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 components of fitness. A growing number of studies shows that individual sociality predicts survival. We used 18 years of data from the Lomas Barbudal Monkey project to quantify social integration 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 integration, survival, accelerated failure time model, fitness

INTRODUCTION

A key question for understanding the evolution of animal sociality is: Do more social individuals have higher fitness? 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). A number of studies link differences in the social behavior of individuals to 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). 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).

Much work has been done investigating whether social relationships that primates develop with some social partners predict longevity (reviewed in Snyder-Mackler et al. 2020). Strong and durable social bonds with either female (Silk et al. 2010; Archie et al. 2014) or male (Archie et al. 2014) partners predict adult female longevity. Some evidence suggest that the number of weak bonds is also predictive of fitness-related benefits (McFarland et al. 2017; Silk et al. 2018). Studying social bonds helps us identify the functional aspects of cultivating social relationships with specific partners (Snyder-Mackler et al. 2020). However, there is no consensus about to measure social bonds (Silk et al. 2013), and furthermore, there is no agreement about what sorts of methods and quantitative thresholds should be used to categorize partnerships as either strong or weak (McFarland et al. 2017; Elis et al. 2019).

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). Another way that individual sociality can be conceptualized is through social integration. Such measures require fewer assumptions regarding specific partnerships and instead emphasize the frequency of interactions and/or total number of social partners that an individual has (Ellis et al. 2019). In human studies these measures are called "structural", with the emphasis being on the individual's position in the social network (Snyder-Mackler et al. 2020). Fitness-related benefits flow to socially integrated individuals through increased social tolerance, better access to resources, and/or beneficial spatial location that results in reduced predation or minimizes the risk of injury during coalitionary conflicts (Ellis et al. 2019). Various versions of social integration measures have been shown to predict longevity in some species (e.g. feral horses, *Equus caballus*: Nuñez et al. 2015; rhesus macaques, *Macaca mulatta:* Brent et al. 2017; chacma baboons, *Papio ursinus:* McFarland et al. 2017).

There is no strong evidence that one type of measure is the most suitable for investigating the relationship between sociality and fitness. The available evidence suggests that dyadic relationships and social integration both predict survival-related benefits within the same system, and most likely these different aspects of sociality are associated with fitness through discrete and heterogeneous pathways (Elis et al. 2019).

Here we ask how an adult white-faced capuchin (*Cebus capucinus*) female's survival is predicted by her social integration into her group. Capuchin monkeys live in stable, well-defined groups (Perry and Manson, 2009; Perry, 2012). We focus on the longevity of adult females because we have the most complete demographic and behavioral records for this class of individuals, the philopatric sex. However, to quantify social integration of the adult females, we

use all observed interactions they had with all of their social partners (not just other females) in order to get as accurate as possible estimate of their overall social integration with to other group members.

To do this, we chose an individual-level metric, by quantifying the individual's base rate of engaging in a behavior relative to that of other individuals in her social group. We aimed to estimate an individual's overall participation in social life. We assume that participating more in some social interactions translates into more survival-related benefits received from the group members in general. Such benefits might include increased access to resources, reduced predation and/or wounding risk, and increased rank (Ostner & Schülke 2018; Thompson 2019; Elis et al. 2019). The pathways from the interactions to survival-related benefits can be either direct or manifested through exchange of beneficial social interactions with others (Ostner & Schülke 2018; Thompson 2019). Although we are testing for predictors of fitness and are not testing specific mechanistic pathways, we provide a non-exhaustive list of pathways linking our measures to survival-related benefits in the supplemental materials.

We aimed to quantify social integration in different contexts of capuchin social life: (1) affiliative interactions (measured via grooming), (2) support in agonistic contexts, and (3) one form of tolerance in feeding context (measured by time spent foraging in proximity, although we do not assume foraging near others measures tolerance from group members in general). We quantified interactions in each domain separately and, where possible (i.e. for grooming and coalitionary support), we estimated a female's role as both a provider and as a receiver of the behavior. If females are trading some services for others, their role as a receiver and a giver might be associated with a different pathway to survival-related benefits (*see supplemental material for detailed descriptions of possible pathways*).

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

Measuring Social Integration

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. We treated each of the five

interaction types (*grooming giving, grooming receiving, support giving, support receiving, foraging in proximity*) as a separate measure of social integration.

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 was a total of 563 monkeys and 13,770 unique dyads. We estimated the posterior mean and standard deviation of each individual-level social integration measure and propagated that measurement uncertainty when estimating the effect of sociality on survival (*see supplemental material*).

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 social integration 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 social integration that

reflect measurement uncertainty, with the uncertainty increasing for infrequently observed individuals.

Social integration estimates from the Social Relations Model can be conceptualized as a 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 social integration estimate then is an offset from the population average. In general, our social integration 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 social integration measure

To investigate whether sociality is associated with adult female survival, we used Bayesian accelerated failure time models (Wei 1992; *see supplemental material*). In separate models, each of the five individual social integration 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 social integration estimated in the same year. As a supplemental analysis, we model survival in year t as a function of social integration in the preceding year, $t-1$. The former approach has a larger sample size whereas the second approach assumes that the benefits social integration are evident over an intermediate timeframe.

In addition to the respective social integration 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 the accelerated failure time model (Wei 1992). 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 social integration 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 social integration 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 social integration on survivorship. Table 1 presents the accelerated failure time 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 social integration 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 social integration estimates.

To facilitate the interpretation of the accelerated failure time model coefficients, we plotted model predictions showing the probability of dying in a given year (Figure 3). Across all five social integration measures, the less integrated females have a greater probability of dying than more integrated 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 social integration 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.

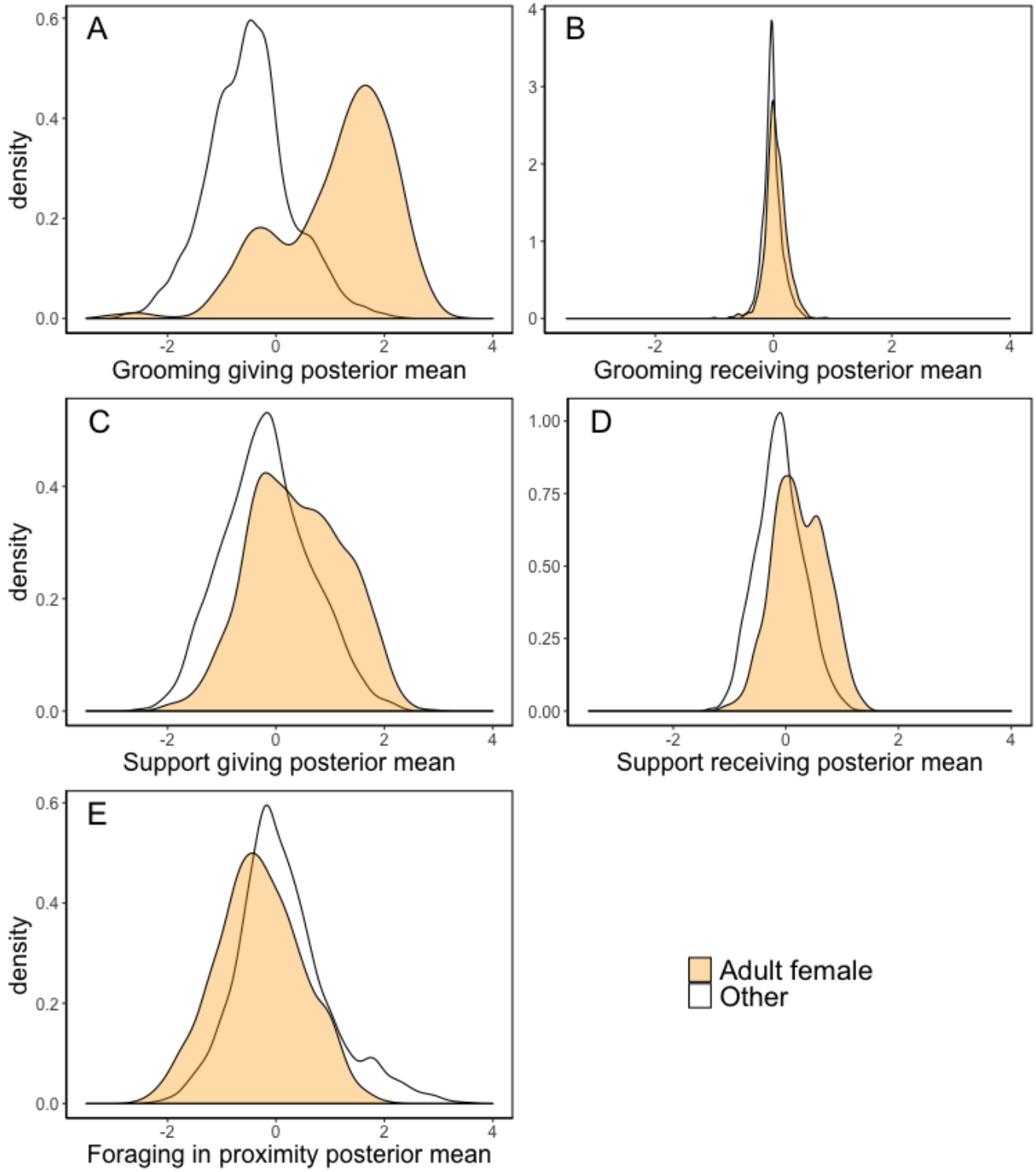


Figure 2. Bivariate correlations of individual social integration measures. Each point represents the posterior mean of an annual estimate for an individual female in the sample.

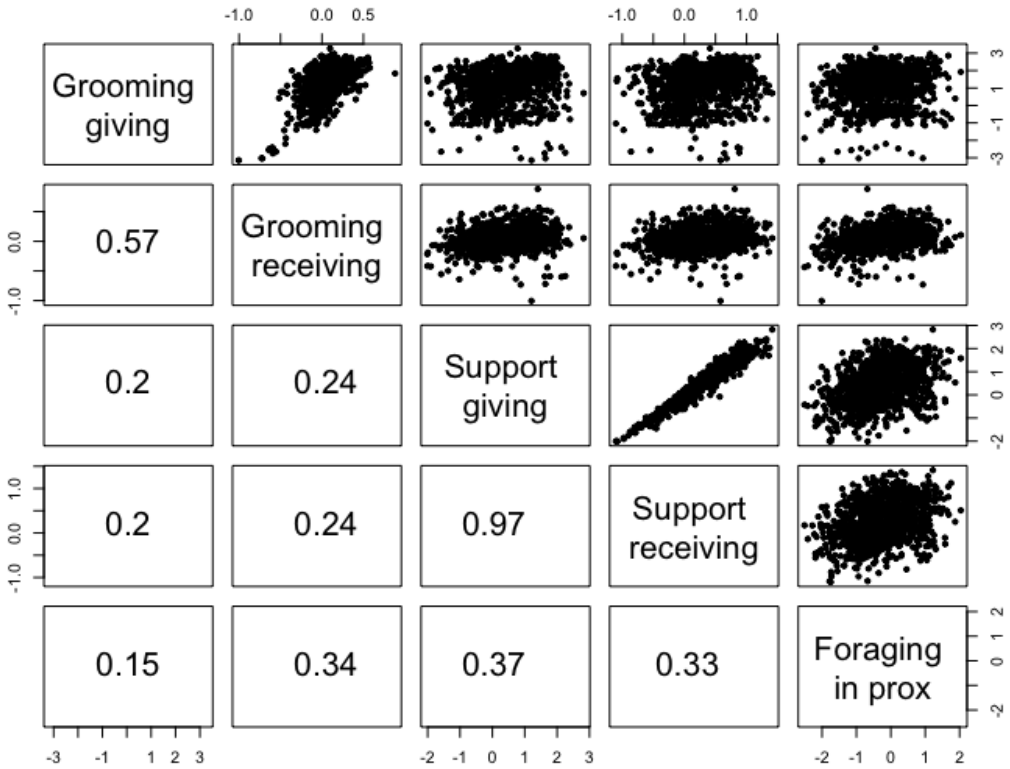
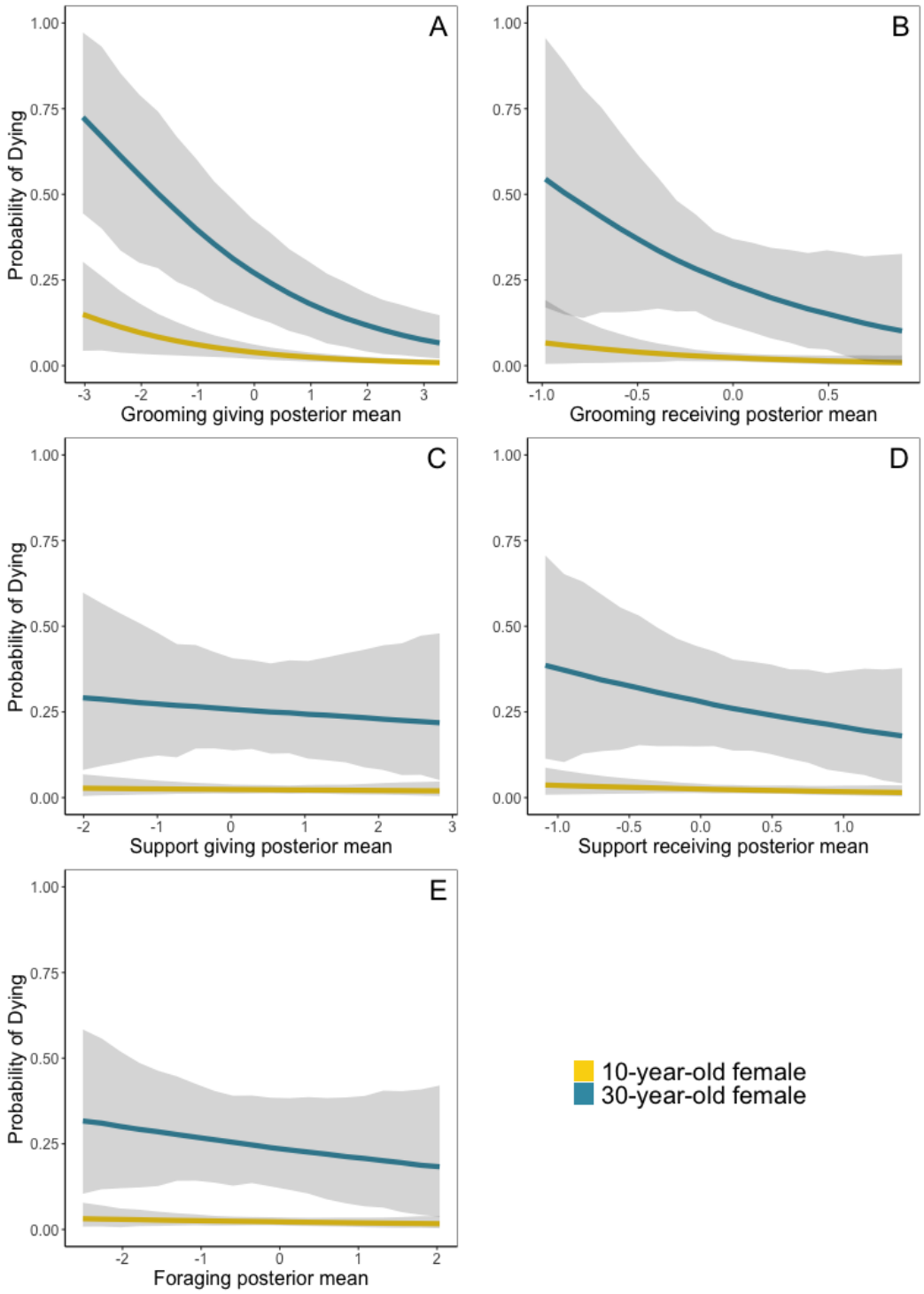


Table 1. Estimates of fixed effects of each of the accelerated failure time models: posterior means and 95% HPDI (see supplemental material for graphical representation of this table).

	Social integration 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 social integration levels in five behavioral domains, as calculated from the accelerated failure time 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

Our results suggest that white-faced capuchin females' social integration into their social group as measured by their grooming of others predicts survivorship. 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).

Female capuchins who were providing most grooming were the least likely to die, but there was no reliable relationship between receiving more grooming and survival. However, the pattern, although uncertain, is similar in *grooming receiving* and *grooming giving* domains. Notably, whereas capuchins vary considerably in the amount of grooming they provide, the variance of the *grooming receiving* is relatively modest, which potentially explains why the effect of this latter variable on survival is positive but statistically inconclusive.

A possible explanation for the difference between giving and receiving grooming is that females might be exchanging grooming for other currencies (Noë and Hammerstein 1995), e.g for food (de Waal 1989, 1997; Jaeggi & Gurven 2013) or tolerance (Tiddi et al., 2011), and therefore their grooming provider estimate correlates with survival, while their grooming receiving estimate does not. Overall, the respective causal pathways that connect giving and receiving behaviors to survival are likely to be non-overlapping. Accordingly, estimating individuals' roles as providers or recipients of directed social behaviors enables insights into the mechanisms by which sociality contributes to fitness.

The causal pathway that connects the providing of grooming to females' survival is potentially mediated by multiple variables. The survivorship benefits might accrue to avid groomers via increased spatial centrality within the group, in which case the females are spending more time around other individuals, plausibly reducing predation risk (Josephs et al., 2016). Trading grooming can open several pathways to survival-related benefits. For example, in return for grooming, females might receive more coalitionary support when in conflict and either avoid injuries or improve their rank, both of which can result in lowered risk of death (Cheney et al. 2010; Haunhorst et al. 2017). However, our model is inconclusive whether receiving coalitionary support predicts survival. The low correlation between *groom giving* and *support receiving* indicates that not all avid groomers are individuals being frequently supported in coalitions. Even if females who groom others frequently trade it for coalitionary support, our analyses do not address that. To test the hypothesis that grooming is exchanged for coalitionary support between females and their partners in this population, future studies could assess whether female grooming is reciprocated by recipients through a different currency such as coalitionary support (Kajokaite et al. in prep).

Another possibility is that females trade grooming for tolerance and engage in conflicts less often, which results in better access to resources (Tiddi et al. 2011, Haushort et al. 2017) and/or less wounding. Although we do not directly test this mediator, or any other pathway, the result that female's grooming giving estimates are only weakly correlated with their support giving and receiving in coalitionary conflicts suggest that those who spend a lot of time grooming are unlikely to receive a lot of coalitionary support in return for these services. Two possible explanations for this pattern are that: (1) avid groomers do not participate in coalitionary conflicts often; (2) avid groomers do participate as often as other classes of individuals, but they

do not receive coalitionary support as often as other classes of individuals. The evidence for the first possibility would be consistent with females gaining survival-related benefits through trade of grooming for tolerance.

Our analysis does not rule out possible confounders that could influence both grooming given and survival, in which case the observed correlation could be caused by other factors (e.g., a favorable genotype that promotes social behavior and survival) (Ostner and Schülke 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 social integration 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.5040066

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