

1 **Deconstructing sociality: the types of social connections that predict longevity in a group-living**
2 **primate**

3
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15
16 **Key words**

17 sociality, fitness, social structure, survival, group living, *Macaca mulatta*

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20 Many species use social interactions to cope with challenges in their environment and a growing
21 number of studies show that individuals that are well-connected to their group have higher fitness
22 than socially isolated individuals. However, there are many ways to be ‘well-connected’ and it is
23 unclear which aspects of sociality drive fitness benefits. Being well-connected can be conceptualised
24 in four main ways: individuals can be socially integrated by engaging in a high rate of social
25 behaviour or having many partners; they can have strong and stable connections to favoured partners;
26 they can indirectly connect to the broader group structure; or directly engage in a high rate of
27 beneficial behaviours, such as grooming. In this study we use survival models and long-term data in
28 adult female rhesus macaques (*Macaca mulatta*) to compare the fitness outcomes of multiple
29 measures of social connectedness. Females that maintained strong connections to favoured partners
30 had the highest relative survival probability, as did females well-integrated due to forming many weak
31 connections. We found no survival benefits to being structurally well-connected or engaging in high
32 rates of grooming. Being well-connected to favoured partners could provide fitness benefits by, for
33 example, increasing the efficacy of coordinated or mutualistic behaviours.
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36 **Introduction**

37 Social relationships are a fundamental component of group life. Individuals often interact or associate
38 with others in an affiliative or non-agonistic manner, and these interactions can have fitness
39 consequences. For example, well-connected humans and other animals can live longer and produce
40 more offspring than less well-connected individuals (e.g. [1–3]; table S1). Yet despite their apparent
41 importance to biological success, the routes by which social connections impact fitness - how and
42 why social connections are beneficial - remains unclear.

43

44 Critical to uncovering the means by which social connections are beneficial is an understanding of
45 what it means for individuals to be ‘well-connected’ [4]. Sociality is multi-dimensional in nature [5,6]
46 and there are many ways for group-living animals to connect to others. For example, an individual
47 might be well-connected in one sense because they have a large number of social partners, but poorly
48 connected in another sense if their partners are all from the same sub-group. By deconstructing
49 sociality into its different dimensions, we can pinpoint the specific types of social connections that are
50 linked to fitness and, as a result, begin to identify the function (or functions) of being well-connected.

51

52 There are four main ways that connectedness has been conceptualised. We describe each here along
53 with the proposed mechanisms by which each might be beneficial. For ease of understanding, we
54 have named the four types of social connectedness as follows: 1) social integration; 2) dyadic
55 connectedness; 3) structural connectedness; and 4) direct connectedness (figure 1).

56

57 Socially integrated individuals are those that engage in a high frequency of interactions with others
58 and/or interact with a large number of partners (figure 1; table 1; table S1). Measures of social
59 integration are blind to the identity of social partners; individuals with a given rate of interaction are
60 considered equivalent, regardless of whether they interact with a single individual or 10 individuals.
61 Socially integrated individuals can also have a large number of weak (infrequent or transient) social
62 partners [7]. Social integration has been proposed to be beneficial because it leads to social tolerance,
63 increasing an individual’s access to contested resources or spatial locations, minimising their chances
64 of injury or death due to aggression [8–10].

65

66 For dyadic connectedness the identity of social partners is important and social relationships are built
67 up over a series of interactions with particular individuals (figure 1; table 1; table S1). Dyadic
68 connections might be considered analogous to friendships in humans [11,12]. Measures of dyadic
69 connectedness rely on inferring an individual's most frequent or consistent partners (figure 1).

70 Frequent and consistent engagement with the same partner may be beneficial because it increases the
71 efficacy of coordinated behaviours [13,14] as well as opportunities for mutualism or reciprocal
72 exchange of behavioural services [15,16].

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Structural connectedness is based on indirect (i.e. with a partner's partners) as well as direct connections, capturing the wider pattern of relationships between all group members (figure 1; table 1; table S1). Measures of structural connectedness include metrics commonly used in social network analysis, such as betweenness and closeness, the benefits of which may include an increased chance of learning new information from others (e.g. [17]), increased access to resources (e.g. [18]), enhanced likelihood of being alerted to the presence of a predator (e.g. [19]), and greater travelling and foraging efficiency (e.g. [20]).

Direct connectedness refers to scenarios where being well-connected is not necessarily about the properties of the social connections themselves, but is instead about the interactions involved in forming those connections (figure 1; table 1; table S1). Grooming, for example, removes parasites [21] and is a common behaviour in many birds and mammals. Reduced parasite burdens could lead to decreased mortality of individuals who are groomed by others the most [22] regardless of the number or identity of their partners or of their position in the broader social structure. Similarly, maintaining spatial proximity to others may provide enhanced protection from predators or increased hunting success [23].

Studies have revealed fitness correlates for each of these four types of social connectedness in a taxonomically broad range of species (table S1). But distinguishing between the proposed ways that sociality contributes to fitness requires studies that evaluate the relationship between fitness and the different types of social connectedness in tandem. To our knowledge, no study to date has evaluated all four types of connectedness in a single study system. Here, we deconstruct the relationship between social connectedness and survival in a long-lived and highly social primate. Although a growing number of studies have linked social connections to the health (e.g. [2,3,24]) and reproduction (e.g. [25]) of individuals, longevity is also a major contributor to fitness, especially in female mammals where limited variation in reproductive rates results in longevity being the main predictor of lifetime reproductive success [26]. However, studies of the relationship between longevity and social connectedness are rare due to a scarcity of datasets with sufficiently large numbers of individuals with known survival outcomes. In this study, we take advantage of a data in a large number of (n =319) adult females from a free-living population of rhesus macaques (*Macaca mulatta*) that has been studied for 80 years [27] to test the relationship between measures of the four different types of social connectedness and survival.

107 **Methods**

108

109 Study subjects and behavioural data

110 We undertook this study on rhesus macaques inhabiting the island of Cayo Santiago, Puerto Rico. The
111 population consists of approximately 500 adults living in 6-9 mixed-sex social groups. The animals
112 are descendants of 409 Indian-origin rhesus macaques introduced in 1938. Subjects were mature adult
113 females, ≥ 6 years old [28]. There is no regular medical intervention and the major causes of death at
114 this provisioned and predator-free site are disease and injury [29]. This population therefore allows us
115 to investigate the fitness benefits of social connections in the absence of starvation and predator-
116 driven mortality [30]. The expected lifespan for a female that reached adulthood in this study was 20
117 years (95% CI: 19-22), with a maximum observed lifespan of 28.

118

119 We collected behavioural data on 319 adult females between the years of 2010–2017, resulting in 754
120 macaque years. Behavioural data were collected on an average of two study groups each year: Group
121 F 2010-2017; Group HH 2014; Group KK 2015; Group R 2015-2016; Group S 2011; Group V 2015-
122 2016. Of our subjects, 34 died during the study (table S2). We collected behavioural data using 10-
123 minute focal animal samples [31]. We selected animals in a pseudo-randomised order balanced within
124 days and years, resulting in roughly the same number of observations per subject per year. We
125 recorded the duration and direction of grooming and identities of all adult social partners. We
126 included only interactions between adult females in analyses. Juveniles' interactions are influenced by
127 their lack of independence from their mothers, while female-male interactions tend to be concentrated
128 in the breeding season, making it difficult to isolate social processes from sexual ones. To establish
129 spatial association (hereafter, spatial proximity), we recorded the identities of all adult females found
130 within two meters of a study subject (but not touching or grooming them) at three evenly-spaced
131 intervals throughout a focal animal sample. Female rhesus macaques have a strict dominance
132 hierarchy with maternal rank inheritance [28]. For each female, dominance rank was established in a
133 given year based on observed submissive, win-loss, interactions [32].

134

135 Quantifying social connectedness

136 As with previous studies (e.g. [33–38]), we used grooming and spatial proximity as indicators of
137 social connections. We calculated a dyadic composite sociality index - DSI [6] - which represents the
138 relative rate at which a pair of individuals (i and j) engage in behaviour x , relative to the mean rate of
139 occurrence of that behaviour by all subjects in their group in a given year (equation 1; [6]). For
140 grooming, x represents the duration (seconds) of grooming given and received between a pair of
141 animals. For proximity, x represents the number of times a pair of females were in proximity to one
142 another relative to the number times they were observed but were not in proximity to one another. As
143 DSI is scaled by the mean rate of behaviour, DSI values are relative to within-group social

144 opportunities, which allows comparisons of individuals from groups with divergent group sizes (table
145 S2) or gregariousness, and avoids potentially confounding within-group differences as individual
146 effects. [6].

147
148 We calculated the DSI between all pairs of females in a group in any given year. This allowed us to
149 represent each female's level of connectedness relative to the group and year in which she lived. DSI
150 forms the basis of all measures of social connectedness, acting in social network terms as the network
151 'edge'. Our measures of connectedness either limit the social connections used or slightly alter the
152 calculation of DSI (figure 1). Measures of social connectedness are described in detail below (see also
153 figure S1).

154

155 *Social integration*

156 We measured social integration in three ways:

157

158 i) Strength of connections. The overall strength of an individual's connections is a measure
159 of social effort relative to other group members: i.e., how frequently an individual
160 engages in social activity regardless of the identity of their social partners. This is
161 calculated as the sum of all an individual's DSIs: their composite sociality index (CSI)
162 and is equivalent to weighted degree in social network analysis.

163 ii) Number of connections. A count of the number of different individuals a subject interacts
164 with, equivalent to 'degree' in social network analysis.

165 iii) Number of weak connections. Classifying connections as 'weak' requires a threshold
166 value above which a connection is considered 'strong' and below which it is considered
167 'weak' [37,39]. Previous studies have used a threshold DSI of 1 as the boundary between
168 strong and weak connections because 1 is the mean DSI in any population when pairs of
169 animals that do and do not (DSI=0) interact are considered (e.g. [37,39]). However, by
170 including connections that are not present, this approach has the potential to categorise
171 many connections as strong and few as weak. Indeed, there was too little variation in the
172 number of weak connections using this approach to perform a reliable test of survival
173 outcomes with our data. There were no clear discontinuities or cut-points in the
174 distribution of DSI values to use as an intuitive threshold to distinguish strong and weak
175 connections (figure S2). There were also no clear biological reasons that a particular
176 threshold value should be chosen. We therefore explored a range of thresholds, using
177 fixed percentages of a group's DSIs as the 'weak' threshold, whereby the lowest 90%,
178 80%, 70%, 60%, 50%, 40%, 30%, 20% and 10% of DSI values in the population were
179 considered weak. For example, under a 50% threshold, half of all connections were
180 considered weak, whereas under a 40% threshold two-fifths of the connections were

181 considered weak, and so on (figure S3). At higher threshold values the ‘number of weak
182 connections’ measure approximates the ‘number of connections’ measure. For each
183 threshold, we counted each subject’s number of weak connections (table S3) and used
184 this value as the fixed effect in a survival model.

185

186 *Dyadic connectedness*

187 We measured dyadic connectedness in three ways:

188 i) Number of strong dyadic connections. A count of the number of different individuals
189 with whom a subject shared a ‘strong’ connection [37,39]. As for weak connections,
190 classifying connections as ‘strong’ required a threshold above which a connection is
191 considered ‘strong’ and below which it is considered ‘weak’ [37,39]. We used variable
192 thresholds that defined the top 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80% and 90% of
193 connections in the population were considered strong (table S4). It is important to note
194 that these are not the inverse of the weak connections measures (i.e. defining 10% of
195 connections as weak will not give the same result as defining 90% as strong) because
196 weak connections are defined as being below the threshold, while strong connections are
197 defined as being above the threshold (figure S3). The distribution of values for weak and
198 strong measures do not therefore overlap.

199 ii) Strength of dyadic connections to ‘top’ partners. The frequency of interactions between
200 an individual and their most frequent partners. Previous studies have typically summed
201 the DSIs between a subject and their partners that fall within the subject’s top (strongest)
202 three DSI values [35,40,41]. We followed this procedure, varying the number of partners
203 considered ‘top’ from 1 to 10 (few individuals in our study had more than 10 social
204 partners). Females were only included in an analysis if they had the number of top
205 partners under consideration in that year (i.e., for the top 8 partners threshold all females
206 included had at least 8 partners).

207 iii) Strength of dyadic connections to stable partners. The frequency of interaction between a
208 subject and its preferred partners that were consistent over time (figure 1). We calculated
209 a female’s total DSI to stable partners that: i) had a DSI > 0 (i.e. any social partner); ii)
210 were within her top three DSI values [40–42]; and, iii) were in the top 50% of her DSI
211 values. Partner stability was only evaluated in Group F since this was the only group with
212 data across at least three consecutive years. To be included in the analysis for the top
213 three stable partners (ii) or top 50% of partners (iii) a female must have had at least 3 or 2
214 partners respectively.

215

216 *Structural connectedness*

217 We quantified structural connectedness using social network metrics of indirect connectedness. A
218 social network integrates individual social interactions into a representation of the social structure of
219 the population [5]. An individual's position within the social structure of the whole group can then be
220 quantified. We used three social network metrics that are among the most commonly used and have
221 been previously correlated with fitness in social species: betweenness, closeness and eigenvector
222 centrality (table S1). Betweenness is the number of shortest paths between all pairs of individuals that
223 pass through a particular individual [5]. Individuals with a high betweenness connect subgroups
224 within a population and can influence the transfer of items, e.g., information, through a network [43].
225 Closeness is the inverse of the average number of paths from a given individual to all others in a
226 network [5]. An individual with high closeness can be connected to all others in a short number of
227 steps and can, for example, disseminate a new piece of information throughout the network quickly.
228 Eigenvector centrality is a measure of the quality of an individual's partners. Individuals with high
229 eigenvector centrality have partners who themselves are well-connected [44]. All network metrics
230 were calculated as their weighted version, where the weight of a social connection was the DSI. As
231 DSI is a relative measure, weights are comparable between years and groups. Individuals without any
232 social partners ($n = 4$) could not be included in this analysis.

233

234 *Direct connectedness*

235 To test whether specific types of interactions, and in particular the amount of grooming individuals
236 received from others, predicted survival, we re-calculated DSI values to include only one type of
237 interaction, resulting in a 'grooming sociality index' and a 'proximity sociality index'. An
238 individual's grooming-CSI and proximity-CSI were calculated by summing the grooming and
239 proximity DSIs for that individual. We also separated grooming based on its direction, and calculated
240 a 'grooming given' index and a 'grooming received' index. We used the ratio of the grooming
241 received index to the grooming given index to isolate the impact of receiving grooming from giving
242 grooming to the greatest extent possible (i.e. separate analyses could result in significant relationships
243 with survival for both the rate of giving and the rate of receiving grooming due to autocorrelation
244 between these terms). Females were only included in this ratio analysis if they were observed both
245 giving and received grooming in a given year.

246

247 *Quantifying mortality*

248 Parentage (maternal from 1956, paternal from 1992) and dates of birth and death (where applicable)
249 are known for all Cayo Santiago animals [27]. Dates of birth and death are typically known to within
250 a few days. For each subject in each year ($n = 754$), we established their age and survival status
251 (number of deaths = 34), which we defined as whether or not they survived through a given year of
252 study.

253

254 Analyses

255 We used extended Cox proportional hazards (Cox PH) models to determine how an individual's
256 instantaneous risk of death varied with their level of social connectedness. An individual's level of
257 social connectedness can vary from year to year - extended Cox PH models allow for the use of these
258 time-dependent covariates [45]. All connectedness measures were normalised to between 0 and 10 by
259 dividing each value by the maximum value for that group and multiplying by ten (the multiplication is
260 to scale hazards to an easily understandable range). The number of mortality events in our data
261 precluded including multiple variables in analyses and the use of model selection. To limit problems
262 with over-parametrisation and autocorrelation of variables (figure S1), we included a single variable
263 per model and compared across models using a concordance analysis. Mortality data is time-linked:
264 individuals in a dataset die in a known order, e.g. individual A died before individual B. Concordance
265 determines the proportion of times that a model correctly predicts the order of death of all pairs of
266 individuals in a dataset [46]. We used concordance as a measure of how well the parameters included
267 in a model reflected real world processes. We also investigated the relationship between survival and:
268 i) group size, ii) dominance rank and iii) hours an individual was observed, each of which is a
269 potentially important correlate of survival in this system [28,30,47], independently of our measures of
270 social connectedness.

271

272 To account for the inherent lack of independence in our relational data we created null models from
273 1000 permutations of individual identity ('node-label permutations': [5,48]). Each permuted dataset
274 had the same structure of social connections as the observed data, but the identities of the animals to
275 which those connections belong were randomised. For each permuted dataset, we derived our
276 measures of social connectedness and ran Cox PH models to establish the relationship between
277 connectedness and survival. P-values were calculated from the number of times the test statistic from
278 our observed data was greater (or less) than the test statistic in the null models [49]. P-values for
279 analyses without social interaction variables (and therefore without relational non-independence), e.g.
280 group size, were taken from the cox model without permutation. To account for multiple comparisons
281 of the same data we adjusted p-values using the Benjamini-Hochberg method [50]. Unadjusted p-
282 values are reported in the supplementary material (table S5).

283

284 Analyses were undertaken in R using the dplyr, stringr, survival, sna, igraph, lme4 and ggplot2
285 packages.

286

287 **Results**

288 Female rhesus macaques had a mean (\pm std. dev.) of 7.96 (\pm 6.26) social connections and a mean CSI
289 (\pm std. dev.) of 47.55 (\pm 43.13). There was a wide distribution of connection strengths. For example, in
290 group F in 2012 the mean DSI was 8.35 (\pm 9.28) but the weakest connection had a DSI of 0.46 and the
291 strongest a DSI of 51.24 (complete distributions shown in figure S2).

292

293 *Social integration and survival*

294 Neither an individual's strength of connections with other adult females nor her number of adult
295 female partners were significant predictors of mortality risk (strength of connections:
296 $\text{Haz.}=0.91\pm 0.08$, $z=-0.93$, $n=754$, $e=34$, $p=0.138$; number of connections: $\text{Haz.}=0.92\pm 0.08$, $z=-0.79$,
297 $n=754$, $e=34$, $p=0.131$; figure 2). However, a female's number of weak connections was a significant
298 predictor of survival for all thresholds where 'weak' connections included more than 20% of
299 connections in the population (figure 2; table S3). Females with a greater number of weak connections
300 typically lived longer than those with fewer weakly connected partners.

301

302 *Dyadic connectedness and survival*

303 A female's number of strong dyadic connections was a significant predictor of survival when the
304 strongest 90% of connections (i.e., almost all connections in the population) were considered 'strong'
305 ($\text{Haz.}=0.91\pm 0.07$, $z=-1.32$, $n=754$, $e=34$, $p=0.008$; figure 2). There was no relationship between a
306 female's number of strong connections and her probability of survival under all other 'strong'
307 connections thresholds (figure 2; table S4).

308

309 There was a significant relationship between the strength of a female's connections to her most
310 frequent partners and her probability of survival. Females with stronger relationships with their top 1-
311 3 partners had a greater probability of survival than those with weaker connections to those top
312 partners (figure 2; table S6). The strength of a female's social connections to her top 4 to 10 partners
313 did not predict survival (figure 2; table S6; table S5). It is important to note that as the number of top
314 partners increases, the proportion of an individual's total CSI that value represents increases, and the
315 strength of connections to top partners begins to approximate total strength of connections (figure S4).

316

317 There was a significant positive relationship between the strength of a female's connections to
318 partners that were stable and her probability of surviving when all stable partners were considered
319 ($\text{Haz.}=0.90\pm 0.09$, $n=469$, $e=24$, $z=-1.17$, $p=0.031$; figure 2). No such relationship was found when
320 stable partners only included a female's top three partners ($\text{Haz.}=0.94\pm 0.08$, $n=467$, $e=24$, $z=-0.75$,
321 $p=0.437$; figure 2) or the strongest 50% of partners ($\text{Haz.}=0.90\pm 0.09$, $n=458$, $e=24$, $z=-1.11$, $p=0.218$;
322 figure 2).

323

324 *Structural connectedness and survival*

325 No measure of structural connectedness was significantly related to mortality risk (betweenness:
326 $\text{Haz.}=0.95\pm 0.08$, $n=750$, $e=33$, $z=-0.64$, $p=0.403$; closeness: $\text{Haz.}=0.82\pm 0.11$, $n=750$, $e=33$, $z=-1.53$,
327 $p=0.260$; eigenvector centrality: $\text{Haz.}=1.0\pm 0.08$, $n=750$, $e=33$, $z=-0.03$, $p=0.276$; figure 2).

328

329 *Direct connectedness and survival*

330 There was no relationship between survival and the amount of time females spent in proximity to
331 others ($\text{Haz.}=0.99\pm 0.07$, $n=754$, $e=34$, $z=-0.86$, $p=0.142$), engaged in grooming ($\text{Haz.}=0.86\pm 0.08$,
332 $n=754$, $e=34$, $z=-1.47$, $p=0.0247$), or the ratio at which females gave and received grooming
333 (received to given, $\text{Haz.}=5.13\pm 4.31$, $n=673$, $e=28$, $z=1.92$, $p=0.414$; given to received,
334 $\text{Haz.}=2.03\pm 2.81$, $n=673$, $e=28$, $z=0.6$, $p=0.121$);).

335

336 *Concordance*

337 There was little variance in the concordance of the models (figure S5), suggesting no model better
338 explained the mortality patterns in the data than any other.

339

340 *Other variables and survival*

341 We found no relationship between group size ($\text{Haz.}=0.84\pm 0.07$, $n=924$, $e=42$, $z=-1.82$, $p=0.695$),
342 dominance rank (high vs low: $\text{Haz.}=0.87\pm 0.42$, $n=871$, $e=34$, $z=-0.26$, $p=0.782$; high vs medium:
343 $\text{Haz.}=1.19\pm 0.56$, $n=871$, $e=34$, $z=0.39$, $p=0.712$) or hours observed ($\text{Haz.}=1.00\pm 0.01$, $n=924$, $e=42$,
344 $z=0.39$, $p=0.149$) and survival. Similarly, group identity did not significantly predict survival (table
345 S6).

346

347

348 **Discussion**

349

350 By quantifying the relationship between survival and four of the most common operational definitions
351 of social connectedness in a single system, this study highlights the fact that being ‘well-connected’ is
352 multi-faceted in nature and provides evidence that some aspects of sociality represent more
353 straightforward routes to biological success than others. In particular, we found support for a
354 relationship between survival and dyadic connectedness: adult female rhesus macaques that
355 frequently interacted with their top partners and that had partners that were stable over time were
356 more likely to survive than females that interacted less often with their preferred and stable partners.
357 However, we found no relationship between a female’s number of strong connections and her
358 probability of survival. For dyadic connections, at least, it appeared as though quality was more
359 important than quantity. We also found some support for a relationship between social integration and
360 survival: females that had a large number of weak connections experienced a lower mortality hazard.
361 Other predictions of the social integration hypothesis were not supported, and there was little
362 evidence that being structurally or directly well-connected resulted in survival benefits.

363

364 Our results add to previous studies linking the quality of dyadic relationships with positive fitness
365 outcomes in social animals (table S1). In this study, rhesus macaque females with the strongest
366 connections to their top partner had an 11% higher probability of survival than females that were less
367 well-connected to their top partner. Repeatedly interacting with the same small number of individuals
368 may facilitate the emergence and maintenance of cooperative relationships, whereby partners
369 exchange behavioural services, such as grooming and coalitionary support, and where the consistency
370 of partner identity may improve coordination of those behaviours and deter cheating [51,52].

371

372 Consistent and frequent partners may also result in benefits related to mutual social tolerance. In
373 despotic, hierarchical, societies, like those of many female Old World primates, tolerated access to
374 necessary resources, including food and space, may be beneficial to individuals [53–55]. Repeated
375 and stable partnerships may initially arise because of shared needs or preferences amongst pairs of
376 individuals. For example, individuals with similar metabolisms, thermoregulatory needs, or
377 preferences for certain foods, may repeatedly find themselves attempting to access the same resource
378 [56,57]. If alliances between pairs of individuals result in tolerance of that pair when accessing a
379 resource, combined with mutualistic joint defence of that resource against competing groupmates,
380 repeated and stable relationships may emerge. This scenario relies on relative stability in resource
381 availability and in individual differences in needs and preferences. Individuals living outside of those
382 conditions may have little need for stable partners, and may therefore exhibit a divergent relationship
383 between dyadic connectedness and fitness [8,9,16]. In these species, a more flexible and generalised

384 strategy of connectedness - via, for example, social integration - may be a better strategy for coping
385 with the challenges of group-living.

386

387 In addition to dyadic connectedness, we found that some aspects of social integration predicted
388 survival in this study; the number of weak connections a female maintained was linked to her
389 mortality hazard. Wide social tolerance derived from these connections may allow a female to feed
390 without disturbance or avoid harassment in a greater number of settings than females with fewer weak
391 connections. Similar to the results presented here, blue monkeys (*Cercopithecus mitis*) survival has
392 been shown to be positively associated with both strong-consistent connections and weak-inconsistent
393 connections [42]. In the current population of rhesus macaques, measures of social integration have
394 been positively linked to reproductive output [36] and proxies of social integration (family size) have
395 been linked to survival [30]. Interestingly, correlations (figure S1) and principal component analysis
396 (figure S6) suggest that dyadic connectedness measures and social integration measures are negatively
397 associated in this population. That is, females with strong dyadic connectedness tend to have weak
398 social integration. Taken together, these results may suggest that both dyadic connectedness and
399 social integration can provide fitness benefits (albeit perhaps of different types) within the same
400 system.

401

402 There was quantitative and qualitative variation in the relationship between survival and a female's
403 number of strong connections, and between survival and number of weak connections depending on
404 the threshold used to define connections as strong or weak. Choice of threshold can therefore have
405 important implications for the conclusions reached by a study, and we suggest that thresholds either
406 be based on features of the data or behaviour of study species. More generally, connectedness is an
407 individual effect. Defining connections as strong or weak at the population-level and then calculating
408 connectedness at the individual-level may not best represent the salient features of the social
409 environment experienced by individuals. This is highlighted by our contrasting results for number of
410 strong connections and strength of connection to top associates (which is a measure defined at the
411 individual-level).

412

413 We found no evidence of a relationship between an individual's position in the broader social network
414 and their probability of surviving. Individuals that are well-connected to their broader social worlds
415 have been suggested to benefit from being among the first to receive useful information when it enters
416 the system. For example, in resident-ecotype killer whales indirect network position predicts male
417 survival, potentially because well-positioned males are more likely to receive information about the
418 presence and location of resources [58]. The rhesus macaques in our study were provisioned at regular
419 intervals and predictable locations and have no predators. The opportunities for individuals to gain
420 survival benefits from social information in this population may therefore be limited,. Although

421 information about the social environment such as mating opportunities, changes in group membership
422 or dominance rank, are likely important for the success of these animals, the benefits of this
423 information might be more tightly born out in terms of reproductive success [36] and less so in terms
424 of survival.

425

426 Measures of direct connectedness were also not important predictors of survival in female rhesus
427 macaques: neither a greater amount of time spent in proximity to others, engaged in grooming, nor the
428 relative amount of grooming received were associated with increased probability of survival. In some
429 primate species grooming rates have been linked to lower parasite loads (e.g. [21]). Our findings
430 suggest that the benefits of sociality are not directly derived from the behaviours involved in sociality,
431 at least in this population. This interpretation aligns with suggestions that relationships are a
432 commodity or resource that are promoted and maintained in some social animals.

433

434 Other social factors not considered in detail here are also likely to influence mortality. Dominance
435 rank has been shown to be an important predictor of fitness and health (e.g. [35]) and a source of
436 variation in social behaviour [59]) in primates, including in rhesus macaques [28,30,60]. Dominance
437 rank did not significantly predict survival when evaluated as a term on its own and it was therefore
438 not included as a main effect in subsequent models. Dominance rank was also not included as an
439 interaction term with social connectedness because of concerns of overfitting. The analyses - in
440 essence - represent the fitness consequences of sociality in females of 'average' rank. Including the
441 interaction between connectedness and rank in future analyses may reveal important subtleties in the
442 relationship between sociality and fitness. It is conceivable, for example, that the importance of social
443 connectedness differs for females of high and low rank. Though it should be noted that including rank
444 has increased the observed benefits of sociality in this study system [30]. Further analyses based on
445 longer observations and increased sample sizes would be needed to reveal how rank, and other
446 behavioural and ecological constraints, influence the relationship between connectedness and
447 longevity.

448

449 Overall, the results presented here demonstrate the value of understanding what exactly is meant by
450 being 'socially well-connected'. Although 'sociality' and 'connectedness' are useful catch-all terms,
451 the methods used to measure them can influence results revealed and the conclusions reached. We
452 have highlighted how different aspects of sociality can result in different biological conclusions.
453 Future work in other species is needed to understand the generality of the conclusions reached here.
454 Testing whether different conceptualizations of being well-connected are related to proxies of fitness
455 other than survival, such as reproductive success, are also required, as are studies investigating how
456 different aspects of connectedness interact in other systems.

457

458 **Ethics**

459 Collection of field data and use of the Cayo Santiago long-term database were approved by the
460 Animal Care and Use Committee of the University of Puerto Rico (A6850108) and by the Ethics
461 Committee for the School of Psychology, University of Exeter.

462

463 **Data accessibility**

464 Anonymised data are included as supplementary material.

465

466 **Competing interests.** We declare we have no competing interests.

467

468 **Authors' contributions**

469 SE and LJNB conceived the study in consultation with NSM. SE performed the analysis in discussion
470 with LJNB on data collected by LJNB and ARL. SE and LJNB drafted the paper with input from
471 NSM and MLP. All authors approved the final version of the manuscript.

472

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488 **References**

489

- 490 1. Silk JB. 2012 The adaptive value of sociality. In *The Evolution of Primate Societies* (eds JC
491 Mitani, J Call, PM Kappeler, RA Palombit, JB Silk), pp. 552–564. London: University of
492 Chicago Press.
- 493 2. Steptoe A, Shankar A, Demakakos P, Wardle J. 2013 Social isolation, loneliness, and all-cause
494 mortality in older men and women. *Proc. Natl. Acad. Sci. U. S. A.* **110**, 5797–801.
- 495 3. Holt-Lunstad J. 2017 The potential public health relevance of social isolation and loneliness:
496 prevalence, epidemiology, and risk factors. *Public Policy Aging Rep.* **27**, 127–130.
- 497 4. Ostner J, Schülke O. 2018 Linking sociality to fitness in primates: a call for mechanisms. *Adv.*
498 *Study Behav.* **50**, 127–175.
- 499 5. Whitehead H. 2008 *Analyzing Animal Soceities: Quantative methods for vertebrate social*
500 *analysis*. Chicago: University of Chicago Press.
- 501 6. Silk JB, Cheney DL, Seyfarth R. 2013 A practical guide to the study of social relationships.
502 *Evol. Anthropol.* **22**, 213–225.
- 503 7. Granovetter M. 1973 The strength of weak ties. *Am. J. Sociol.* **78**, 1360–1380.
- 504 8. Barrett L, Henzi SP, Weingrill T, Lycett JE, Hill RA. 1999 Market forces predict grooming
505 reciprocity in female baboons. *Proc. R. Soc. B Biol. Sci.* **266**, 665.
- 506 9. Henzi SP, Barrett L. 2007 Coexistence in female-bonded primate groups. *Adv. Study Behav.*
507 **37**, 43–81.
- 508 10. Mcfarland R, Fuller A, Hetem RS, Mitchell D, Maloney SK, Henzi SP, Barrett L. 2015 Social
509 integration confers thermal benefits in a gregarious primate. *J. Anim. Ecol.* **84**, 871–878.
- 510 11. Brent LJM, Chang SWC, Gariépy JF, Platt ML. 2014 The neuroethology of friendship. *Ann. N.*
511 *Y. Acad. Sci.* **1316**, 1–17.
- 512 12. Hruschka DJ. 2010 *Friendship: Development, Ecology, and Evolution of a Social*
513 *Relationship*. Univeristy of California Press.
- 514 13. Dunbar RIM, Shultz S. 2010 Bondedness and sociality. *Behaviour* **147**, 775–803.
- 515 14. Croft DP, James R, Thomas POR, Hathaway C, Mawdsley D, Laland KN, Krause J. 2006
516 Social structure and co-operative interactions in a wild population of guppies (*Poecilia*
517 *reticulata*). *Behav. Ecol. Sociobiol.* **59**, 644–650.
- 518 15. Schino G, Aureli F. 2017 Reciprocity in group-living animals: partner control versus partner
519 choice. *Biol. Rev.* **92**, 665–672.
- 520 16. Gilby IC. 2012 Cooperation among non-kin: reciprocity, markets and mutualism. In *The*
521 *Evolution of Primate Societies* (eds JC Mitani, J Call, PM Kappeler, RA Palmobit, JB Silk),
522 pp. 514–530. London: University of Chicago Press.

- 523 17. Aplin LM, Farine DR, Morand-Ferron J, Sheldon BC. 2012 Social networks predict patch
524 discovery in a wild population of songbirds. *Proc. R. Soc. B Biol. Sci.* **279**, 4199–4205.
- 525 18. Ellis S, Franks DW, Robinson EJH. 2017 Ecological consequences of colony structure in
526 dynamic ant nest networks. *Ecol. Evol.* **7**, 1170–1180.
- 527 19. Heathcote RJP, Darden SK, Franks DW, Ramnarine IW, Croft DP. 2017 Fear of predation
528 drives stable and differentiated social relationships in guppies. *Sci. Rep.* **7**, 1–10.
- 529 20. Cook Z, Franks DW, Robinson EJH. 2013 Exploration versus exploitation in polydomous ant
530 colonies. *J. Theor. Biol.* **323**, 49–56.
- 531 21. Akinyi MY, Tung J, Jeneby M, Patel NB, Altmann J, Alberts SC. 2013 Role of grooming in
532 reducing tick load in wild baboons (*Papio cynocephalus*). *Anim. Behav.* **85**, 559–568.
- 533 22. Godfrey SS. 2013 Networks and the ecology of parasite transmission: A framework for
534 wildlife parasitology. *Int. J. Parasitol. Parasites Wildl.* **2**, 235–245.
- 535 23. Krause J, Ruxton GD. 2002 *Living in Groups*. Oxford: Oxford University Press.
- 536 24. Balasubramaniam KN, Beisner BA, Hubbard JA, Vandeleest JJ, Atwill ER, McCowan B.
537 2019 Affiliation and disease risk: social networks mediate gut microbial transmission among
538 rhesus macaques. *Anim. Behav.* **151**, 131–143.
- 539 25. Cameron EZ, Setsaas TH, Linklater WL. 2009 Social bonds between unrelated females
540 increase reproductive success in feral horses. *Proc. Natl. Acad. Sci.* **106**, 13850–13853.
- 541 26. Clutton- Brock TH. 1988 *Reproductive success: studies of individual variation in contrasting*
542 *breeding systems*. Chicago: University of California Press.
- 543 27. Rawlings R, Kessler M. 1986 *The Cayo Santiago Macaques: History, Behaviour and Biology*.
544 New York: State University of New York Press.
- 545 28. Blomquist GE, Sade DS, Berard JD. 2011 Rank-related fitness differences and their
546 demographic pathways in semi-free-ranging rhesus macaques (*Macaca mulatta*). *Int. J.*
547 *Primatol.* **32**, 193–208.
- 548 29. Widdig A *et al.* 2016 Genetic studies on the Cayo Santiago rhesus macaques: A review of 40
549 years of research. *Am. J. Primatol.* **78**, 44–62.
- 550 30. Brent LNJ, Ruiz-Lambides A, Platt ML. 2017 Family network size and survival across the
551 lifespan of female macaques. *Proc. R. Soc. B* **284**.
- 552 31. Altmann J. 1974 Observational study of behavior: sampling methods. *Behaviour* **49**, 227–267.
- 553 32. Brent LNJ. 2010 The causes and consequences of sociality in adult female rhesus macaques
554 using a social network approach. University of Roehampton, London, UK.
- 555 33. Silk JB, Alberts SC, Altmann J. 2003 Social bonds of female baboons enhance infant survival.
556 *Science.* **302**, 1231–1235.
- 557 34. Silk JB, Altmann J, Alberts SC. 2006 Social relationships among adult female baboons (*Papio*

- 558 *cynocephalus*) I. Variation in the strength of social bonds. *Behav. Ecol. Sociobiol.* **61**, 183–
559 195.
- 560 35. Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM,
561 Seyfarth RM, Cheney DL. 2010 Strong and consistent social bonds enhance the longevity of
562 female baboons. *Curr. Biol.* **20**, 1359–1361.
- 563 36. Brent L J N, Heilbronner SR, Horvath JE, Gonzalez-Martinez J, Ruiz-Lambides A, Robinson
564 AG, Pate Skene JH, Platt ML. 2013 Genetic origins of social networks in rhesus macaques.
565 *Sci. Rep.* **3**, 1–8.
- 566 37. McFarland R, Murphy D, Lusseau D, Henzi SP, Parker JL, Pollet T V., Barrett L. 2017 The
567 ‘strength of weak ties’ among female baboons: fitness-related benefits of social bonds. *Anim.*
568 *Behav.* **126**, 101–106.
- 569 38. Archie EA, Tung J, Clark M, Altmann J, Alberts SC. 2014 Social affiliation matters : both
570 same-sex and opposite-sex relationships predict survival in wild female baboons. *Proc. R. Soc.*
571 *B* **281**, 20141261.
- 572 39. Silk JB, Seyfarth RM, Cheney DL. 2018 Quality versus quantity: do weak bonds enhance the
573 fitness of female baboons? *Anim. Behav.* **140**, 207–211.
- 574 40. Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM,
575 Seyfarth RM, Cheney DL. 2009 The benefits of social capital: close social bonds among
576 female baboons enhance offspring survival. *Proc. R. Soc. B Biol. Sci.* **276**, 3099–3104.
- 577 41. Silk JB, Alberts SC, Altmann J. 2006 Social relationships among adult female baboons (*Papio*
578 *cynocephalus*) II . Variation in the quality and stability of social bonds. *Behav. Ecol. Sociobiol.*
579 **61**, 197–204.
- 580 42. Thompson NA, Cords M. 2018 Stronger social bonds do not always predict greater longevity
581 in a gregarious primate. *Ecol. Evol.* , 1–11.
- 582 43. Freeman L. 1977 A set of measures of centrality based on betweenness. *Sociometry* **40**, 35–41.
- 583 44. Wasserman S, Faust K. 1994 *Social Network Analysis: Methods and Applications*. Cambridge:
584 Cambridge University Press.
- 585 45. Kleinbaum DG, Klein M. 2013 *Survival Analysis: a self learning text*. Third Edit. Springer.
- 586 46. Newson RB. 2010 Comparing the predictive powers of survival models using Harrell’s C or
587 Somers’ D. *Stata J.* **10**, 339–358.
- 588 47. Silk JB. 2007 The adaptive value of sociality in mammalian groups. *Philos. Trans. R. Soc. B*
589 *Biol. Sci.* **362**, 539–559.
- 590 48. Farine DR, Whitehead H. 2015 Constructing, conducting and interpreting animal social
591 network analysis. *J. Anim. Ecol.* **84**, 1144–1163.
- 592 49. Ruxton GD, Neuhäuser M. 2013 Improving the reporting of P-values generated by

- 593 randomization methods. *Methods Ecol. Evol.* **4**, 1033–1036.
- 594 50. Benjamini Y, Hochbery Y. 1995 Controlling the false discovery rate: a practical and powerful
595 approach to multiple testing. *J. R. Stat. Soc.* **57**, 289–300.
- 596 51. Seyfarth RM. 1977 A model of social grooming among adult female monkeys. *J. Theor. Biol.*
597 **65**, 671–698.
- 598 52. Cheney DL, Moscovice LR, Heesen M, Mundry R, Seyfarth RM. 2010 Contingent
599 cooperation between wild female baboons. *Proc. Natl. Acad. Sci. U. S. A.* **107**, 9562–9566.
- 600 53. Mayagoitia LM, Santillan-Doherty AM, Lopez-Vergara L, Mondragon-Ceballos R. 1993
601 Affiliation tactics prior to a period of competition in captive groups of stumptail macaques.
602 *Ethol. Ecol. Evol.* **5**, 435–446.
- 603 54. de Waal FBM. 1997 The chimpanzee's service economy: food for grooming. *Evol. Hum.*
604 *Behav.* **18**, 375–386.
- 605 55. Ventura R, Majolo B, Koyama N, Hardie S, Schino G. 2006 Reciprocation and interchange in
606 wild Japanese macaques: grooming, cofeeding and agonistic support. *Am. J. Primatol.* **68**,
607 1138–1149.
- 608 56. McPherson M, Smith-Lovin L, Cook JM. 2002 Birds of a feather: homophily in social
609 networks. *Annu. Rev. Sociol.* **27**, 415–444.
- 610 57. Christakis NA, Fowler JH. 2007 The spread of obesity in a large social network over 32 Years.
611 *N. Engl. J. Med.* **357**, 370–379.
- 612 58. Ellis S, Franks DW, Natrass S, Cant MA, Weiss MN, Giles D, Balcomb KC, Croft DP. 2017
613 Mortality risk and social network position in resident killer whales: sex differences and the
614 importance of resource abundance. *Proc. R. Soc. B* **284**, 20171313.
- 615 59. Schülke O, Ostner J. 2012 Ecological and social influences of sociality. In *The Evolution of*
616 *Primate Societies* (eds JC Mitani, J Call, PM Kappeler, RA Palmobit, JB Silk), pp. 195–219.
617 London: University of Chicago Press.
- 618 60. Vandeleest JJ, Beisner BA, Hannibal DL, Nathman AC, Capitanio JP, Hsieh F, Atwill ER,
619 McCowan B. 2016 Decoupling social status and status certainty effects on health in macaques:
620 A network approach. *PeerJ* **2016**, 1–25.

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622

623 Figure 1. Hypothetical network demonstrating how the same social connections were deconstructed in
624 this study. Nodes represent individuals and lines between nodes represent a social connection. The
625 width of lines increases as the strength of the connection between a pair of nodes increases. The large
626 central node shows a focal individual but analyses were conducted using all individuals
627 simultaneously. Solid lines show connections used to calculate a given measure of connectedness,
628 dashed lines show connections not relevant to a given measure. Blue nodes represent measures of
629 social integration: where we expect fitness benefits to be greatest for individuals spending more time
630 socialising or with more social partners or with many social connections. Green nodes are measures
631 of dyadic connectedness: with highest fitness predicted for females with many strong connections or
632 strong connections to their most important and consistent partners. Yellow nodes show measures of
633 structural connectedness where individuals with higher indirect connectedness are predicted to have
634 higher fitness. Pink nodes are measures of direct connectedness: female's receiving more grooming or
635 in proximity to others more often are predicted to have higher fitness. Social interactions in the
636 context of this paper include grooming and spatial proximity represented as a dyadic sociality index,
637 which differs from the direct connectedness measures (red nodes) where social interactions are
638 derived separately for proximity and grooming.
639

640 Figure 2. The relationships between different measures of social connectedness and mortality
641 hazard (Hazard \pm Std. Err.) of adult female rhesus macaques. The first 3 columns (from left)
642 show the mortality hazard under each measure of connectedness used in this study. Hazards
643 of 1 indicate no change in survival in relation to social connectedness, while hazards less than
644 1 indicate models where mortality decreases (and the probability of survival increases) as
645 social connectedness increases. Solid error bars indicate measures that significantly predicted
646 survival. Dashed error bars indicate measures did not significantly predict survival. Colours
647 indicate the type of connectedness measure: blue are *social integration*, green are *dyadic*
648 *connectedness*, yellow are *structural connectedness* and pink are *direct connectedness*. For
649 ‘strong connections’ and ‘weak connections’, *x* axis labels indicate the proportion of
650 connections in the population considered ‘strong’ or ‘weak’. In ‘top partners’, *x* axis labels
651 indicate the number of partners considered to be ‘top’. In ‘stable partners’ *x* axis labels
652 indicate the definition of stability used: *I* is any partner, *II* is a top 3 partners and *III* is a top-
653 50% of all partners. In contrast to the other measures, ratio of grooming given to grooming
654 received does not show the changing mortality hazard as ‘connectedness’ increases, it instead
655 represents a ratio. The *y*-axis in this plot is expanded to accommodate its divergent scale.
656 ‘Survival examples’ (furtherest right column) show an example of the relationship between
657 age and survival probability for one of the measures used under each type of connectedness
658 measure. Curves show the predicted survival probability for individuals with low (lighter
659 colour; 10th quartile of observed values) and high (darker colour; 90th quartile of observed
660 values) connectedness.
661