

Nuñez, C. M., Adelman, J. S., & Rubenstein, D. I. (2014). Sociality increases juvenile survival after a catastrophic event in the feral horse (Equus caballus). *Behavioral Ecology*, *26*(1), 138–147.

Ostner, J., & Schuelke, O. (2018). Linking sociality to fitness in primates: A call for mechanisms. In *Advances in the Study of Behavior* (Vol. 50, pp. 127–175). Elsevier.

Perry, S. (1996). Female-female social relationships in wild white–faced capuchin monkeys, *Cebus capucinus*. *American Journal of Primatology*, *40*(2), 167–182.

Perry, S. (2012). The behavior of wild white-faced capuchins: Demography, life history, social relationships, and communication. In *Advances in the study of behavior* (Vol. 44, pp. 135–181). Elsevier.

Perry, S., Godoy, I., & Lammers, W. (2012). The Lomas Barbudal Monkey Project: Two decades of research on Cebus capucinus. In *Long-term field studies of primates* (pp. 141–163). Springer.

Perry, S., Manson, J. H., & Perry, S. (2009). *Manipulative Monkeys*. Harvard University Press.

Porter, C. A., Page, S. L., Czelusniak, J., Schneider, H., Schneider, M. P. C., Sampaio, I., & Goodman, M. (1997). Phylogeny and Evolution of Selected Primates as Determined by Sequences of the ε-Globin Locus and 5’ Flanking Regions. *International Journal of Primatology*, *18*(2), 261–295. https://doi.org/10.1023/A:1026328804319

R Core Team. (2020). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Roelfs, D. J., Shor, E., Kalish, R., & Yogev, T. (2011). The rising relative risk of mortality for singles: Meta-analysis and meta-regression. *American Journal of Epidemiology*, *174*(4), 379–389.

Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology*, *20*(24), 2207–2210.

Shor, E., & Roelfs, D. J. (2015). Social contact frequency and all-cause mortality: A meta-analysis and meta-regression. *Social Science & Medicine*, *128*, 76–86.

Shor, E., Roelfs, D. J., & Yogev, T. (2013). The strength of family ties: A meta-analysis and meta-regression of self-reported social support and mortality. *Social Networks*, *35*(4), 626–638.

Silk, J. B. (2009). Nepotistic cooperation in non-human primate groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1533), 3243–3254.

Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science*, *302*(5648), 1231–1234.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, *20*(15), 1359–1361.

Silk, J., Cheney, D., & Seyfarth, R. (2013). A practical guide to the study of social relationships. *Evolutionary Anthropology: Issues, News, and Reviews*, *22*(5), 213–225.

Snijders, T. A., & Kenny, D. A. (1999). The social relations model for family data: A multilevel approach. *Personal Relationships*, *6*(4), 471–486.

Stan Development Team. (2020). RStan: The R interface to Stan (Version 2.19.1).

Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, *41*(5), 291–309. https://doi.org/10.1007/s002650050390

Thompson, N. A. (2019). Understanding the links between social ties and fitness over the life cycle in primates. *Behaviour*, *1*(aop), 1–50.

Thompson, N. A., & Cords, M. (2018). Stronger social bonds do not always predict greater longevity in a gregarious primate. *Ecology and Evolution*, *8*(3), 1604–1614.

Yee, J. R., Cavigelli, S. A., Delgado, B., & McClintock, M. K. (2008). Reciprocal affiliation among adolescent rats during a mild group stressor predicts mammary tumors and lifespan. *Psychosomatic Medicine*, *70*(9), 1050.