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

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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. A growing number of studies shows that interactions with individuals of both sexes, and both weak and strong bonds predict survival. We used 18 years of data from the Lomas Barbudal Monkey project to quantify sociality in 11 capuchin (*Cebus capucinus*) groups and tested whether females' tendencies to interact with their group members are associated with survival. We found that females who provide more grooming to other group members survive longer. The association is stronger for older females. These benefits were independent of females' rank, presence of their adult daughters and mothers, and their group size. Receiving more grooming from others showed a similar effect on survival, but confidence in the estimated effect was unclear. Participation in coalitionary aggression and foraging in close proximity of others were not predictive of increased survival. The results presented here suggest that females' general propensities to affiliate with members of their group may result in survival-related benefits. Females might enjoy these benefits through exchanging grooming for other currencies, such as coalitionary support or tolerance.

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

INTRODUCTION

A key question for understanding the evolution of animal sociality is: Do more social individuals have higher fitness? A number of studies link components of reproductive success, such as fertility (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 life-time reproductive success that contributes to variation in fitness (Clutton-Brock, 1998) and there is evidence that aspects of individual sociality are associated with lifespan in humans and nonhuman animals (Snyder-Mackler et al., 2020).

It has been hypothesized that social animals have evolved cognition characterized by skills and motivations to monitor their social world and interact with conspecifics in fitness-enhancing ways (Jolly, 1966; Humphrey, 1976; Whiten and Byrne, 1997). Individuals cultivate differentiated social relationships through these interactions, which, in turn, affect their fitness. Discussion of causal pathways by which the social integration of an individual contributes to their fitness is just starting to emerge in the literature (Ostner and Schülke, 2018; Thompson, 2019, Snyder-Mackler et al., 2020). The task is complicated by the fact that there are multiple ways one can measure how social animals connect to others (Cheney et al., 2016; Ellis et al., 2019), and different measures may be associated with different pathways linking social behavior to fitness.

Here we ask how an adult white-faced capuchin (*Cebus capucinus*) female's survival is predicted by various kinds of social interactions. To choose a measurement of sociality that is well suited to address this question, we consider three different types of social interactions:

grooming, foraging near others, and coalitionary aggression. These interactions are characterized by varying qualities that define the social relationships: affiliative touch, affiliation through spatial proximity in the vicinity of food resources, and cooperation respectively (Hinde, 1976). We quantified interactions in each domain separately and, where possible, we estimated a female's role as a provider and as a receiver of the behavior. In order to better understand the pathways by which females translate their social interactions into survival-related benefits (e.g., reduced wounding, increased rank, better access to resources, reduced predation risk), it is important to document whether females are providing or receiving these services (*see supplemental material for detailed descriptions of pathways*). Although we are testing for predictors of fitness and are not testing specific pathways, our approach of estimating individuals' roles separately in each behavioral domain generates hypotheses that can be tested subsequently regarding causal pathways connecting these interactions to fitness.

Measures of individual sociality (Silk et al., 2013; Ostner and Schülke 2018; Thompson 2019; Ellis et al. 2019), vary according to the emphasis on the interaction frequency and/or numbers of partners being incorporated into the metric. We chose an individual-level metric that is best conceptualized as a social integration measure, where interaction frequency rather than the number of partners is quantified. We aimed to estimate a female's overall participation in social life without making arbitrary distinctions between strong and weak partnerships (McFarland et al., 2017), because important interindividual variation in affiliation tendency, number of partners, and number of strong bonds can be neglected when focusing only on the strongest affiliative relationships (Ostner and Schülke, 2018; Thompson and Cords, 2018).

Our measure of a female's sociality can be conceptualized as an individual's base rate of engaging in a behavior relative to that of other individuals in her social group, regardless of the number of partners, their sex, their age or the presence of specific social bonds in her life. We assume that participating more in some social interactions translates into more survival related benefits received, from the group members in general. In species where individuals live in stable, well-defined groups, like white-faced capuchin monkeys, daily interactions occur with all types of partners (Perry and Manson, 2009; Perry, 2012). Interactions with both males and females are associated with female longevity in wild yellow baboons (*Papio cynocephalus*) whose social groups resemble those of capuchin monkeys (Archie et al., 2014).

We hypothesize that females who are more socially integrated experience fitness benefits associated with survival. Specifically, we predicted that the more females provide and receive either grooming or coalitionary support, the better they will survive. We also predicted that females who are more likely to forage in close proximity of others will survive longer. We tested these predictions using data spanning 18 years of capuchin monkeys' social interactions and demography from the Lomas Barbudal Monkey Project dataset.

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

111 this study were observed during at least 7 calendar years (mean = 13.5, SD = 4.4). The primary
112 subjects of this analysis were 132 adult females (adulthood defined as beginning at 5 years of
113 age). Sixty-two females died during the study period. The behavioral and demographic data on
114 each group were collected by experienced observers during visits lasting at least 6 hours/day.

115 *Measuring Sociality*

116 As measures of female sociality, we focused on three behavioral domains: grooming,
117 coalitionary aggression, and foraging. We treated grooming and coalition formation as directed
118 behaviors, and we used observations of individuals as both initiators and recipients of the
119 behavior. We did not have information about which individual had initiated the proximity when
120 foraging, and therefore foraging in proximity was treated as an undirected behavior. We
121 treated each of the five interaction types (*grooming giving, grooming receiving, support giving,*
122 *support receiving, foraging in proximity*) as a separate measure of sociality.

123 In calculating the frequency with which adult females engaged in these interactions,
124 we used behavioral records from all the individuals who resided in the 11 respective groups
125 during the study period. There was a total of 563 monkeys and 13,770 unique dyads. In addition
126 to the aforementioned theoretical reasons for considering interactions with partners of both
127 sexes and all age groups, using all recorded interactions provided more information per adult
128 female. We estimated the posterior mean and standard deviation of each individual-level
129 sociality measure and propagated that measurement uncertainty when estimating the effect of
130 sociality on survival (*see supplemental material*).

131 *Grooming (grooming giving and grooming 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 an *ij* dyad to engage in grooming, was calculated as the sum of the focal follows of *i* and the focal follows of *j* at times when *i* and *j* were co-resident. A count of 1 was assigned if *i* groomed *j* at least once during a focal follow, otherwise 0 was assigned. The same was done when evaluating if *j* groomed *i*.

Joining an ongoing 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 *i* is identified as joining monkey *j* if *i* performed an aggressive behavior toward either monkey *j*'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 *i* joining monkey *j* 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 estimates of grooming, coalitionary support, and foraging in close proximity (*see supplemental material*). This method provided estimates of individual sociality that reflect measurement uncertainty, with the uncertainty increasing for infrequently observed individuals.

Sociality estimates from the Social Relations Model can be conceptualized as female's base rate of either providing or receiving behavior, after accounting for average rates for the population and the individual's social group. Conceptually, it describes how likely a female is to participate in an interaction (either as a recipient or as a provider, if applicable) with another

individual in her social group. The measure is estimated as a random effect in the statistical model and centered on zero, which conceptually represents an average monkey in the population. The sociality estimate then is an offset from the population average. In general, our sociality measures are similar to nodal in- and out-degree centrality in the social networks tradition (Hasenjager and Dugatkin, 2015).

Modeling survival as a function of the individual sociality measure

To investigate whether sociality is associated with adult female survival, we used Bayesian Cox proportional hazards models (*see supplemental material*). In separate models, each of the five individual sociality measures (mean and SD) was modeled as a predictor of survival probability over one-year periods. In the main text, we report models in which survival in year t is modeled as a function of sociality observed in the same year. As a supplemental analysis, we model survival in year t as a function of sociality in the preceding year, $t-1$. The former approach has a larger sample size whereas the second approach assumes that the benefits sociality are evident over an intermediate timeframe.

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; *see supplemental material*), the average number of individuals in her group (including juveniles and infants) throughout the year, 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*).

We used a Bayesian approach to fit Cox proportional hazards models (Singer and Willett, 2003). 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 respective 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.

In Figure 2, we plotted the pairwise correlations between each of the individual sociality measures (*see supplemental materials section 3.A*) 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. The effect of *grooming giving* exhibited a clear positive effect ($\beta = 0.49$), suggesting that females who groomed others more frequently exhibited greater survivorship. The other sociality measures (particularly *grooming receiving)* had posterior estimates consistent with sociality predicting greater survival but their 95% HPDI intervals were wider and included zero, suggesting uncertainty about the effects of these sociality 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 *grooming giving* confidently suggest a beneficial effect on survivorship (Figure 3, panel A).

The supplemental analysis, in which survival in year *t* is modeled as a function of sociality in year *t−1*, provides qualitatively similar results.

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.

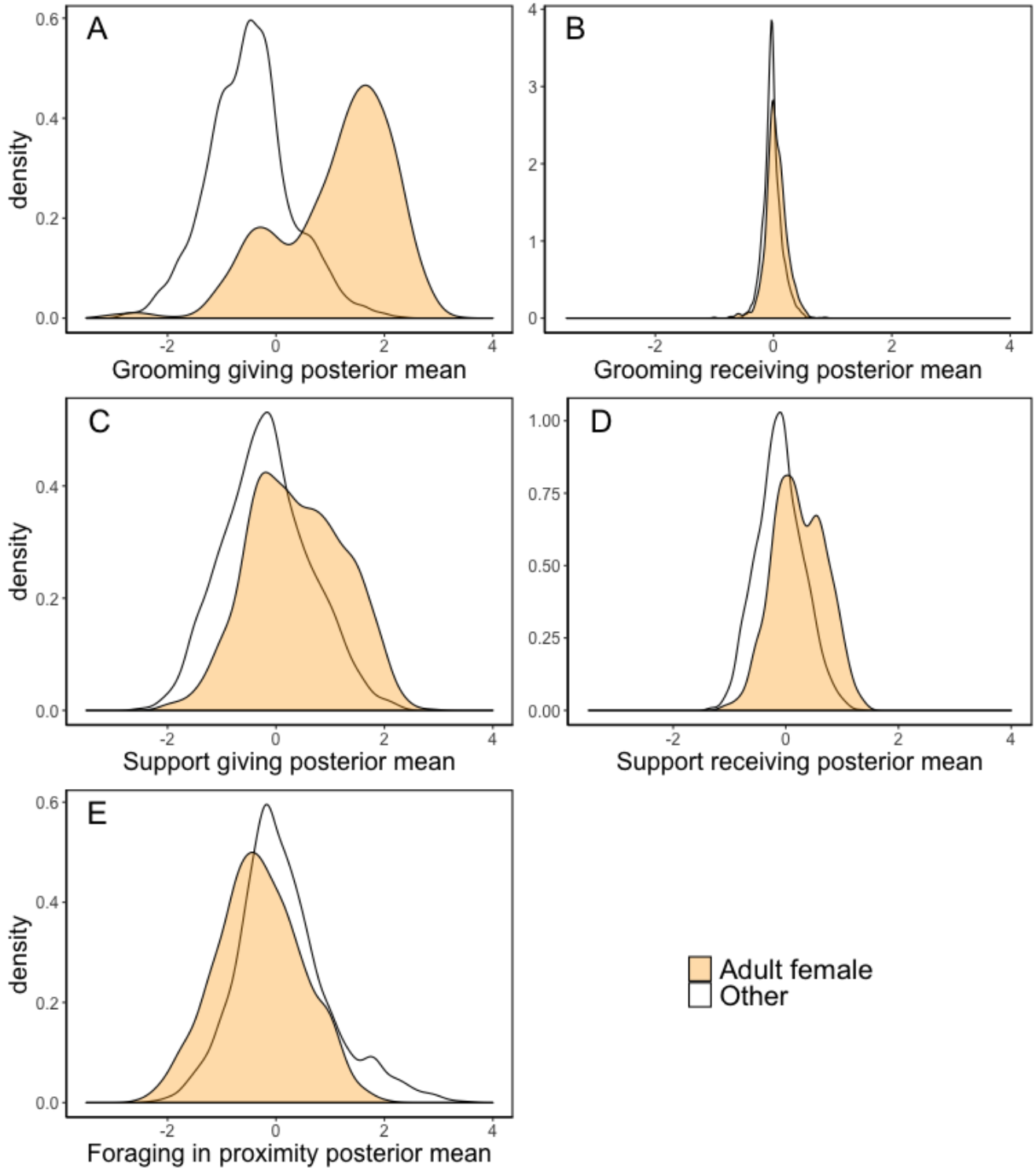


Figure 2. Bivariate correlations of individual sociality measures. Each point represents the posterior mean of an annual estimate for an individual female in the sample.

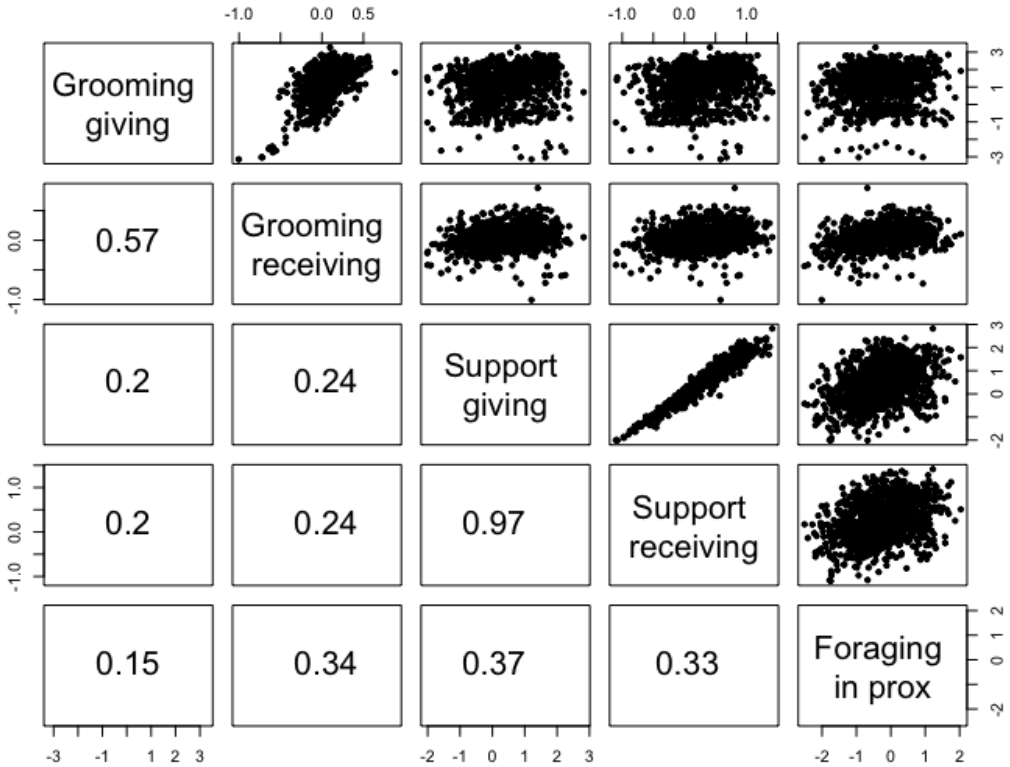
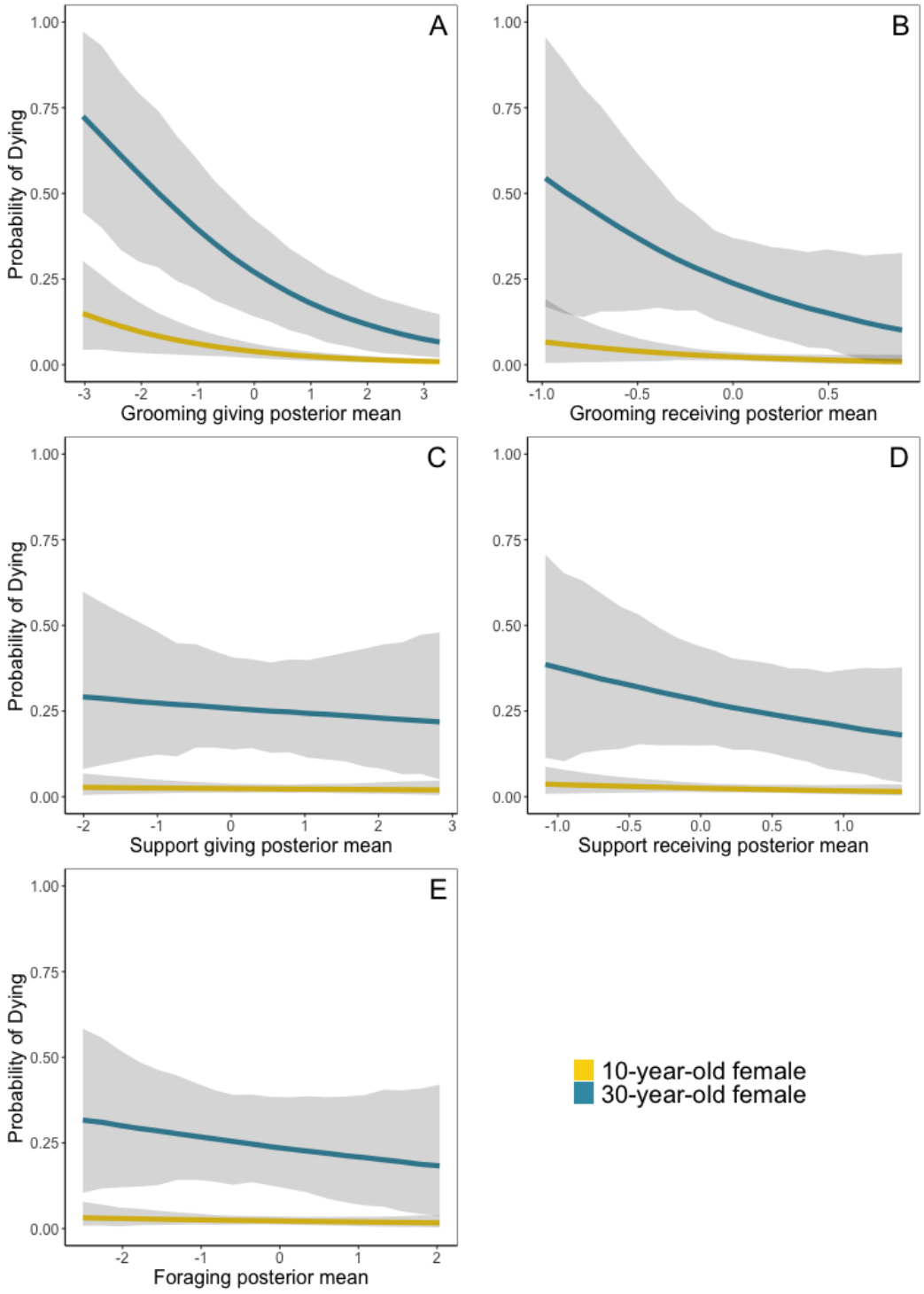


Table 1. Estimates of fixed effects of each of the Cox proportional hazards models: posterior means and 95% HPDI (see supplemental material for graphical representation of this table).

	Sociality measure				
Parameter	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 [–0.10,0.49]	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.



DISCUSSION

In female white-faced capuchin monkeys, providing grooming to others is associated with greater survival rates. 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 broadly consistent with previous findings that variation in social behavior is associated with survival (Holt-Lunstad et al., 2010, Fagen and Fagen, 2004; Yee et al., 2008; Silk et al., 2010; Archie et al., 2014; Brent et al., 2017), but depart from previous studies by considering interactions with all social partners. Multiple studies reported that interacting with various partners (Archie et al., 2014) and both strong (Silk et al., 2010) and weak bonds (McFarland et al., 2017; Silk et al., 2018) predict survival. Our results suggest that females' propensity to affiliate with all of her group members predicts survivorship.

Our study also adds a new dimension by considering the direction of the social interaction: female capuchins who were providing most grooming were the least likely to die, but there was no reliable relationship between receiving most grooming and survival. If females are exchanging grooming for food sharing (de Waal 1989, 1997; Jaeggi & Gurven 2013) or tolerance (Tiddi et al., 2011) their grooming provider estimate should correlate with survival, while their grooming receiving estimate might not. Notably, whereas capuchins vary considerably in the amount of grooming they provide, the variance of the *groom receiving* is relatively modest, which potentially explains why the effect of this latter variable on survival is positive but statistically inconclusive. Overall, the respective causal pathways that connect giving and receiving behaviors to survival are likely to be non-overlapping. Accordingly,

274 estimating individuals' roles as providers or recipients of directed social behaviors enables
275 insights into the mechanisms by which sociality contributes to fitness.
276 The causal pathway that connects the providing of grooming to females' survival is
277 potentially mediated by multiple variables. The survivorship benefits might accrue to avid
278 groomers via increased spatial centrality within the group, in which case the females are
279 spending more time around other individuals, plausibly reducing predation risk (Josephs et al.,
280 2016). Another alternative is that females might be trading grooming for other benefits. For
281 example, in return for grooming, females might receive more coalitionary support when in
282 conflict and either avoid injuries or improve their rank, both of which can result in lowered risk
283 of death. To test the hypothesis that grooming is exchanged for coalitionary support, future
284 studies could assess whether female grooming is reciprocated by recipients through a different
285 currency such as coalitionary support (Kajokaite et al. in prep). Another possibility is that
286 females trade grooming for tolerance and engage in conflicts less often, which results in better
287 access to resources and/or less wounding. Although we do not directly test this mediator, or
288 any other pathway, the result that female's grooming giving estimates are only weakly
289 correlated with their support giving and receiving in coalitionary conflicts suggest that those
290 who spend a lot of time grooming are unlikely to receive a lot of coalitionary support in return
291 for these services.
292 Our analysis does not rule out possible confounders that could influence both grooming
293 given and survival, in which case the observed correlation could be caused by other factors
294 (e.g., a favorable genotype that promotes social behavior and survival) (Ostner and Schülke
295 2018). Also, although our supplemental models examine the effects of sociality and survival in

successive years, it is possible that physical senescence induces a correlation between social behavior and survival on longer timescales. Although assessments of health are logistically challenging among habituated primate groups, it would be beneficial for future studies to consider variation in physical condition as a proximate mechanism of the patterns reported here.

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. Therefore, this study adds a neotropical primate species to the list of mammalian species where a similar association between sociality and survival has been demonstrated. These results accentuate the need for greater attention to the mechanistic pathways that connect sociality to fitness (Ostner and Schülke, 2018; Thompson, 2019). 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.4036211

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