Fitness benefits of providing services to others: Sociality 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. 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 impact survivorship. To estimate female sociality in each of these domains, we built an adaptation of the Social Relations Model. This approach enabled us to estimate individual rates of giving and receiving interactions and take into account the 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 estimate, 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. 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. These results add a neotropical primate species to the growing list of mammals, including humans, where greater sociality is associated with longevity.

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 (white-faced capuchins, *Cebus capucinus:* Fedigan et al., 2008; Assamese macaques, *Macaca assamensis*: Schülke et al., 2010; chimpanzees, *Pan troglodytes schweinfurthii*: Gilby et al., 2013) and offspring survival (yellow baboons, *Papio cynocephalus ursinus*: Silk, 2009; savannah baboons, *Papio cynocephalus*: Silk et al., 2003; white-faced capuchins, *Cebus capucinus:* Kalbitzer et al., 2017), to differences in the social behavior of individuals.

In long-lived species, lifespan is also an important component of reproductive success contributing to fitness variation (Clutton-Brock, 1998). The most abundant evidence that individual sociality affects lifespan has accumulated in human literature. Both the presence and the absence of social relationships affects lifespan. That is, 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 individual sociality is associated with lifespan. Among baboons, females who maintain stable social relationships with other males and females live longer (chacma baboons, *Papio hamadryas ursinus,* Silk et al., 2010; Archie et al., 2014). Prime-aged female macaques of Cayo Santiago who have more living adult female relatives live longer (Brent et al., 2017). Blue monkey females (*Cercopithecus mitis stuhlmanni)* who have strong and

enduring social relationships consistently with the same partners tend to live longer in comparison to females whose strong partnerships are inconsistent across years (Thompson and Cords, 2018). Female rats who cultivate reciprocal affiliations with their sisters survive longer (Yee et al., 2008), and brown bear cubs who play longer during summer survive better (*Ursus arctos*) (Fagen and Fagen, 2004). More social juvenile feral horses (*Equus caballus*) live longer than their less social peers. However, facultatively social yellow-bellied marmots (*Marmote flaviventer*) show the opposite pattern: more social marmots live shorter lives than less social marmots (Blumstein et al., 2018).

Neotropical primates are not represented among the studies that report the link between sociality and longevity. Capuchin monkeys are an excellent neotropical primate species for the investigation of these associations: Despite the long evolutionary history that separates them from humans and cercopithecines (Porter et al., 1997), their social structure is similar to cercopithecine primates (Perry, 2012).

In this paper, we investigate whether more social white-faced capuchin females live longer than less social females. We analyzed eighteen years of capuchin monkeys' social interactions taken 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. To deal with different amounts of observations for each individual, we used the multilevel Social Relations Model (Snijders and Kenny, 1999; Koster et al. 2019) to decompose the observations of exchanges of these interactions into separate individual giving, individual receiving, and dyadic

relationship components. This approach allowed us to estimate the uncertainty in sociality estimates, which can be substantial for individuals with small numbers of observations. Then, we used the individual giving and individual receiving posterior means and standard deviations (SD) from these models as sociality measures to model adult female longevity using the Bayesian Cox proportional hazards model.

We found that adult female capuchins provide most of the grooming in the population. However, they display considerable variation in their propensity for grooming others, and some adult females are among the least frequent groomers in the population. The variation in *giving grooming* measures predicts longevity: Females who provide more grooming live longer than the females who provide less grooming. Measures in other interactions – *receiving of grooming*, *giving* and *receiving of coalitionary support*, and *foraging in close proximity* – were similar in their distribution to the rest of the population. In addition, females were more similar to each other in these interactions, especially in how much grooming they received, i.e. the females who were the most and the least likely to be groomed were not very different from an average monkey in the population. The females who engaged more in these interactions seemingly experienced some benefits associated with longevity, but the model estimates were uncertain. Therefore, the evidence does not support a strong association between longevity and the sociality measures we considered (*grooming receiving, participating in coalitionary support,* and *foraging in close proximity of others*).

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 Lomas Barbudal Monkey Project dataset has longitudinal records on individuals living in 11 capuchin social groups. It contains detailed records including demographic information, pedigree information, and data regarding social interactions that are necessary for quantifying individual sociality.

White-faced capuchins live in multimale, multifemale social groups (Perry, 2012). Females are philopatric – they stay in their natal groups for their entire lives – which allows researchers to collect data about the social interactions from large portions of their lives (Fragaszy et al., 2004; Perry et al., 2008). As a result, females' demographic and behavioral records are more complete than males' records because males transfer to different groups multiple times in their lives and often leave the study area. This makes female capuchins more suitable subjects for the investigation of the relationships between individual sociality and survival.

The records on capuchin behavior were collected between January 2002 and December 2019. The subjects were 132 adult females, living in eleven different social groups over 146 group years (average years of observation per group = 13.27; range = 7 – 18 years). The females were considered adults once they reached the age of 5 years. The behavioral and demographic data on each group were collected by experienced observers during censuses lasting at least 6 hours/day.

Measuring Sociality

To measure female sociality, we chose 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 groups during the study period. There were a total of 563 monkeys, residing in 11 social groups, comprising 13,770 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)

Allogrooming, or social grooming, is a common behavior in capuchin monkeys (Perry, 1996). Grooming serves a hygienic and social bonding function and is thought to impose costs on groomers of loss of time and increased vigilance (Manson et al., 2004). These features of grooming behavior make it a good candidate for providing information regarding an individual's sociality.

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

155 at times when A and B were residents of the same social group. The dyadic counts of
156 giving and receiving grooming were assigned as follows: a count of 1 was assigned if A
157 groomed B at least once during a focal follow, otherwise 0 was assigned. The same was
158 done when evaluating if B groomed A.

159 *Joining a coalitionary conflict (support giving and support receiving)*

160 Coalitionary aggression is frequent in capuchin monkeys (Perry, 2012).
161 Intergroup encounters are characterized by high rates of coalitionary lethal aggression
162 (Gros-Louis et al., 2003), and coalitions play an important role in male competition for
163 reproductive opportunities (Perry, 2012). Intragroup conflicts are far less dangerous;
164 they often do not result in physical fighting, and individuals are rarely injured (Perry,
165 2012). Capuchins have stereotyped signals for recruiting allies in conflicts (Perry, 2012),
166 and participation in coalitionary aggression is likely based on social relationships
167 between the partners (Kajokaite et al., 2019).

168 The behavior of joining a coalitionary conflict was defined as an individual
169 intervening on one side during an ongoing aggressive conflict. This definition only
170 indicates the functional aspect of joining a side; it entails no inferences about internal
171 psychological states such as the intent to help a specific individual. Since aggressive
172 interactions are salient and harder to miss than quiet activities like grooming or foraging
173 in proximity, aggressive interactions were collected both *ad libitum* and during focal
174 follows. The chronological stream of aggressive behaviors was divided into 5 min.
175 segments. In order to identify instances of joining a coalitionary conflict, monkey A is
176 identified as joining monkey B if A performed an aggressive behavior toward either

monkey B's opponent or victim within the context of the 5-minute segment. Even if multiple instances of A joining monkey B were observed during the 5 min segment, we scored only one instance of A joining B. To calculate the opportunities to join a coalitionary conflict, all individuals who were co-resident during the aggressive conflict were counted as having had an opportunity to join on either side during the conflict.

Foraging in proximity

Although foraging is a seemingly asocial behavior, the way individuals distribute themselves across space can be indicative of their social relationships with group members. It can be costly to tolerate another individual near you (more competition for food) and monkeys might only tolerate proximity of individuals with whom they maintain good social relationships.

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 min. segments (i.e. if they were observed doing this more than once within 10 min., only one instance was counted). 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 min. apart, where one of the individuals is a subject of a group scan.

The Social Relations Model and Individual sociality measures

Detailed longitudinal behavioral records are necessary for relating an individual's social behavior patterns to longevity (Clutton-Brock, 1988). Such data is hard to collect and resources are limited; therefore the more individuals we observe, the less information we collect on each one of them. The data for these analyses were collected across eighteen years and the number of social groups and individuals observed increased over time. As a result, data density is uneven across time periods, social groups, and individuals.

We incorporated uneven distribution of the data into our analyses as follows. First, we aggregated the data annually and used adaptations of the multilevel Social Relations Model (Snijders and Kenny, 1999; Koster et al. 2019) to estimate individual annual rates of grooming, coalitionary support, and foraging. This provided us with mean and standard deviation of individual sociality measures (see the supplemental material). Second, we used these distributions of individual sociality measures as predictors of longevity and to investigate the effects of social behavior on survivorship.

The Social Relations Model (Snijders and Kenny, 1999) decomposes the variance in giving and receiving behaviors into separate giving, receiving, and dyadic relationship components. We fitted a Bayesian multilevel Social Relations Model with the following parameters: the intercept parameter (base rate), social group-level, individual giving, individual receiving, dyadic symmetric, and dyadic asymmetric random effects parameters (see Koster at al. 2015). We used data collected on the entire population (i.e. adult males, females, and immatures) since the Social Relations Model is a multilevel model and can take advantage of additional data to estimate the average

221 rates of interactions in the population (McElreath, 2020). Although we estimated the
222 random effects for all the individuals in the population, we used the adult female annual
223 individual posterior mean and SD of *grooming giving, grooming receiving, support*
224 *giving, support receiving*, and non-directional *foraging in proximity* rate estimates as our
225 five measures of annual individual sociality.

226 The posterior estimates of mean and SD of female giving and receiving random
227 effects capture the extent to which an individual female deviates from the estimated
228 average rate of engaging in this behavior in the population. The individual sociality
229 measures are centered on zero, which represents the population mean (an average
230 monkey). Each behavior domain has its own population average estimate. For example,
231 the individual estimates of *grooming giving* ranges from –3.14 to 3.27 across the entire
232 population. For a particular individual, a posterior mean closer to the minimum (–3.14)
233 indicates that this individual grooms others much less than the average monkey grooms
234 her partners in the population. The inverse is true for a posterior mean estimate close to
235 the maximum of the range (3.27). The SD reflects the measurement uncertainty from
236 heterogenous sampling effort, where individuals who were observed less have posterior
237 estimates with wider distributions around the posterior mean estimate.

238 *Modeling survival as a function of individual sociality measure*

239 To investigate whether sociality is associated with adult female longevity, we
240 used Bayesian Cox proportional hazards models. In separate models, each of the five
241 individual sociality measures was modeled as a predictor of survival probability over
242 one-year periods. These models included the following time-varying (calendar year-

specific) covariates: the female's age, her dominance index, 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.

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 each mother had a two-year interbirth interval (Fedigan and Rose, 1995; Perry, 2012).

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.

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.

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.

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-a}, divided by the total number of dominance interactions that the focal had with her alters, s_{i-a}:

$$DDI_i = \frac{\sum w_{i-a}}{\sum s_{i-a}}. \quad (1)$$

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

$$ADI_i = \frac{1}{n} \sum_{i=1}^{n} DDI_i \ . \quad (2)$$

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 (Archie et al. 2014; Brent et al. 2017). Females who live in larger groups might experience greater survival rates due to reduced predation risks (Sterk et al., 1997). Higher-ranking females possibly enjoy reduced mortality in comparison to lower-ranking females due to their central position in the group (Kalbitzer et al., 2017), 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 (Brent et al., 2017).

Having many covariates in the model can result in "included variable bias" (McElreath, 2020) 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 (McElreath, 2020). 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 (Archie et al., 2014). 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. The DAG assumed is provided in the supplemental materials.

Modeling approach

To take into account that some females contributed different numbers of years to the analysis, we modeled individual differences using a random effect term. 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).

More formally, we specified the following model for the number of days before death, D_i,. The probability for the number of days before death come from the cumulative probability distribution:

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

For females who did not die during the observation period, the probability of waiting D_i without dying 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

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

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}, b_{grsize} describe the impact of sociality, rank, age, number of daughters, mother's presence, and group size, respectively. We took a latent variable approach to model the sociality estimates, since individual sociality estimates are not point estimates, but rather posterior distributions with mean and SD reflecting measurement uncertainty about the true rate. Under this approach, we assumed that each female had some true underlying sociality measure, $true\ sociality\ estimate[id]$, which was normally distributed with mean and SD equal to the mean and SD of the individual estimate of sociality drawn from the Social Relations Model results.

We used the Bayesian approach to fit Cox proportional hazard model (Singer and Willett 2003). We assumed 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)

prior. For individual-level random effects, $\alpha[id]$, 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), while the results of the other two types of models are reported in the supplemental material (Table S1 and Table S2). All of the covariates, except the number of daughters, were standardized by subtracting the mean and dividing it by the standard deviation. As noted previously, the number of daughters was centered by subtracting the mean number of daughters for each age.

RESULTS

(1) Measures of sociality: How do adult females compare to the rest of the population?

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, while a majority of the adult males and immatures (78%) groom less than an average monkey (Figure 1, panel A). The female distributions for the rest of the behavioral domains are very similar to the other age-sex distributions, indicating that females behave similarly to adult males and immatures in those domains.

Figure 1 illustrates how the individual sociality measures of *grooming, coalitionary support,* and *foraging in proximity* by adult females compare to the estimates for other age-sex classes. The distribution in orange represents adult female posterior means estimated by the Social Relations Model, while the distribution in white

375 represents a combination of adult males and immature capuchins. The zero represents
376 an average individual in the population.
377 Grooming behavioral domain distributions show both the greatest and the
378 smallest amount of variation. Females display the greatest range in *grooming giving*
379 posterior estimates (*grooming giving* variance=2.02), and the narrowest range in
380 *grooming receiving* posterior estimates (*grooming receiving* variance=0.12). The
381 difference in variation suggests that the most avid groomers and the least enthusiastic
382 groomers differ a lot from an average monkey. However, as recipients of grooming,
383 both females who receive the most and the least amount of grooming are much more
384 similar to an average monkey in the population in comparison to any other type of
385 interaction that we measured.
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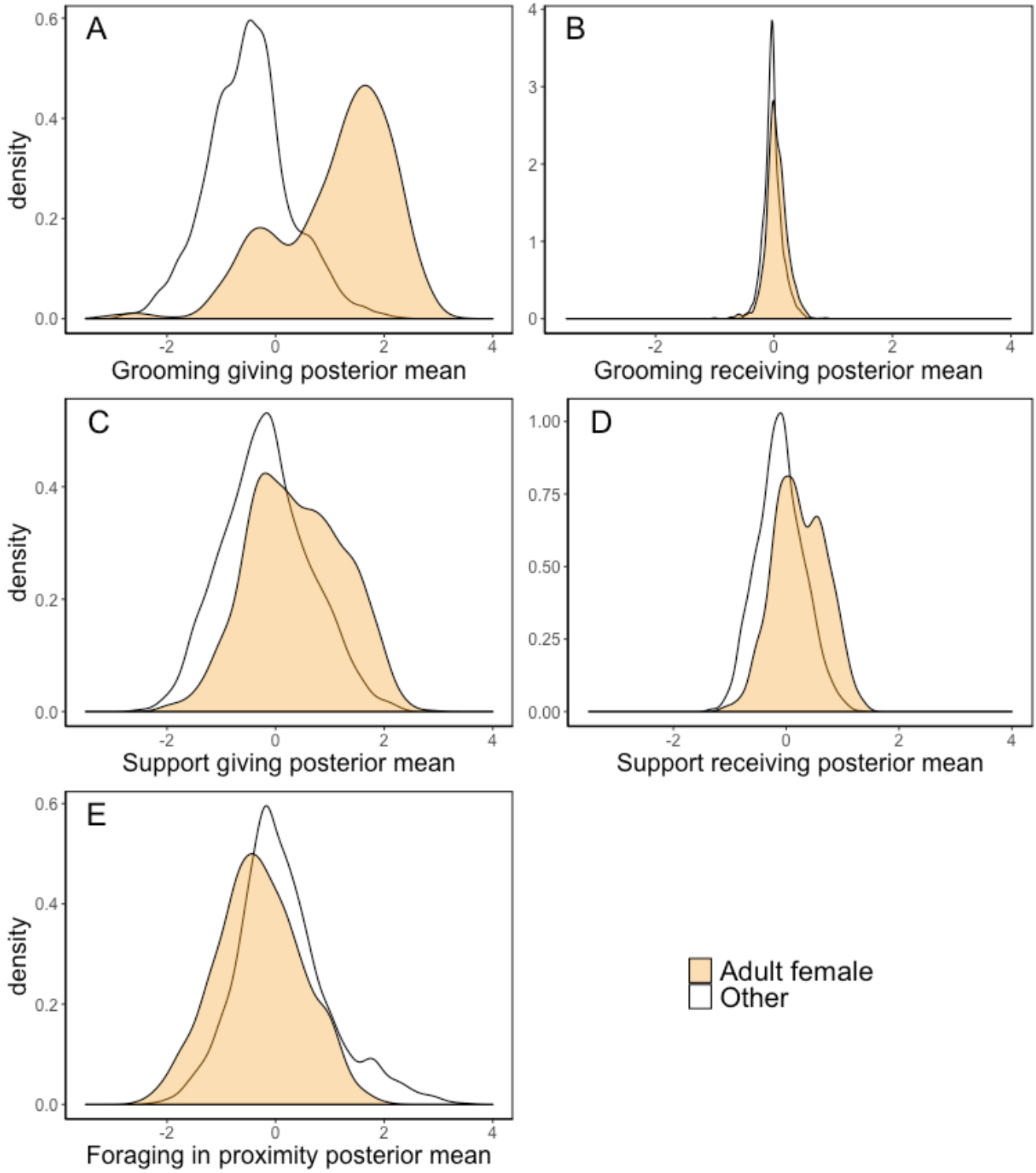
Figure 1. Posterior mean distributions of annual individual sociality measures for each type of behavior. The orange density represents adult females whereas the white density represents the rest of the population. The population base rate is at approximately zero.

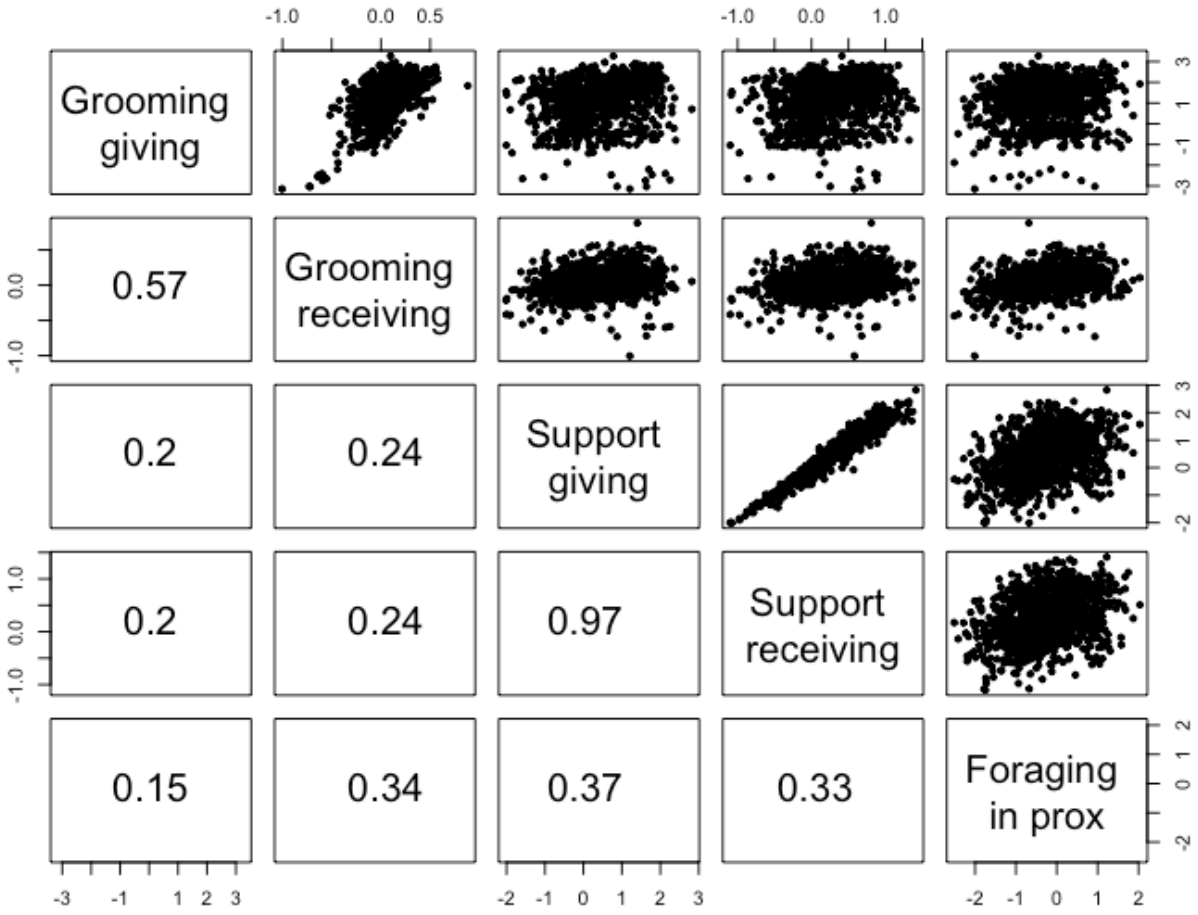


(2) Measure of sociality: Do females behave similarly across the behavioral domains?

Each female has five annual sociality measures. 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, i.e. 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). Females who intervene on someone's side during a conflict also tend to receive a lot of support from others. This suggests that there is a small subset of females that participate in coalitionary aggression more frequently than others. However, females vary less in their *support receiving* than in their *support giving* estimates (Figure 1, Panel C–D). In the grooming domain, the correlation between giving and receiving estimates was moderate (r=0.57). Some of the females who groom others the most are not among those who receive the most grooming. In addition, Figure 1 panel B shows a narrow distribution of the receiving measurements, which implies that females overall distribute their grooming evenly among their group members.

The correlation across behavioral domains is smaller than within a domain, between 0.15 and 0.37: If a female is among those who engage a lot in coalitionary aggression, she is not necessarily involved a lot in grooming interactions and in foraging in close proximity. The pairwise correlations show that females have different profiles of interactions depending on the behavioral domain.

Figure 2. Bi-variate correlations of individual sociality measures. Each point represents an annual observation of an individual female.



(3) Do more social females survive better?

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 (age, dominance rank, group size, number of adult daughters, co-residence with mother), females who groomed others more survived at higher rates than other females. The other sociality measures had mean estimates consistent with sociality

435 predicting greater survival, but their HPDI intervals were wide and included zero

436 indicating that the models are uncertain about these estimates.

437

438 **Table 1.** Estimates of fixed effects of each of the Cox proportional hazards models:
439 posterior means and 95% HPDI.

	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 [–0.1,0.49]	0.18 [–0.10,0.46]	0.19 [–0.10,0.48]	0.18 [–0.1,0.46]	0.18 [–0.09,0.46]

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442 We plotted the posterior means and their standard errors across five Cox

443 proportional hazard models in Figure 3 to better illustrate how model estimates

444 compare across all five models. Apart from sociality, all of the covariates have mean

445 estimates with wide HPDI intervals that include zero. The only exception is age,

446 indicating that female survival declines with age.

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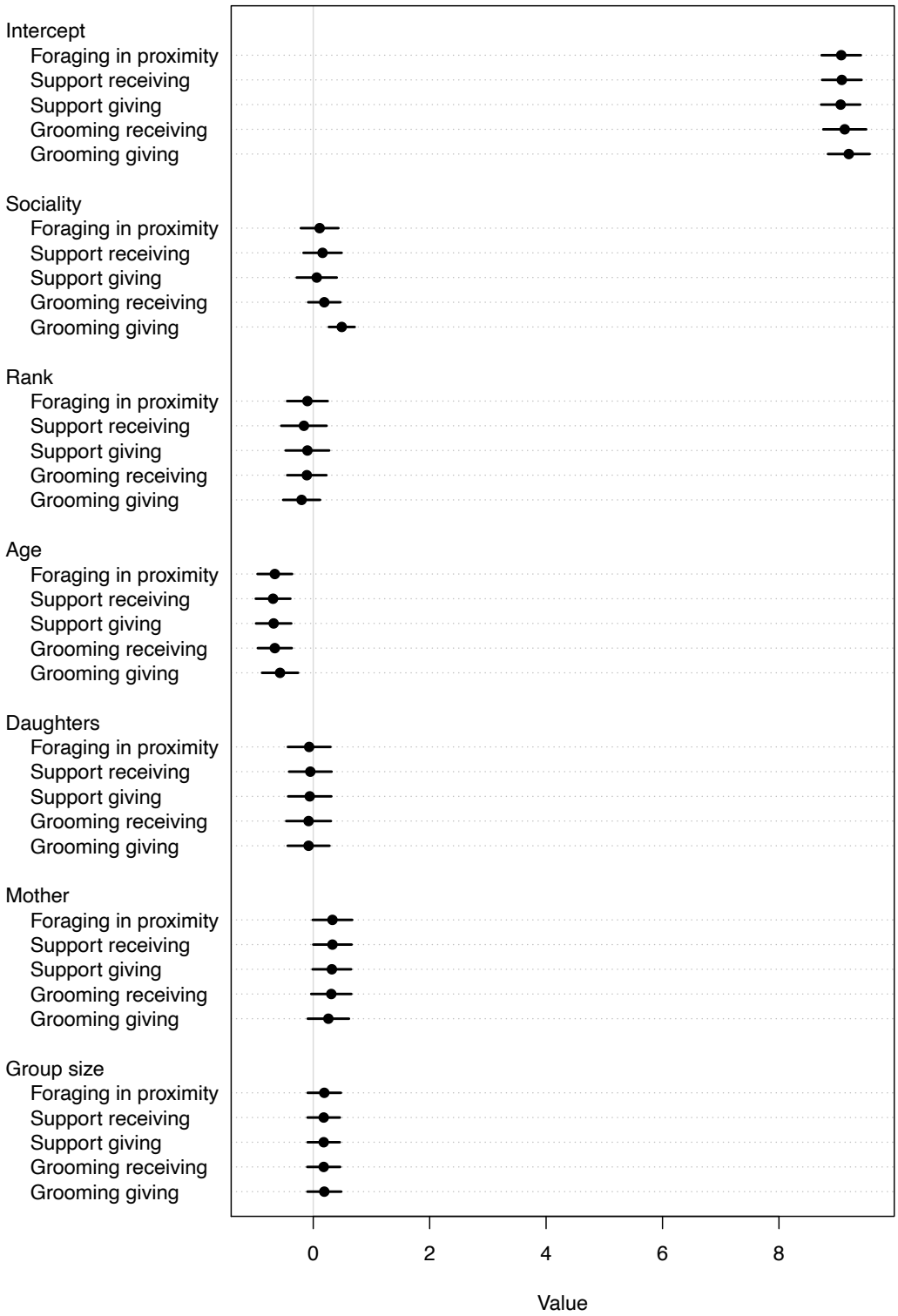
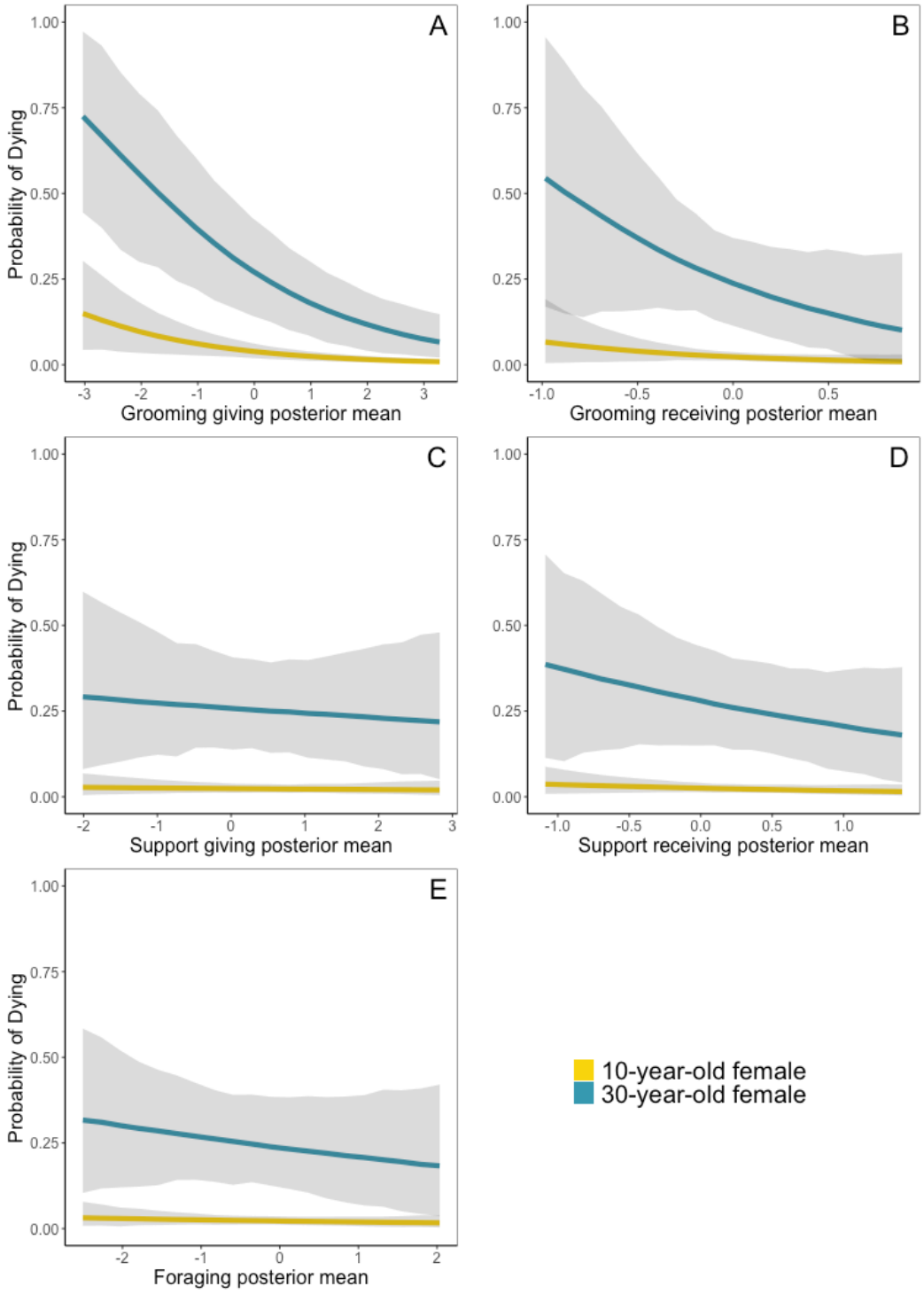
Figure 3. Posterior means and standard deviations of 5 Cox proportional hazards models in which annual survivorship varied as a function of five measures of sociality (*foraging in proximity, support receiving, support giving, grooming receiving,* and *grooming giving*) and covariates.



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 4). We have varied females' sociality measure to compute the predictions. Figure 4 illustrates the annual probability of dying as a function of a female's sociality level measure where a yellow line represents a 10-year-old female and a blue line represents a 30-year-old female (holding all other covariates fixed at the values described above).

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 4, panel A). Predictions for *groom receiving* likewise suggest a beneficial effect of sociality, but the model predictions are less certain (Figure 4, panel B). Meanwhile, the slopes for *coalitionary supp*ort and *foraging in close proximity* are quite shallow, indicating that the survival varies little as a function of these sociality measures (Figure 4, panels C, D, and E). These model predictions reflect the uncertainty associated with these estimates (Table 1 and Figure 3). Overall, there is less certainty in the estimates for older females, partly owing to their scarcity in the sample.

Figure 4. Cox proportional hazard model predicted annual probabilities of dying at two representative ages (10 and 30) as a function of the sociality levels in five behavioral domains. 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 (Silk et al., 2010; Archie et al., 2014; Brent et al., 2017; Yee et al., 2008; Nuñez et al., 2014; Fagen & Fagen, 2004).

Despite great interest by primatologists in studying social relationships and their impact on primate lives, there is no established consensus on how to measure the properties of social relationships in primates (Silk et al., 2013). The conceptual foundation for studying primate social relationships dates back to Robert Hinde's seminal paper (1976), where he argued that analyses of multiple types of interactions should be included in measuring social relationships. However, the details of how to combine these interactions into a meaningful measure have been under-theorized. There are some well-established measures that combine the rates of behaviors from different domains into a single measure of sociality (reviewed in Silk, 2013), but the

implications of averaging over multiple rates of different behaviors have not been analyzed.

We do not suggest that combining information about interactions from multiple domains should not be our goal in principle, but we want to draw attention to the idea that doing so imposes inferential tradeoffs. For example, we demonstrated that the distributions of the rates for each interaction type are very different (Figure 1) and, for example, the females who frequently groom others are not always the same females who frequently participate in coalitionary aggression (Figure 2). Averaging estimates across all five behaviors would result in the same point estimates for females who have very different profiles. For example, it is possible that a female who is an avid groomer and seldom participates in coalitionary aggression through simple averaging could appear identical to a female who rarely grooms others, but who often joins coalitionary aggression. The interpretation of such measures is problematic because sociality indices that draw on multiple behaviors may conceal important differences between individuals. We suggest that it is useful to understand the variation of these behaviors within a population before constructing a single measure.

We selected three behavioral domains, each of which represents a different type of social engagement in capuchins – grooming, coalitionary conflicts, and foraging – and estimated the individual sociality measures separately. We argue that doing so: (1) enabled us to incorporate the uncertainty about our measures, and (2) aided our interpretation of the results.

527 *Incorporating the uncertainty.* One of the challenges in analyzing observational
528 longitudinal datasets is data resolution as a result of uneven sampling. Data from the
529 natural habitats are notoriously difficult to gather. Inevitably, the records for social
530 interactions are sparse (Farine 2015) and some individuals are observed more often
531 than others for multiple reasons (Silk et al., 2013). Analysts therefore face a high risk of
532 false negatives when estimating dyadic relationships, i.e. some pairs are inferred to
533 have no social relationship at all, whereas if behavioral sampling were sufficiently dense,
534 they would be observed to interact, although rarely (Farine, 2015).
535 To address the uneven sampling of individuals and social groups in our dataset,
536 we used a Social Relations Model (Snijders and Kenny, 1999). This approach allowed us
537 to estimate individual rates of giving and receiving interactions and the uncertainty
538 associated with those estimates due to the varying number of observations. To increase
539 data resolution, we did not focus on adult female interactions with only other adult
540 females (e.g. Silk et al., 2010; Kalbitzer et al., 2017; Archie et al., 2014) or with only adult
541 males (e.g. Archie et al., 2014). We used to use each female's entire observation history
542 with her group members to ensure as complete as possible a picture of a female's true
543 sociality (Farine and Whitehead, 2015). As a multilevel model (McElreath 2020), the
544 Social Relations Model takes advantage of partial pooling across the entire population
545 when estimating individual female estimates (McElreath, 2020), which reduces
546 overfitting on the available data. To reflect the latent uncertainty in observational data,
547 our sociality measures were modeled as distributions, rather than point estimates,
548 which we subsequently used to model female survival.

549 *Interpretation of results.* Our analysis reveals several insights about grooming,
550 coalitionary support, and foraging interactions by showing how adult females compare
551 to each other and to the rest of the population (Figures 1–2). The most informative
552 behavior is grooming. Adult females are the most avid groomers in the capuchin
553 population with the majority of the females grooming more than an average monkey.
554 However, some of the individuals who groom the least are also adult females.

555 Knowing how an individual female's measures in one behavior correlate with
556 other behaviors that same year provides additional insights into the heterogenous
557 effects that the respective sociality measures exhibit on survivorship. As noted,
558 *grooming giving* measures are reliably associated with longevity. Yet, because *grooming*
559 *giving* is only weakly correlated with *support in coalitionary aggression* and *foraging in*
560 *close proximity*, females who are providing the most grooming are usually not the same
561 females who participate most often in coalitionary aggression or most often foraging in
562 close proximity of others.

563 Within the grooming domain, our results make sense in light of the respective
564 grooming distributions (Figure 1). *Grooming giving* and *grooming receiving* are
565 moderately correlated (r = 0.57, Figure 2), suggesting that many females occupy a
566 similar position relative to other females within the grooming network when quantifying
567 their grooming rates with other group members. However, there is substantially more
568 variation in how much grooming females provide, i.e. the most and the least avid
569 groomers are much more different from an average monkey in the population than the
570 females who receive the most and the least grooming. The narrow distribution of groom

receiving estimates suggests that grooming is somewhat equally distributed within the population and that individuals do not differ from each other a lot in how likely they are to be groomed by a group member. Unsurprisingly, these relatively small differences are not reliably associated with survival.

Finally, a biologically interesting question deals with the mechanisms that facilitate the relationship between sociality and longevity. Recently there has been a call for understanding exactly how sociality is affecting fitness in primates (Ostner and Schülke 2018; Thompson, 2019). Individual sociality as a construct is likely to be composed of the many types of relationships that an animal has: affiliative, agonistic and others. The lifespans that we observe are a consequence of many decisions that animals make and there is arguably more than one pathway through which sociality can affect survival in a particular species (Ostner & Schülke, 2018; Thompson, 2019). Behaviors such as grooming, coalitionary support and foraging in proximity of others indicate social relationships that individuals cultivate, but are probably not the sole indicators of those relationships.

Our study was not designed with the purpose of identifying a mechanism linking sociality and longevity. It is possible that females derive direct benefits from grooming others, such as social bonding through the release of hormones (Dunbar 2010). Indirectly, grooming interactions might contribute to structuring a female's overall social life. Capuchin monkeys spend a lot of time grooming, and providing grooming to multiple partners might allow females to develop social relationships which eventually structure other types of interactions. For example, the distributions of coalitionary

aggression interactions suggest that a small group of individuals participate in coalitionary aggression because female estimates of giving and receiving support are very highly correlated (Figure 2). Since the females who groom others the most are usually not the same females who participate in coalitionary aggression the most, it is possible that the frequent groomers experience less aggression and, as a result, fewer of the detrimental consequences associated with it. Alloparenting might be another domain where frequent groomers receive more help from other group members. To better understand the mechanisms that contribute to the relationship between sociality and longevity and to design studies to test them, we need to investigate the interaction patterns themselves. Understanding the natural structure of different types of interaction types can help in developing better sociality measures and further our understanding how sociality contributes to fitness.

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

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