

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

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23 ABSTRACT

24 Across multiple species of social mammals, evidence is accumulating that
25 sociality is associated with fitness. In long-lived species, like primates, lifespan is one of
26 the main fitness components. Here, we provide the first direct evidence that females
27 who provide more in social services live longer. We used 18 years of data from the
28 Lomas Barbudal Monkey project to quantify sociality in 11 capuchin (*Cebus capucinus*)
29 social groups using three interaction types: grooming, support in coalitionary
30 aggression, and foraging in close proximity. We analyzed each domain separately to
31 understand how giving and receiving social favors impact survivorship. To estimate
32 female sociality in each of these domains, we built an adaptation of the Social Relations
33 Model. This approach enabled us to estimate individual rates of giving and receiving
34 interactions and take into account the uncertainty in these estimates due to varying
35 amounts of observations of each individual. Subsequently, we modeled adult females'
36 survival as a function of their sociality estimate, rank, age, group size, and maternal kin
37 presence using a Bayesian Cox proportional hazards model. We found that females who
38 provide more grooming to other group members survive longer. There was no strong
39 evidence that females who receive more grooming, participate more often in
40 coalitionary aggression, and forage more often in close proximity of others also have
41 higher survivorship. These results add a neotropical primate species to the growing list
42 of mammals, including humans, where greater sociality is associated with longevity.

43

44

45 INTRODUCTION

46 A key question for understanding the evolution of animal sociality is: Do animals
47 that are more social enjoy greater fitness benefits? A number of studies link
48 components of reproductive success, such as fecundity (white-faced capuchins, *Cebus*
49 *capucinus*: Fedigan et al., 2008; Assamese macaques, *Macaca assamensis*: Schülke et
50 al., 2010; chimpanzees, *Pan troglodytes schweinfurthii*: Gilby et al., 2013) and offspring
51 survival (yellow baboons, *Papio cynocephalus ursinus*: Silk, 2009; savannah baboons,
52 *Papio cynocephalus*: Silk et al., 2003; white-faced capuchins, *Cebus capucinus*: Kalbitzer
53 et al., 2017), to differences in the social behavior of individuals.

54 In long-lived species, lifespan is also an important component of reproductive
55 success contributing to fitness variation (Clutton-Brock, 1998). The most abundant
56 evidence that individual sociality affects lifespan has accumulated in human literature.
57 Both the presence and the absence of social relationships affects lifespan. That is, being
58 socially connected is associated with a lower probability of dying (Holt-Lunstad et al.,
59 2010; Shor and Roelfs, 2015; Shor et al., 2013), while having few and poor social
60 relationships is associated with a higher risk of death (Roelfs et al., 2011).

61 In nonhuman species there is similar evidence that individual sociality is
62 associated with lifespan. Among baboons, females who maintain stable social
63 relationships with other males and females live longer (chacma baboons, *Papio*
64 *hamadryas ursinus*, Silk et al., 2010; Archie et al., 2014). Prime-aged female macaques of
65 Cayo Santiago who have more living adult female relatives live longer (Brent et al.,
66 2017). Blue monkey females (*Cercopithecus mitis stuhlmanni*) who have strong and

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

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

80 In this paper, we investigate whether more social white-faced capuchin females
81 live longer than less social females. We analyzed eighteen years of capuchin monkeys'
82 social interactions taken from the Lomas Barbudal Monkey dataset. To quantify
83 individual sociality, we selected interactions from three domains to represent the
84 variety of social behaviors that capuchin monkeys engage in: grooming, coalitionary
85 aggression, and foraging in proximity to others. To deal with different amounts of
86 observations for each individual, we used the multilevel Social Relations Model (Snijders
87 and Kenny, 1999; Koster et al. 2019) to decompose the observations of exchanges of
88 these interactions into separate individual giving, individual receiving, and dyadic

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

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

110

111 METHODS

112 *Study subjects and the dataset*

113 We studied members of the wild white-faced capuchin population at the Lomas
114 Barbudal Biological Reserve and surrounding private lands in Guanacaste, Costa Rica
115 (Perry et al., 2012). The Lomas Barbudal Monkey Project dataset has longitudinal
116 records on individuals living in 11 capuchin social groups. It contains detailed records
117 including demographic information, pedigree information, and data regarding social
118 interactions that are necessary for quantifying individual sociality.

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

127 The records on capuchin behavior were collected between January 2002 and
128 December 2019. The subjects were 132 adult females, living in eleven different social
129 groups over 146 group years (average years of observation per group = 13.27; range = 7
130 – 18 years). The females were considered adults once they reached the age of 5 years.
131 The behavioral and demographic data on each group were collected by experienced
132 observers during censuses lasting at least 6 hours/day.

133 *Measuring Sociality*

134 To measure female sociality, we chose three behavioral domains: grooming,
135 coalitionary aggression, and foraging. We treated grooming and coalition formation as
136 directed behaviors, and we used observations of individuals as both initiators and
137 recipients of the behavior. We did not have information about which individual had
138 initiated the proximity when foraging, and therefore foraging in proximity was treated
139 as an undirected behavior. In calculating the frequency with which adult females
140 engaged in these interactions, we used behavioral records from all the individuals who
141 resided in the 11 groups during the study period. There were a total of 563 monkeys,
142 residing in 11 social groups, comprising 13,770 dyads. We treated each of the five
143 interaction types (*grooming giving, grooming receiving, support giving, support*
144 *receiving, forage in proximity*) as a separate measure of sociality.

145 *Grooming (groom giving and groom receiving)*

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

151 Grooming rates were estimated using data collected during 10-minute focal
152 follows. To estimate individual grooming rates, we calculated dyadic counts of grooming
153 and dyadic opportunities for grooming. The opportunity for a dyad, A-B, to engage in
154 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

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

182 *Foraging in proximity*

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

188 *Foraging in close proximity* was estimated from group scans that occurred in
189 the context of foraging. In group scans, the identity of the scanned individuals, their
190 activity and their proximity to other individuals within 10 body lengths (~2 m) was
191 noted. We considered individuals to be foraging in close proximity if they were scanned
192 within 5 body lengths (~1m) of each other. For each dyad, we scored whether they were
193 observed foraging within close proximity in 10 min. segments (i.e. if they were observed
194 doing this more than once within 10 min., only one instance was counted). The number
195 of opportunities that the dyad had to forage within close proximity is a sum of group
196 scans in the foraging context that are 10 min. apart, where one of the individuals is a
197 subject of a group scan.

198 *The Social Relations Model and Individual sociality measures*

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

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

213 The Social Relations Model (Snijders and Kenny, 1999) decomposes the variance
214 in giving and receiving behaviors into separate giving, receiving, and dyadic relationship
215 components. We fitted a Bayesian multilevel Social Relations Model with the following
216 parameters: the intercept parameter (base rate), social group-level, individual giving,
217 individual receiving, dyadic symmetric, and dyadic asymmetric random effects
218 parameters (see Koster et al. 2015). We used data collected on the entire population
219 (i.e. adult males, females, and immatures) since the Social Relations Model is a
220 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-

243 specific) covariates: the female's age, her dominance index, the average number of
244 individuals in her group, the proportion of time during that year that her mother was
245 alive, and the number of adult daughters that she had.

246 Age: Focal female ages were assigned based on demographic records of births
247 and deaths collected from 1990 – 2019. The ages of females who were born before
248 1990 were estimated in part by retroactively comparing photos taken then with photos
249 of known-aged females collected later in the study. In addition, we inferred
250 reproductive histories via genetic maternity data. We assumed that the age of first birth
251 for each mother was six years, and each mother had a two-year interbirth interval
252 (Fedigan and Rose, 1995; Perry, 2012).

253 Average number of individuals in her group: This is the mean number of adult
254 females, adult males, and immatures that resided in the female's group during the days
255 when researchers spent at least six hours of observation with the group, averaged for
256 the year.

257 Mother's presence: The proportion of the year that the female's mother was
258 alive and co-resided with her. The measure varies from 0 to 1, where 1 indicates that
259 the mother was alive and co-resident with the focal female for the entire year, and 0
260 indicates that the mother died in some previous year.

261 Number of daughters: The number of daughters that a focal female had was
262 very highly correlated with her age (0.72). To control for the effect of age on the
263 number of daughters, we grouped all of the females that were the same age together
264 and centered the number of daughters for each age group. For every age group we

265 subtracted the mean number of daughters for that age group to reduce the confounding
266 between age and number of daughters. The resulting variable was not correlated with
267 age (~ 0). This is equivalent to modeling an interaction between age and number of
268 daughters, with age treated as a categorical variable.

269 Annual dominance index: The annual dominance index represents the proportion
270 of group members that the female dominated, on average, that year. For each
271 observation day that the female (the focal) resided in a social group, we identified all of
272 the other co-resident individuals (alters). To assess whether the female was dominant to
273 an alter on a particular day,
274 we first identified the dominance interaction immediately preceding and following the
275 day of interest for each focal-alter dyad. The total number of these interactions across
276 all focal–alter dyads represents the number of opportunities for the focal to dominate
277 someone. For each interaction, we identified that the focal individual was dominant if
278 she was either the animal performing the supplanting, or being cowered at, or being
279 avoided, or fled from. The daily dominance index, DDI_i , of a focal individual, i , is a sum of
280 dominance interactions where focal was dominant to their alters, w_{i-a} , divided by the
281 total number of dominance interactions that the focal had with her alters, s_{i-a} :

282

$$283 \quad DDI_i = \frac{\sum w_{i-a}}{\sum s_{i-a}}. \quad (1)$$

284

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

287

288

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

289

290 In some cases, either one or no dominance interactions were available for a focal-alter

291 dyad. As a result, the individuals who did not have dominance interactions with the

292 focal did not contribute to the calculation of the daily dominance index.

293 We included the covariates, because each of them is likely to influence

294 females' probability of survival. An adult female's probability of dying in a given year is

295 expected to increase with age (Archie et al. 2014; Brent et al. 2017). Females who live in

296 larger groups might experience greater survival rates due to reduced predation risks

297 (Sterk et al., 1997). Higher-ranking females possibly enjoy reduced mortality in

298 comparison to lower-ranking females due to their central position in the group

299 (Kalbitzer et al., 2017), which also reduces risks of predation. The presence of a mother

300 and/or adult daughters approximate female's close kin network benefits: Females who

301 have a more extensive kin network might experience reduced mortality (Brent et al.,

302 2017).

303 Having many covariates in the model can result in "included variable bias"

304 (McElreath, 2020) where predictors are not only causally influencing the outcome, but

305 also influencing each other. This can result in predictor induced statistical selection

306 within the model and manifest itself through misleading statistical, but not causal,

307 associations between the variables we are interested in (McElreath, 2020). A female's

308 rank and age are likely to influence how much the female participates in social

309 interactions. Females who reside in larger groups are likely to have different interaction
310 networks in comparison to females in smaller social groups due to a larger number of
311 social partners available (Archie et al., 2014). To check if the above assumed
312 relationships justify the inclusion of all of the predictor variables in the model, we drew
313 a directed acyclical graph (DAG) using the package *daggity* (v.3.0) and analyzed implied
314 functional relationships. The DAG assumed is provided in the supplemental materials.

315 *Modeling approach*

316 To take into account that some females contributed different numbers of
317 years to the analysis, we modeled individual differences using a random effect term.
318 Models were run using Stan (v.2.19.1) and the *rethinking* package (v. 1.93: McElreath
319 2020) in R (v. 3.6.2; R Core Team 2019).

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

323

$$324 \quad \Pr(D_i | \lambda_i) = \lambda_i \exp(-\lambda_i D_i) . \quad (3)$$

325

326 For females who did not die during the observation period, the probability of waiting D_i
327 without dying comes from the complementary cumulative probability distribution:

328

$$329 \quad \Pr(D_i | \lambda_i) = \exp(-\lambda_i D_i) . \quad (4)$$

330

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

332
$$\lambda_i = 1/\mu_i . \quad (5)$$

333 where μ_i is the expected number of days till death

334
$$\log(\mu_i) = \alpha + a[id] + b_{sociality} * true\ sociality\ estimate[id] + b_{rank} * rank_s \quad (6)$$

335
$$+ b_{age} * age + b_{daughters} * daughters$$

336
$$+ b_{mother} * mother + b_{grsize} * group\ size .$$

337

338 α denotes the intercept or the base rate of number of days survived, $\alpha[id]$ denotes

339 individual female random effects corresponding to the observation period. The model

340 coefficients $b_{sociality}$, b_{rank} , b_{age} , $b_{daughters}$, b_{mother} , b_{grsize} describe the impact of

341 sociality, rank, age, number of daughters, mother's presence, and group size,

342 respectively. We took a latent variable approach to model the sociality estimates, since

343 individual sociality estimates are not point estimates, but rather posterior distributions

344 with mean and SD reflecting measurement uncertainty about the true rate. Under this

345 approach, we assumed that each female had some true underlying sociality measure,

346 *true sociality estimate[id]*, which was normally distributed with mean and SD equal to

347 the mean and SD of the individual estimate of sociality drawn from the Social Relations

348 Model results.

349 We used the Bayesian approach to fit Cox proportional hazard model (Singer

350 and Willett 2003). We assumed Normal (8, 0.5) prior for a base rate of survival, α , which

351 places most of the prior mass between 0 to 20 years with the mean of 8 years and a

352 long tail allowing more extreme values. For fixed effects, we assumed Normal (0, 1)

353 prior. For individual-level random effects, $\alpha[id]$, we compared three types of models:
354 one with no random effects and two with individual-level random effect priors assumed
355 as Normal (0, 0.2) or Normal (0, 1). All three model types resulted in similar estimates;
356 therefore here we are reporting the results with individual-level random effect prior
357 Normal (0, 1), while the results of the other two types of models are reported in the
358 supplemental material (Table S1 and Table S2). All of the covariates, except the number
359 of daughters, were standardized by subtracting the mean and dividing it by the standard
360 deviation. As noted previously, the number of daughters was centered by subtracting
361 the mean number of daughters for each age.

362

363 RESULTS

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

365 Females differ the most from the other age-sex classes in their distribution of
366 *grooming giving* measures. A majority of the females (80%) groom more than an
367 average monkey in the population, while a majority of the adult males and immatures
368 (78%) groom less than an average monkey (Figure 1, panel A). The female distributions
369 for the rest of the behavioral domains are very similar to the other age-sex distributions,
370 indicating that females behave similarly to adult males and immatures in those domains.

371 Figure 1 illustrates how the individual sociality measures of *grooming*,
372 *coalitional support*, and *foraging in proximity* by adult females compare to the
373 estimates for other age-sex classes. The distribution in orange represents adult female
374 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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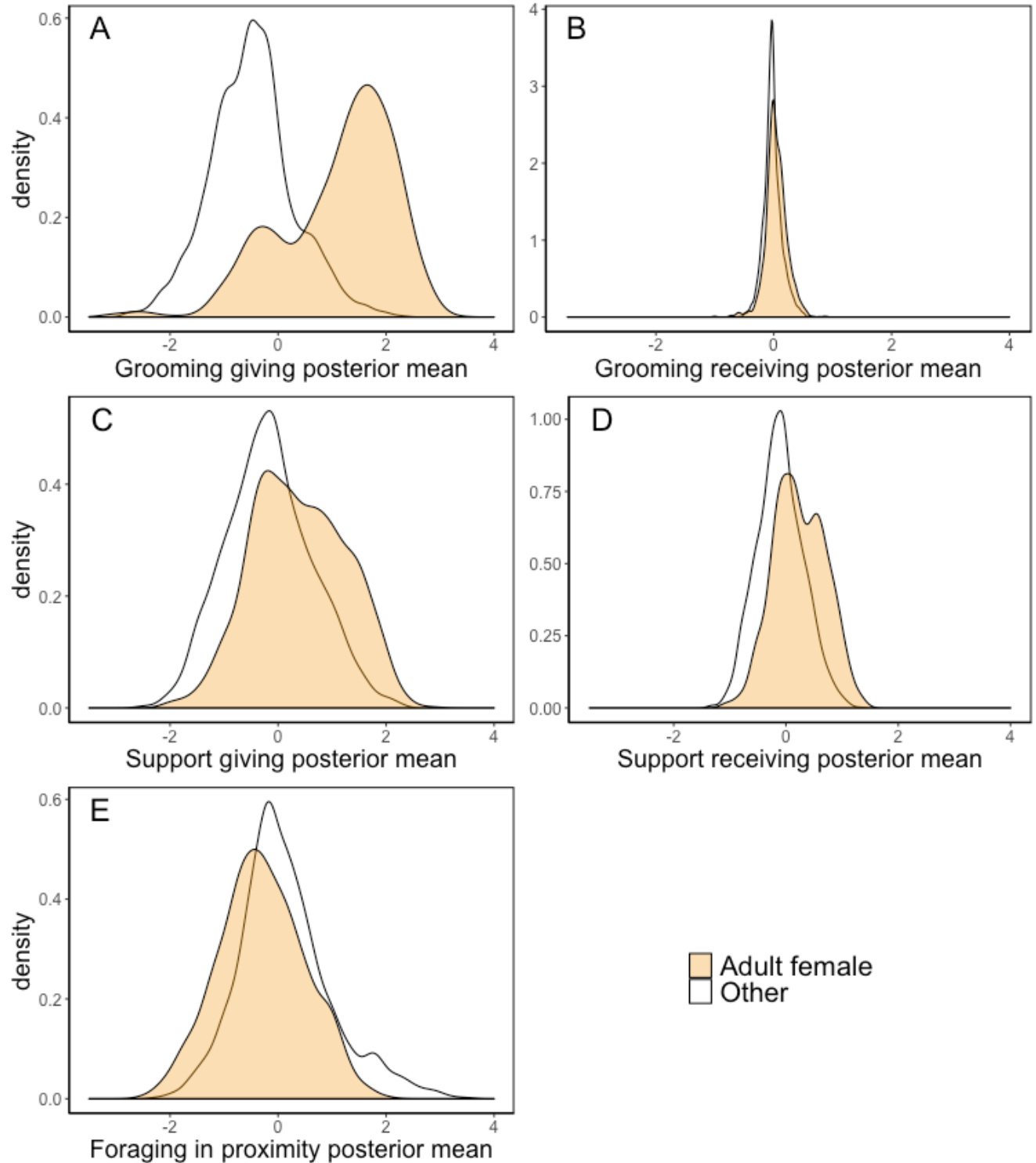
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397 **Figure 1.** Posterior mean distributions of annual individual sociality measures for each
398 type of behavior. The orange density represents adult females whereas the white
399 density represents the rest of the population. The population base rate is at
400 approximately zero.
401



402

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

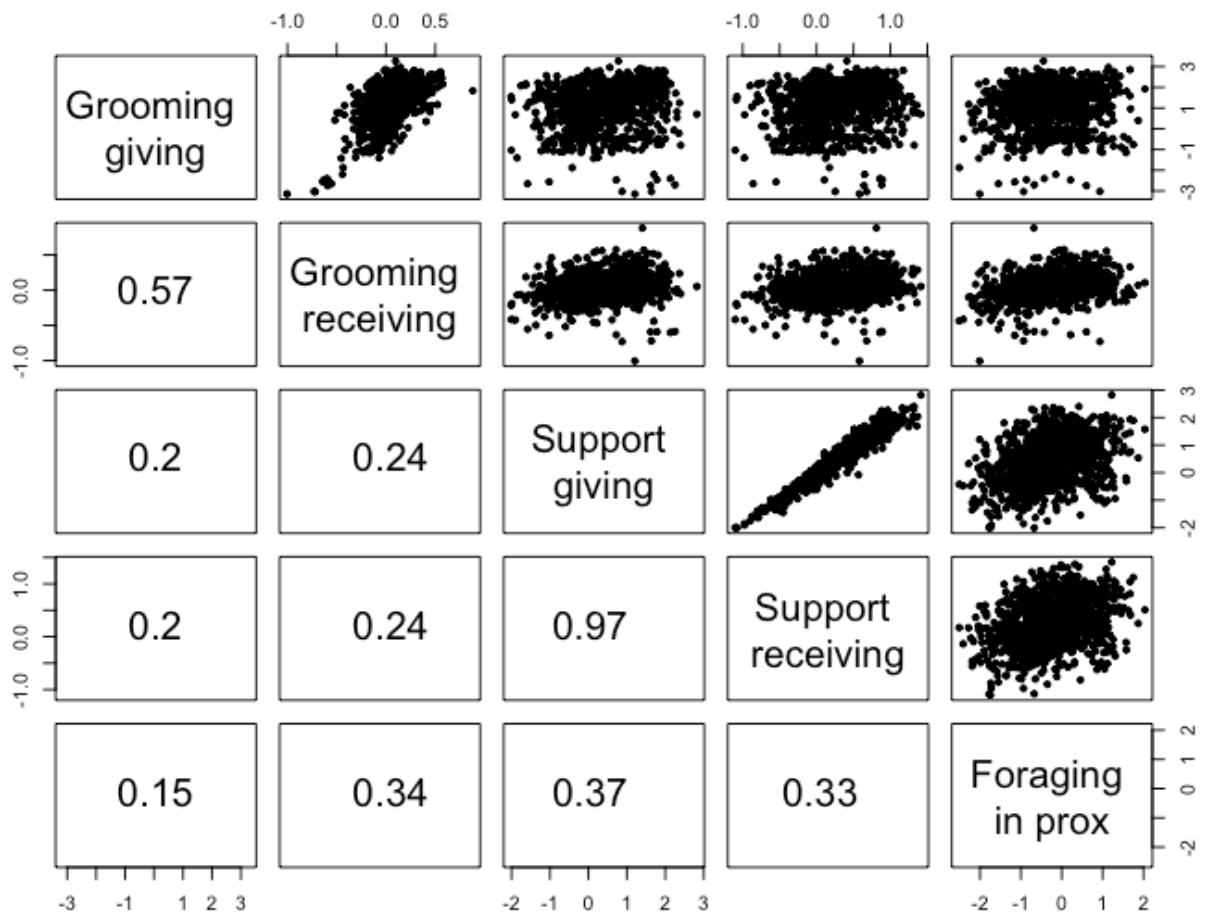
404 Each female has five annual sociality measures. We plotted the pairwise
405 correlations between each of the sociality measures in Figure 2 in order to investigate if
406 female profiles are similar across all five measures, i.e. is a frequent groomer also a
407 frequent recipient of grooming and coalitional support? Within the coalitional
408 aggression domain, estimates of female giving and receiving coalitional support were
409 highly correlated ($r=0.97$). Females who intervene on someone's side during a conflict
410 also tend to receive a lot of support from others. This suggests that there is a small
411 subset of females that participate in coalitional aggression more frequently than
412 others. However, females vary less in their *support receiving* than in their *support giving*
413 estimates (Figure 1, Panel C–D). In the grooming domain, the correlation between giving
414 and receiving estimates was moderate ($r=0.57$). Some of the females who groom others
415 the most are not among those who receive the most grooming. In addition, Figure 1
416 panel B shows a narrow distribution of the receiving measurements, which implies that
417 females overall distribute their grooming evenly among their group members.

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

423

424

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



427

428 (3) Do more social females survive better?

429 Table 1 presents the Cox proportional hazards model posterior mean estimates

430 and the 95% Highest Posterior Density Interval (HPDI), representing the narrowest

431 interval containing the 95% probability mass. Independent of the effects of covariates

432 (age, dominance rank, group size, number of adult daughters, co-residence with

433 mother), females who groomed others more survived at higher rates than other

434 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.

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

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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.

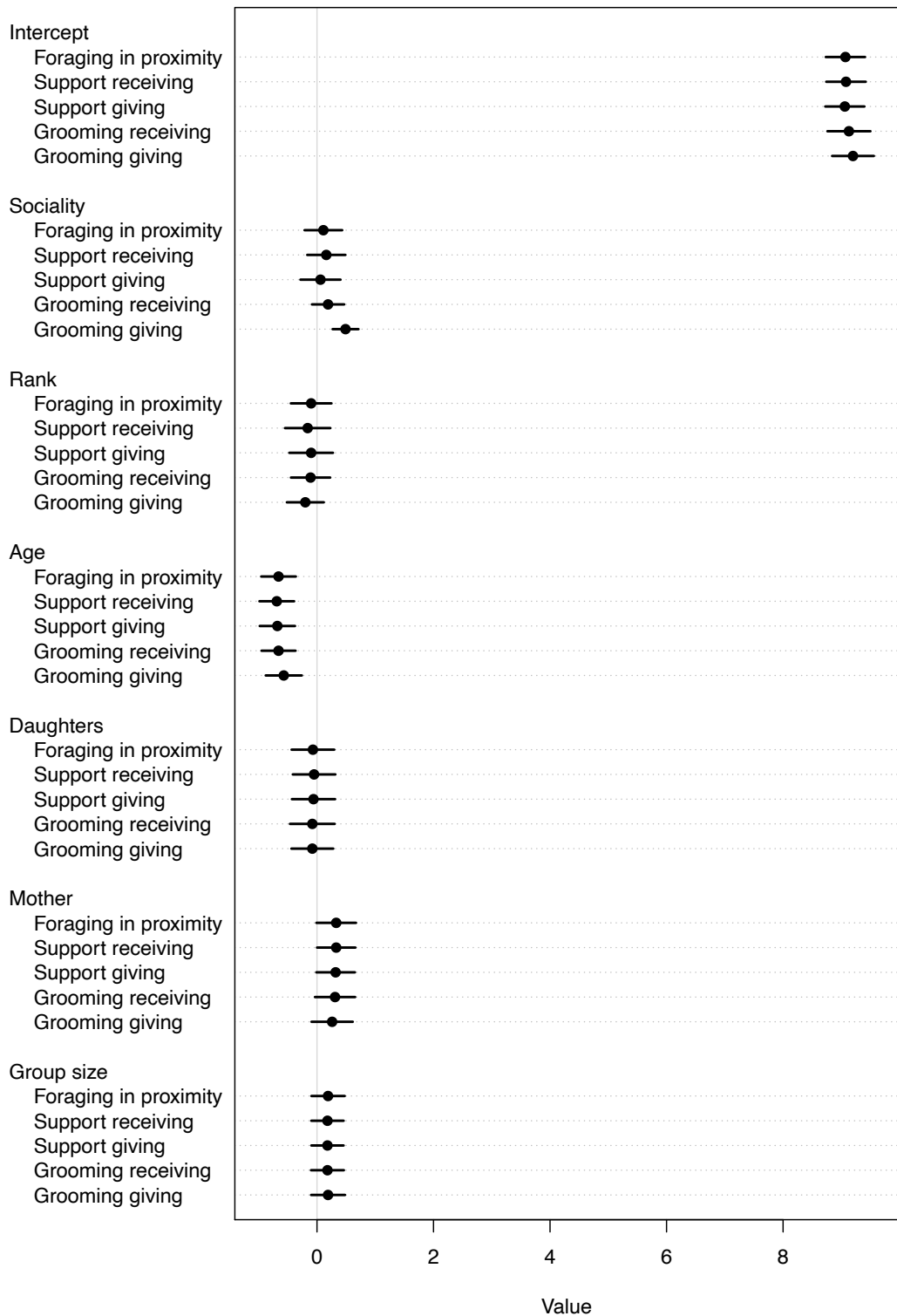
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451 **Figure 3.** Posterior means and standard deviations of 5 Cox proportional hazards models
452 in which annual survivorship varied as a function of five measures of sociality (*foraging*
453 *in proximity, support receiving, support giving, grooming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



456 To facilitate the interpretation of the Cox proportional hazards model
457 coefficients, we plotted model predictions showing the probability of dying in a given
458 year (Figure 4). We have varied females' sociality measure to compute the predictions.
459 Figure 4 illustrates the annual probability of dying as a function of a female's sociality
460 level measure where a yellow line represents a 10-year-old female and a blue line
461 represents a 30-year-old female (holding all other covariates fixed at the values
462 described above).

463 Across all five sociality measures, the less social females have a greater
464 probability of dying than more social females, but only the slopes for *groom giving*
465 confidently suggest a beneficial effect on survivorship (Figure 4, panel A). Predictions for
466 *groom receiving* likewise suggest a beneficial effect of sociality, but the model
467 predictions are less certain (Figure 4, panel B). Meanwhile, the slopes for *coalitionary*
468 *support* and *foraging in close proximity* are quite shallow, indicating that the survival
469 varies little as a function of these sociality measures (Figure 4, panels C, D, and E). These
470 model predictions reflect the uncertainty associated with these estimates (Table 1 and
471 Figure 3). Overall, there is less certainty in the estimates for older females, partly owing
472 to their scarcity in the sample.

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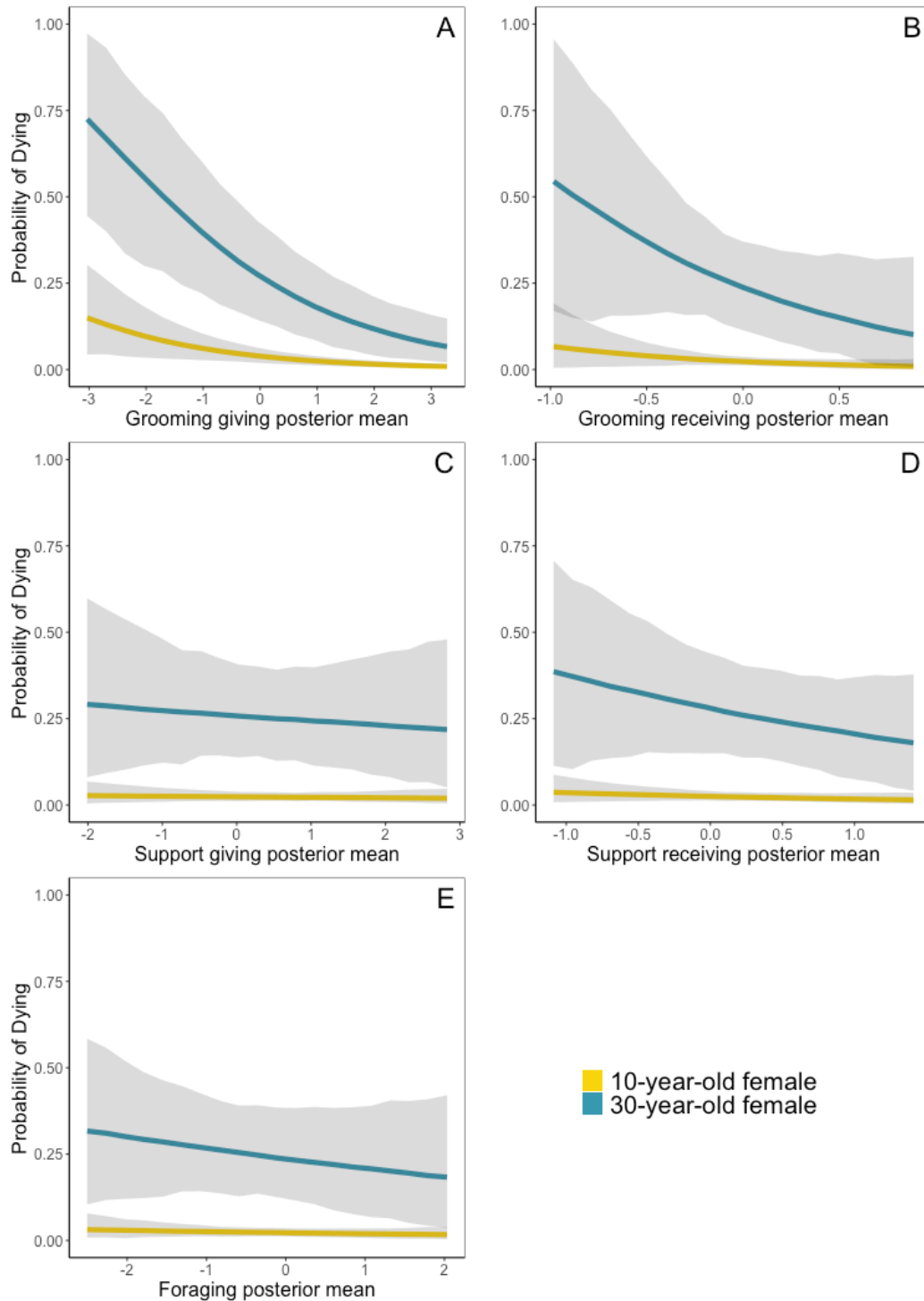
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478 **Figure 4.** Cox proportional hazard model predicted annual probabilities of dying at two
479 representative ages (10 and 30) as a function of the sociality levels in five behavioral
480 domains. For both ages, we assumed median group size, median rank, and average
481 number of daughters for the age. For 10-year-old females, we assumed a co-resident
482 mother, while predictions for the 30-year-old assume the mother is deceased.
483



485 DISCUSSION

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

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

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

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

522 We selected three behavioral domains, each of which represents a different
523 type of social engagement in capuchins – grooming, coalitionary conflicts, and foraging –
524 and estimated the individual sociality measures separately. We argue that doing so: (1)
525 enabled us to incorporate the uncertainty about our measures, and (2) aided our
526 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

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

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

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

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

605 DATA AND CODE ACCESSIBILITY

606 The data and code used to produce the analyses in this paper are available at:

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608

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