

## **Re-evaluating the relationship between female social bonds and infant survival in wild baboons**

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## 1 **ABSTRACT**

2 Over the past few decades studies have provided strong evidence that the robust links between the  
3 social environment, health, and survival found in humans also extend to non-human social animals.  
4 A number of these studies emphasize the early life origins of these effects. For example, in several  
5 social mammals, more socially engaged mothers have infants with higher rates of survival  
6 compared to less socially engaged mothers, suggesting that positive maternal social relationships  
7 causally improve offspring survival. Here we show that the relationship between infant survival  
8 and maternal sociality is confounded by previously underappreciated variation in female social  
9 behavior linked to changes in reproductive state and the presence of a live infant. Using data from  
10 a population of wild baboons living in the Amboseli basin of Kenya – a population where high  
11 levels of maternal sociality have previously been linked to improved infant survival – we find that  
12 infant- and reproductive state-dependent changes in female social behavior drive a statistically  
13 significant relationship between maternal sociality and infant survival. After accounting for these  
14 state-dependent changes in social behavior, maternal sociality is no longer positively associated  
15 with infant survival in this population. Our results emphasize the importance of considering  
16 multiple explanatory pathways—including third-variable effects—when studying the social  
17 determinants of health in natural populations.

18

## 19 **INTRODUCTION**

20 In social species, social interactions play a major role in determining an animal's access to  
21 resources (Wenzel & Pickering, 1991; Ranta et al., 1993; Wright et al., 2001; Silk, 2007), exposure  
22 to pathogens (Kappeler et al., 2015), protection against predators (Sterck et al., 1997; Wright et  
23 al., 2001; Krause & Ruxton, 2002; Silk, 2007), and adoption of novel behaviors (Burkart, 2017).  
24 Consistent with this idea, the social environment has been linked to health and survival outcomes  
25 in a wide variety of social mammals, including humans (Silk et al., 2010; Archie et al., 2014; Brent  
26 et al., 2017; Ellis et al., 2019; Campos et al., 2020; Snyder-Mackler et al., 2020). For the dependent  
27 young of many species, the social environment is primarily determined by the social bonds of their  
28 mothers. For this reason, maternal social traits have been proposed to influence offspring survival,  
29 with evidence supporting this link presented in non-human primates (Silk et al., 2003a; Silk et al.,  
30 2009; Kalbitzer et al., 2017; McFarland et al., 2017; Schneider-Crease et al., 2022; Blersch et al.,

31 2023), dolphins (Frère et al., 2010), sheep (Vander Wal et al., 2015), and horses (Cameron et al.,  
32 2009).

33

34 Because of their long period of maternal dependence and close evolutionary relationship to  
35 humans, non-human primates have been a particular focus of studies linking maternal sociality to  
36 offspring survival. In the Amboseli baboon population of southern Kenya (an admixed population  
37 of yellow, *Papio cynocephalus*, and anubis, *P. anubis*, baboons) females that have the strongest  
38 social bonds show the highest relative infant survival over their lifetime (Silk et al., 2003a). In a  
39 long-term study of chacma baboons in Botswana (*P. ursinus*), offspring of females with stronger  
40 social bonds also live significantly longer lives (Silk et al., 2009). Similarly, in the De Hoop  
41 chacma baboons of South Africa, baboon infants whose mothers have many weak social bonds are  
42 also more likely to survive the first 12-months of life than infants whose mothers have fewer weak  
43 social bonds (McFarland et al., 2017) and evidence in vervet monkeys (*Chlorocebus pygerythrus*)  
44 suggests infant survival increases with the number of maternal spatial partners (Blersch et al.,  
45 2023). These studies suggest a positive role of maternal sociality in bolstering offspring survival.  
46 However, Schneider-Crease et al. (2022) recently revealed no significant relationship between  
47 maternal sociality and offspring survival in kinda baboons (*P. kindae*) and in white-faced  
48 capuchins (*Cebus imitator*), the offspring of highly social females exhibit higher survivorship than  
49 those of less social females during socially stable periods, but lower survivorship during the less  
50 stable periods surrounding alpha male turnover (Kalbitzer et al., 2017). Therefore, associations  
51 between maternal sociality and offspring survival within primates appear to vary as a function of  
52 species, population, and/or prevailing demographic conditions.

53

54 Notably, all analyses of the relationship between maternal social behavior and infant survival  
55 face a key challenge: the amount of time a mother has a living infant may itself drive patterns of  
56 female sociality. For example, in a number of primate species, conspecific adult females are  
57 attracted to young infants (Seyfarth, 1976; Altmann, 1980; Small, 1982; Silk et al., 2003b; Tiddi  
58 et al., 2010; Dunayer & Berman, 2018). This effect could cause mothers with surviving infants to  
59 appear more social than mothers whose infants die, simply because they have a socially attractive  
60 infant for a longer time period (Barrett et al., 2007). Under this scenario, infant survival drives  
61 estimates of female sociality, instead of female sociality driving infant survival, providing an

62 explanation that is plausible regardless of whether maternal sociality is measured over the lifetime  
63 (e.g., Silk et al., 2003a) or over fixed yearly intervals (e.g., Kalbitzer et al., 2017, Silk et al., 2009;  
64 McFarland et al., 2017; Schneider-Crease et al., 2022). Similarly, the relationships females have  
65 with males may depend on patterns in infant survival. In many primates the death of an infant is  
66 followed by the rapid resumption of sexual cycling (the state during which grooming and  
67 proximity to males peak) and males may also be socially attracted to young neonates (e.g., Nguyen  
68 et al., 2009; Baniel et al., 2016). Some approaches to avoiding infant-dependent variation in female  
69 social relationships in such analyses include discarding maternal social interactions that occur  
70 when infants are very young (e.g., less than 100 days: Silk et al., 2009) or measuring maternal  
71 sociality before an infant is born (Blersch et al., 2023). However, these approach have limitations.  
72 The first approach does not eliminate infant-dependent variation in maternal sociality that occurs  
73 after the discarded time window (e.g., cycling resumption following an infant's death). Moreover,  
74 both approaches by design eliminate the social interactions that are likely to be the most  
75 consequential for infant survival, possibly obscuring the true causal effects of maternal social  
76 relationships on offspring survival.

77

78 Here, we directly address the potential influence of infant-driven variation in maternal  
79 social behavior by measuring and adjusting for the magnitude of this potential confound in a study  
80 of the baboons living in the Amboseli basin of southern Kenya – a population where higher levels  
81 of maternal lifetime sociality have previously been linked to improved infant survival (Silk et al.,  
82 2003a). We use a previously established measure of maternal social behavior (maternal social  
83 connectedness, or SCI; Archie et al., 2014, see Methods) to demonstrate that a female's social  
84 interactions with both adult females and adult males are strongly dependent upon her reproductive  
85 state along with the age and survival status of any current infant. Next, we demonstrate how the  
86 relationships between a female's reproductive state, infant age/presence, and her rates of social  
87 interactions produce statistically significant associations between maternal SCI and infant survival  
88 that can change in both direction and magnitude depending upon the time interval over which SCI  
89 is measured. After accounting for infant- and reproductive state-driven variation in maternal  
90 sociality, we find no compelling evidence that sociality positively predicts infant survival in the  
91 present analysis. Finally, we demonstrate that the same confounds attenuate the original effect

92 reported in Silk et al. (2003a) and present some post-hoc analyses assessing the eco-evolutionary  
93 consequences of a trade-off between maternal sociality's effect on adult versus offspring survival.

94

95

## 96 **RESULTS**

### 97 **MATERNAL SOCIAL BEHAVIOR STRONGLY DEPENDS ON REPRODUCTIVE STATE**

#### 98 **AND INFANT PRESENCE**

99 Social connectedness of adult female baboons to other females (SCI-F, a non-dyadic measure of  
100 the quantity/overall rate of grooming, the primary affiliative social behavior in baboons) tends to  
101 peak for mothers with infants in the first one to six months of life (Fig. 1A; Table S1). This pattern  
102 is consistent with the idea that having a young living infant increases a mother's social interactions  
103 with females e.g., by attracting other females to groom with her. Females do not experience this  
104 peak in grooming interactions if their infants die in the first year of life (Fig. S1A).

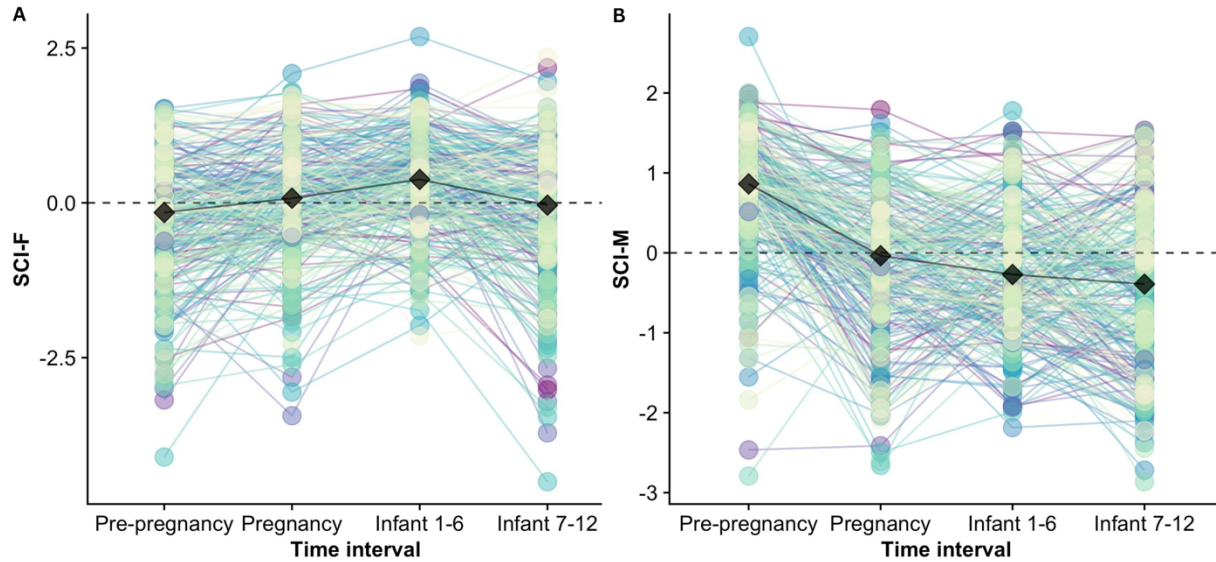
105

106 Social connectedness to males (SCI-M) peaks during the pre-pregnancy period when  
107 females are cycling, and steadily declines from pregnancy through the first year of a surviving  
108 infant's life (Fig. 1B; Table S2). If an infant dies, the mother's connectedness to males returns to  
109 pre-pregnancy levels as she resumes cycling (Fig. S1B).

110

111 Associations between the presence of a live infant, reproductive state, and maternal SCI  
112 could confound an apparent effect of maternal sociality on infant survival. The same concern  
113 affects analyses using alternative measures of social integration such as the dyadic sociality index  
114 (DSI; Silk et al., 2006; Silk et al., 2013) and the composite sociality index (CSI, which combines  
115 data on grooming and proximity to individuals of both sexes; Silk et al., 2003a), which are also  
116 affected by reproductive state and infant presence (albeit less so for CSI; Figs. S2 and S3). These  
117 patterns indicate that the association between infants, reproductive state, and maternal sociality are  
118 not unique to SCI, our specific social measure of interest.

119



120  
121 Figure 1: Comparison of A) social connectedness to females (SCI-F) and B) social connectedness  
122 to males (SCI-M) for mothers with infants who survived to one year across four six-month time  
123 intervals (six months prior to pregnancy, pregnancy, one to six months following birth, and seven  
124 to 12 months following birth). Black diamonds show the median for each time interval. Each series  
125 of connected dots represents a single infant ID for 257 unique infant births ( $n=146$  unique mothers)  
126 where behavioral data for the mother was available for all four time intervals and the mother did  
127 not have a young infant (less than six months old) from a previous pregnancy during the pre-  
128 pregnancy period.

129  
130 THE RELATIONSHIP BETWEEN MATERNAL SOCIALITY AND INFANT SURVIVAL  
131 VARIABLES DEPENDING ON WHEN MATERNAL SOCIALITY IS MEASURED

132 After confirming that mothers experience patterns of social behavior that depend on infants and  
133 reproductive state, we investigated the effects of this relationship on the association between  
134 maternal social behavior and infant survival. To do so, we analyzed the link between the  
135 probability of infant mortality within the first year of life and, in separate models, social  
136 connectedness to females (SCI-F) and social connectedness to males (SCI-M) measured during  
137 four different time intervals. These time intervals included (i) the fixed six-month window after an  
138 infant's conception (i.e., the pregnancy period in baboons, where gestation lasts an average of six  
139 months; Altmann et al., 1977), (ii) the fixed six-month window beginning with the infant's live  
140 birth, (iii) the fixed six-month window beginning seven months after an infant's birth, and (iv) a

141 ‘shifting time window’ that represents the six months prior to each infant’s death or – if it survived  
142 – its first birthday. The shifting time window was designed to exclude any maternal social behavior  
143 occurring after (and possibly as a result of) an infant’s death while also capturing key parts of the  
144 infant’s life which were likely critical to its survival. The other time intervals occur over the same  
145 fixed time period relative to birth for all mothers, regardless of infant outcome, and thus more  
146 closely parallel approaches taken in previous studies connecting maternal sociality to infant  
147 survival (e.g. Silk et al., 2009; McFarland et al., 2017; Blersch et al., 2023).

148

149 We used binomial Generalized Linear Models (GLMs) implemented in R to test the  
150 relationship between SCI-F and SCI-M measured over each of the four time intervals and infant  
151 survival, controlling for other variables that could influence infant survival (maternal social rank,  
152 age, parity, group size, and sexual receptivity; see Methods). In these models the outcome was  
153 scored as 1 (if the infant died within one year) or 0 (if the infant survived). The total number of  
154 infants included in these analyses varied between 824 and 923 depending on the time interval of  
155 interest. This variation in sample sizes was a result of gaps in behavioral data for some mothers  
156 during some time intervals when behavioral sampling was constrained (e.g., if groups ranged  
157 outside of the study area or demographic events decreased sampling opportunities; see sample  
158 sizes reported in Tables S3 to S10). In all data sets, approximately 20% of infants died before their  
159 first birthday (range 19 – 24%). For example, in the shifting time window case, 873 infants were  
160 included in the analysis, 203 of whom died before reaching age one.

161

162 The relationship between SCI-F and infant survival varied dramatically in direction and  
163 magnitude depending when SCI-F was measured. SCI-F showed no statistically significant  
164 relationship with infant survival when measured over the pregnancy period (coefficient=-0.125;  
165 odds ratio (OR)=0.882; p=0.109; Fig. 2; Table S3) or seven to 12 months after an infant’s birth  
166 (coef=0.109; OR=1.116; p=0.240; Fig. 2; Table S5). However, when SCI-F was measured over  
167 the fixed six-month window directly following a live birth, SCI-F positively predicted survival:  
168 infants born to mothers with higher SCI-F experienced lower mortality rates compared to infants  
169 born to mothers with a lower SCI-F (coef=-0.208; OR=0.812; p=0.013; Fig. 2; Table S4). In  
170 contrast, when measured over the shifting time window, which excludes all time periods after an  
171 infant’s death, higher SCI-F negatively predicted survival: infants born to mothers with higher

172 SCI-F experienced higher mortality rates compared to infants born to mothers with a lower SCI-F  
173 (coef=0.374; OR=1.454;  $p < 0.001$ ; Fig. 2; Table S6).

174

175 These contrasting results are consistent with what should be expected if adult females'  
176 attraction to infants, and hence their mothers (Fig. 1A) explain observed associations between  
177 infant survival and maternal sociality. Specifically, measuring SCI-F during the fixed six-month  
178 time window after birth means that females whose infants survive the entire six-month period  
179 appear more social than females whose infants die during that period. Using a shifting time  
180 window, however, would cause females whose infants die to appear more social than females  
181 whose infants survive because in cases of infant death the mother's SCI-F tends to be measured  
182 earlier in the infant's life, when infants are most likely to attract social attention.

183

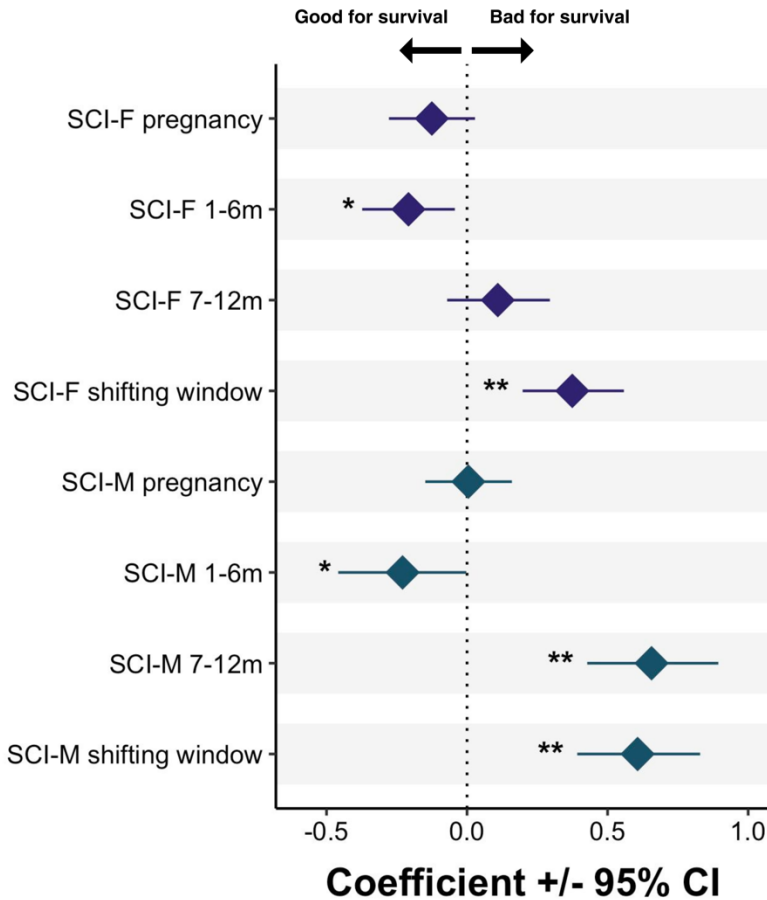
184 Similar to SCI-F, the link between SCI-M and infant mortality depended upon the time  
185 interval over which SCI-M was measured (Fig. 2). Specifically, SCI-M did not predict infant  
186 survival when measured during pregnancy (coef=0.005; OR=1.005;  $p = 0.952$ ; Fig. 2; Table S7).  
187 When measured during the six months following birth, higher SCI-M was associated with  
188 somewhat lower infant mortality (coef=-0.229; OR=0.795;  $p = 0.048$ ; Fig. 2; Table S8). On the  
189 other hand, when measured during the seven to 12 months following birth or using the shifting  
190 time window, higher SCI-M was associated with considerably higher infant mortality (coef=0.656;  
191 OR=1.928;  $p < 0.001$ ; Fig. 2; Table S9 and coef=0.607; OR=1.834;  $p < 0.001$ ; Fig. 2; Table S10,  
192 respectively).

193

194 As with the SCI-F results, results with SCI-M were consistent with the idea that the  
195 reproductive state-dependent nature of female relationships with males affects the apparent  
196 relationship between SCI-M and infant survival. Specifically, high levels of sociality with males  
197 may be negatively associated with infant survival when measured seven to 12 months after birth  
198 because mothers with surviving infants of this age typically have not yet resumed sexual cycling  
199 (Gesquiere et al., 2018) and are less social with adult males than females in any other reproductive  
200 state (Fig. 1B). In contrast, mothers whose infants die resume sexual cycling and return to their  
201 pre-pregnancy levels of social interactions with adult males soon after infant death, resulting in  
202 high levels of social interactions with males seven to 12 months after their (non-surviving) infants'



203 births (Fig. S1B). Similarly, when using the shifting time window, SCI-M for mothers whose  
204 infants survive is measured when those mothers are least likely to be interacting with adult males  
205 (i.e., when their infants are older but the mothers are not yet cycling).  
206



207  
208 **Figure 2:** Infant survival as a function of maternal SCI-F and SCI-M measured over different time  
209 intervals relative to infant birth; a coefficient (i.e., the natural logarithm of the odds ratio) = 0  
210 (shown by vertical dashed line) indicates no effect of the social measure of interest on infant  
211 survival. See Tables S3 to S10 for full model results and sample sizes. + $p \leq 0.1$ ; \*  $p < 0.05$ ; \*\*  $p < 0.01$   
212

213 INFANT-DEPENDENT AND REPRODUCTIVE STATE-DEPENDENT TRENDS IN  
214 MATERNAL SOCIAL BEHAVIOR EXPLAIN THE RELATIONSHIP BETWEEN INFANT  
215 SURVIVAL AND MATERNAL SOCIALITY MEASURED OVER MULTIPLE TIME  
216 INTERVALS

217

218 To determine whether infant-dependent and reproductive state-dependent changes in  
219 female social behavior could completely account for the associations between maternal sociality  
220 and infant survival in our observed data sets, we used a data randomization procedure to force  
221 independence between maternal sociality and infant survival. In this data randomization (hereafter  
222 the ‘Randomization of SCI Values’), maternal SCI-F and SCI-M values were assigned randomly  
223 to the infant outcomes used in our actual analyses, removing any possible influence of maternal  
224 sociality on infant survival. These randomly assigned SCI values were then changed systematically  
225 over time, as a function of time since infant’s birth, depending only on whether and when an infant  
226 died (see further explanation below). If the confounds we described above were sufficient to  
227 account for the observed links between maternal social behavior and infant survival, then the  
228 randomized SCI data should drive effects comparable to those obtained with the observed data.

229  
230 To randomize SCI-F values, we randomly sampled SCI-F trajectories, with replacement,  
231 from the set of trajectories shown in Figure 1A (where infant death never occurred), and matched  
232 them one-by-one to infant-mother pairs in the true data set (randomization procedure visualized in  
233 Fig. S4). For all infants in the true data set we directly substituted the randomly matched SCI-F  
234 value during pregnancy for the real SCI-F value during pregnancy. For cases in the real data set  
235 where the infant survived to 12 months of age, we also directly substituted the randomly matched  
236 SCI-F value in the first six-month interval and the seven to twelve month interval following birth.  
237 For cases in the real data where the infant died, we followed the same procedure as for surviving  
238 infants with one exception: for all months following the infant’s death we assigned the maternal  
239 SCI-F value for pre-pregnancy from the randomly sampled SCI-F trajectory (recall that a female’s  
240 pre-pregnancy SCI-F values closely match her SCI-F values after the loss of her infant, Fig. S1).  
241 We repeated this procedure across all observed infant outcomes 1,000 times, resulting in 1,000  
242 data sets with randomized SCI-F values.

243  
244 We randomized SCI-M values as described above for SCI-F, but with an additional control  
245 for patterns in sexual cycling (since sexual cycling attracts social attention from males; see Fig.  
246 S5) using data from Fig. S6 (randomization procedure visualized in Fig. S7). For all months after  
247 birth where a female had a live infant and had not resumed cycling, we substituted the matching  
248 SCI-M value from the randomly sampled female trajectory (i.e., representing the period when the

249 randomly sampled female's infant was alive and its mother had not yet resumed cycling). For all  
250 months after birth where a female had a live infant and had resumed sexual cycling, we substituted  
251 the SCI-M values from the randomly sampled trajectory during pre-pregnancy. For cases in which  
252 an infant died, we assigned the mother the randomized trajectory SCI-M value in pre-pregnancy,  
253 starting two months after the infant's death and lasting for four months (reflecting rapid resumption  
254 of cycling in baboons after infant death and mean cycling length before the next conception: Zippel  
255 et al., 2017). After four months we assigned the pregnancy SCI-M value from the randomized  
256 trajectory.

257

258 We averaged the randomized monthly SCI values described above to get a mean SCI-F  
259 and SCI-M value for each infant's mother during pregnancy, six months following birth, seven to  
260 12 months following birth, and the shifting time window. We then ran parallel binomial GLMs on  
261 the randomized data sets to estimate the association between SCI measured over each time interval  
262 and infant survival, controlling for the same fixed effects as in analyses with observed data. The  
263 set of infant outcomes for each time interval matched the sample of outcomes for complementary  
264 analyses with real data in Tables S3 to S10.

265

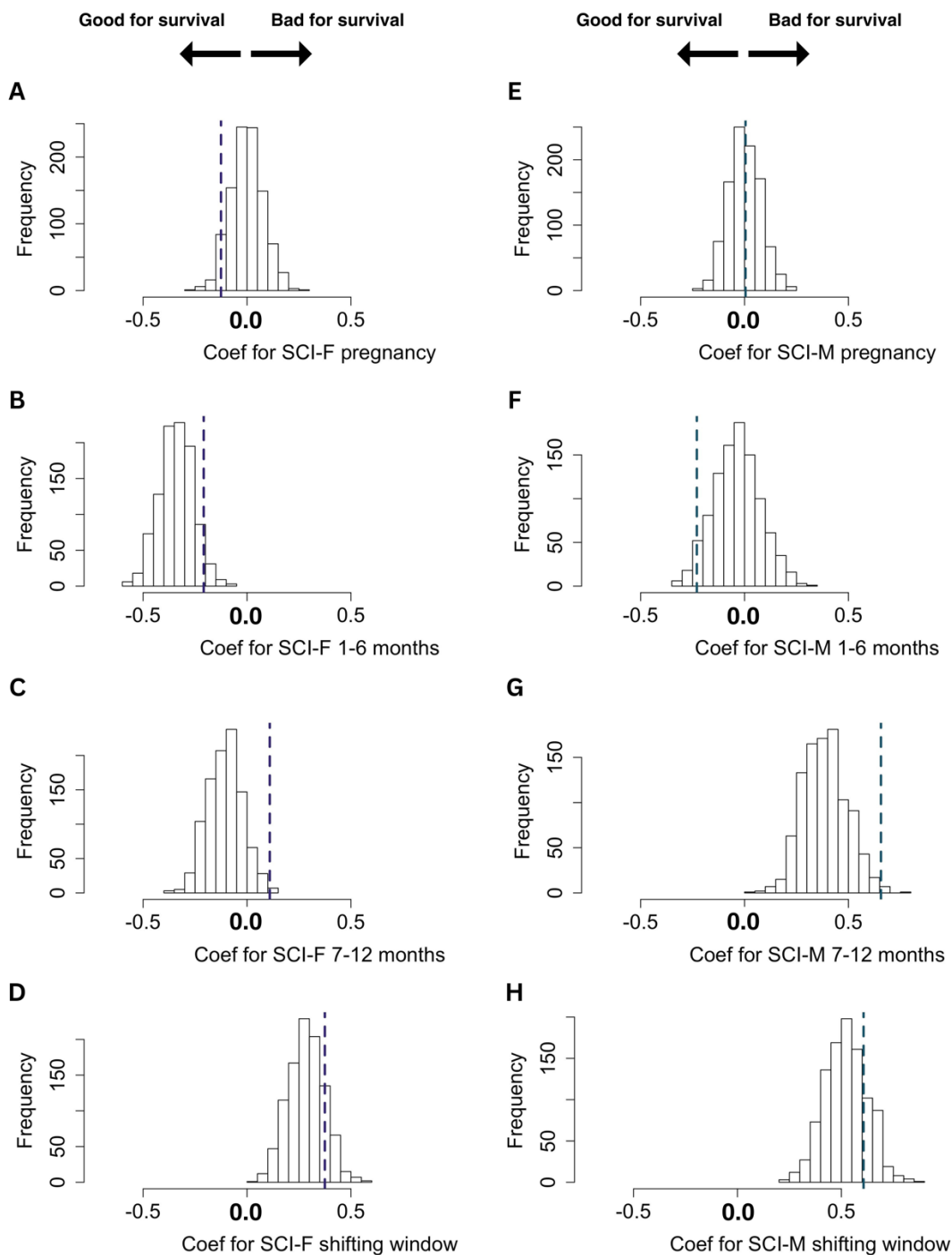
266 After repeating this process across 1,000 randomized data sets, we found that in many cases  
267 the distribution of effect sizes generated from analyses with randomized data did not center on  
268 zero, indicating that infant-dependent and reproductive state-dependent changes in maternal social  
269 behavior indeed present a detectable confound over these time intervals (Fig. 3; Table S11).  
270 Furthermore, for both SCI-F and SCI-M, we found that all of the observed effect sizes fell well  
271 within the distribution of effect sizes generated from randomized data sets, indicating the observed  
272 effect sizes could be entirely explained by infant-dependent and reproductive state-dependent  
273 changes in maternal social behavior (Fig. 3; Table S11). In several cases the observed effects fell  
274 within the tails of the distributions (Fig. 3A, 3B, 3C, 3F, and 3G) making these effects less likely  
275 to be entirely explained by the confound than cases where effects fell within the center of the  
276 distribution. Among cases where the observed coefficients fell within one tail of a distribution,  
277 effects generated from SCI-F and SCI-M measured seven to 12 months after birth were the least  
278 likely to be entirely explained by the confound: less than one percent of coefficients from  
279 randomized data were larger than the observed coefficient (Fig. 3C and 3G; Table S11), in the

280 direction of higher maternal sociality in this time interval being associated with *higher* infant  
281 mortality. Overall, these results suggest that infant-dependent and reproductive state-dependent  
282 patterns in maternal behavior are sufficient to produce non-zero associations between maternal  
283 sociality and infant survival when they are not taken into account, and that any evidence for  
284 maternal sociality having a consistent positive effect on infant survival is weak at best.

285

286 As a complementary test of this hypothesis, we conducted a second data randomization  
287 (hereafter ‘Randomization of Time Intervals’) that was designed to avoid (rather than quantify)  
288 any potential confound. Here, we randomly sampled, with replacement, the age at death for infants  
289 who died within one year, and assigned that age as the last day of the time interval used for SCI  
290 calculation for infants who survived. This approach avoids both the problem of sampling maternal  
291 behavior that occurs after an infant has died and the problem of measuring SCI at later ages for  
292 infants who survive. We then calculated maternal SCI-F and SCI-M over the six months prior to  
293 either the true death date (for dead infants) or the randomly sampled death date (for surviving  
294 infants). We analyzed data from 100 of these randomized data sets each with between 766 and 793  
295 infant outcomes, depending on the number of infants whose mothers had complete behavioral data  
296 available for the sampled six month time interval, using GLMs that paralleled those applied above.  
297 These analyses provided no evidence that SCI-F or SCI-M predict infant survival (mean coef=-  
298 0.025; mean OR=0.975; 0% of p-values < 0.05 and mean coef=-0.029; mean OR=0.971; 0% of p-  
299 values < 0.05, respectively; distribution of coefficients shown in Fig. S8A and S8B).

300



301  
302 Figure 3: Results of the “Randomization of SCI Values” analysis. Histograms show the  
303 distribution of coefficients (i.e., the natural logarithm of the odds ratio) from binomial GLMs using  
304 randomized SCI data; vertical dashed lines show coefficients from GLMs with observed data (see  
305 Fig. 2). Left column shows SCI-F estimated over A) pregnancy, B) the six months following birth,  
306 C) the seven to 12 months following birth, and D) a shifting data window (six months prior to

307 infant death or first birthday depending on survival outcome). Right column shows SCI-M  
308 estimated over E) pregnancy, F) the six months following birth, G) the seven to 12 months  
309 following birth, and H) a shifting data window. Negative coefficients mean high SCI is associated  
310 with low risk of mortality and thus high survival, while positive coefficients mean high SCI is  
311 associated with high risk of mortality and thus low survival. If an observed coefficient (dashed  
312 line) is to the *left* of the distribution of permuted coefficients, then high maternal sociality is  
313 associated with high infant survival after accounting for the confounding effect of infant and  
314 reproductive variation in maternal social behavior. If an observed coefficient is to the *right* of the  
315 distribution, then high maternal sociality is associated with high infant mortality after accounting  
316 for the confound. See Table S11 for median coefficient values and variances associated with  
317 distributions of coefficients from analyses on randomized data sets.

318

319 REPRODUCTIVE STATE AND INFANT-DEPENDENT TRENDS IN MATERNAL SOCIAL  
320 BEHAVIOR EXPLAIN THE EFFECT OF LIFETIME MATERNAL SOCIALITY ON INFANT  
321 SURVIVAL

322 The present analysis was motivated in part by previous results from Silk et al. (2003a), who  
323 showed that more socially integrated mothers experience higher infant survivorship. Silk et al.  
324 (2003a) used the individual mother (i.e., a female's lifetime success at producing surviving infants)  
325 as the unit of analysis while the analyses reported above used the infant as the unit of analysis.  
326 Furthermore, Silk et al. (2003a) used a lifetime estimate of the "composite sociality index" (CSI),  
327 which combines data on female social relationships with both males and females (captured by  
328 grooming and proximity to others during focal points; see Supplementary Methods), as the  
329 measure of maternal sociality. This approach is in contrast to the measures we used above, which  
330 were summarized over short time intervals, sex-specific (SCI-F and SCI-M), and used only  
331 grooming data. These differences could mitigate the influence of the confound described above.  
332 To test this possibility, we recreated the analysis reported in Silk et al. (2003a) using an expanded  
333 data set that included an additional 22 years of behavioral and demographic data that have since  
334 accumulated. A total of 295 adult females were included in our recreation, compared to 108 in Silk  
335 et al. (2003a). See the Supplementary Methods for more details about our recreation.

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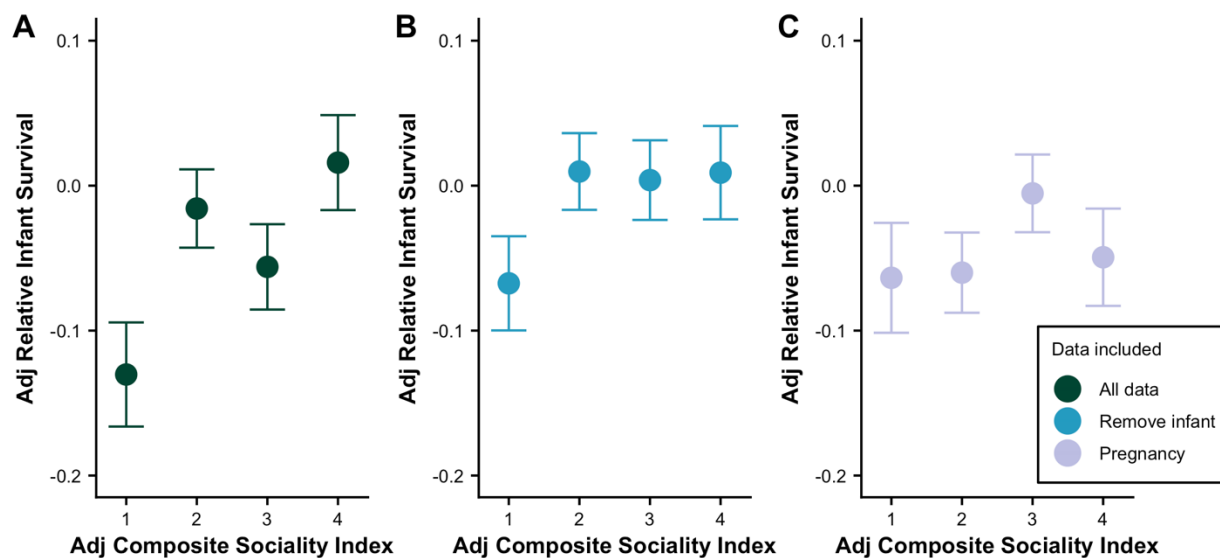
337 We conducted three analyses on the expanded data set. First, following Silk et al. (2003a),  
338 we analyzed the relationship between a mother's lifetime relative infant survival and her lifetime  
339 CSI (an estimate of her tendency to groom with and be in proximity to other adults). In this  
340 analysis, we recovered a similar pattern to the original paper: higher maternal sociality was  
341 associated with higher relative infant survival ( $B=0.095$ ;  $p=0.027$ ) (Fig. 4A), although the effect  
342 size was notably smaller than originally estimated (original paper reports  $B=0.321$ ;  $p=0.015$ ).

343

344 Next, we repeated the analysis twice more, first removing time periods from the CSI  
345 calculation in which mothers had infants less than one year old, and second removing all time  
346 periods except pregnancy (when females typically do not have young infants and all share the same  
347 reproductive state). These two analyses limit the measures of maternal social behavior to periods  
348 when the mother's behavior is least likely to be influenced by the presence of an attractive infant  
349 or by sexual cycling. In neither of these analyses did the relationship between maternal CSI and  
350 offspring mortality reach statistical significance (removing time periods where mothers had infants  
351 less than one year of age:  $B=0.031$ ,  $p=0.268$ ,  $n=256$ , Fig. 4B; restricting the analysis to periods of  
352 pregnancy:  $B=0.025$ ,  $p=0.332$ ,  $n=268$ , Fig. 4C). These results support the idea that the original  
353 result reported in Silk et al. (2003a) is primarily explained by infant-dependent and reproductive  
354 state-dependent trends in maternal social behavior.

355

356



357

358 Figure 4: Recreation of Fig. 1 in Silk et al. (2003a) using an updated data set (1984 – 2022),  
359 showing the relationship between a mother’s lifetime Composite Sociality Index (CSI) score and  
360 relative infant survival. Panels from left to right show estimates: A) including all data from  
361 mothers’ adult lives (green), B) removing periods in the CSI calculation when mothers had a young  
362 infant less than one year old (blue), and C) only including data from periods of pregnancy (purple)  
363 in the CSI calculation.

364

### 365 EFFECTS OF SOCIALITY ON ADULT SURVIVAL OUTWEIGH EFFECTS OF SOCIALITY 366 ON OFFSPRING SURVIVAL

367 Our analysis revealed some limited evidence that mothers who are highly social during certain  
368 periods of their infant’s early life may experience modestly reduced offspring survival (Fig. 3C  
369 and 3G). At the same time, high SCI and DSI scores are associated with higher survival for adult  
370 female baboons themselves (Silk et al., 2010; Archie et al., 2014; Campos et al., 2020; Lange et  
371 al., 2023). If maternal sociality does indeed have conflicting influences on infant and maternal  
372 survival, how is the resulting tradeoff between maternal and infant survival resolved? To probe  
373 this question, we built a simple matrix projection model based on the life cycle of female baboons.  
374 The model’s parameters were chosen to roughly match the life history of our study population,  
375 and infant and adult female survival rates were assumed to be a function of SCI (males were not  
376 explicitly modeled; see Supplementary Methods for details).

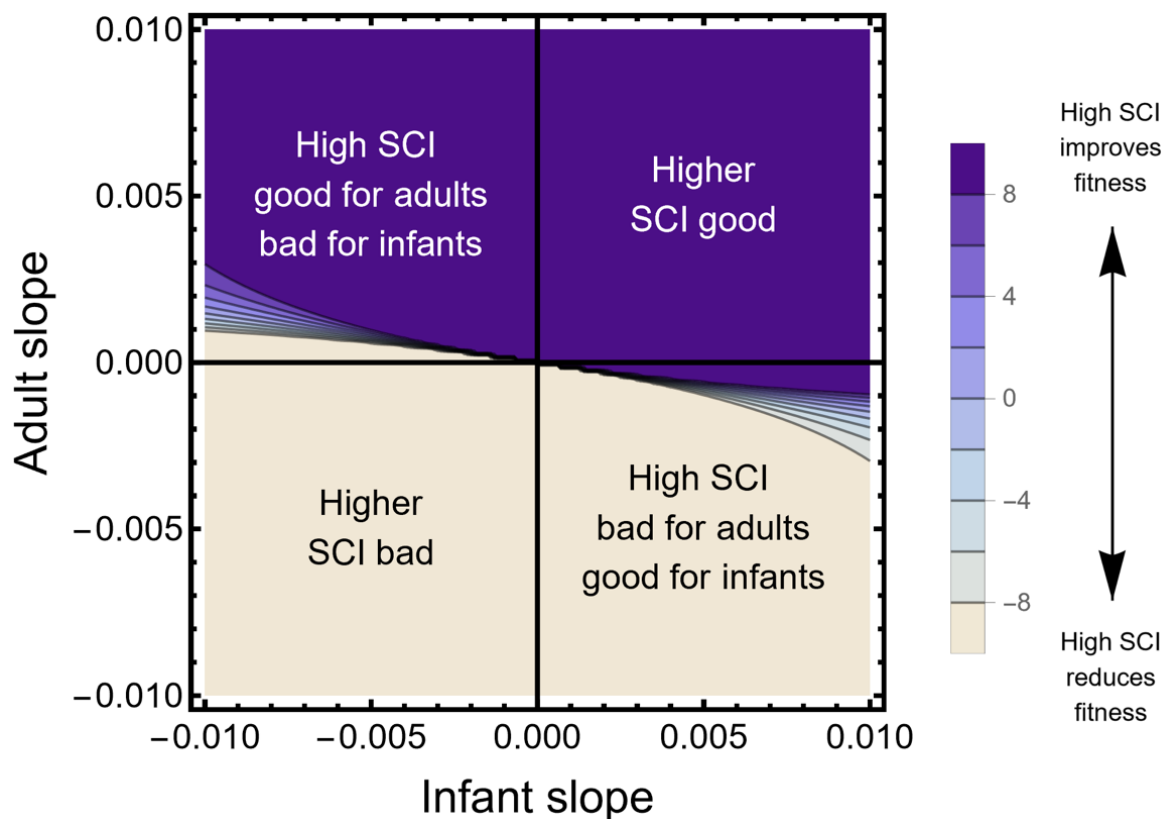
377 Our primary goals were to determine what values of SCI maximize  $\lambda_1$ —the leading  
378 eigenvalue from the transition matrix representing long-term per capita growth rate (the estimate  
379 of female fitness generated by the model; see Supplementary Methods)—and to understand how  
380 the relationship between SCI and  $\lambda_1$  changes depending on how SCI affects infant survival versus  
381 adult survival in our model. If  $\lambda_1$  is greatest when SCI is relatively high, this result would indicate  
382 that high levels of maternal sociality confer net fitness benefits for females. If  $\lambda_1$  is greatest when  
383 SCI is relatively low, this result would indicate that low levels of maternal sociality confer net  
384 fitness benefits (and conversely that high levels of maternal sociality impose net fitness costs).

385 We found that the effect of SCI on overall female fitness ( $\lambda_1$ ) depends almost entirely on  
386 how SCI affects adult female survival, regardless of the outcome for infants (Fig. 5). In Fig. 5,  
387 both of the top quadrants (where SCI is *positively* associated with adult survival) are almost



388 entirely dark in color, indicating that high SCI *improves* fitness ( $\lambda_1$ ) when high SCI is good for  
389 adult survival (positive values on the y-axis), regardless of the effect of SCI on infant survival.  
390 Meanwhile both of the bottom two quadrants (where SCI is *negatively* associated with adult  
391 survival) are almost entirely light in color indicating that high SCI *reduces* fitness ( $\lambda_1$ ) when high  
392 SCI is bad for adult survival (negative values on the y-axis), regardless of the effect of SCI on  
393 infant survival. Notably, exceptions occur where the effects of SCI on adult survival are quite weak  
394 (i.e., the adult slope is close to zero): in these cases the infant slope becomes more influential in  
395 determining how SCI effects female fitness. The fact that SCI mainly influences fitness based upon  
396 its effects on adult survival likely follows from there being more adults in the population than  
397 infants at any given time.

398



399

400 Figure 5: Colored landscape showing the value of SCI that maximizes  $\lambda_1$  (female fitness) in our  
401 matrix projection model. Dark colors correspond to cases where relatively high values of SCI  
402 improve female fitness, while light colors correspond to cases in which high values of SCI reduce  
403 female fitness (see color legend). Axes show the slope of infant survival (x-axis) and adult survival

404 (x-axis) as a function of SCI when SCI = 0 (the population mean). More positive slopes correspond  
405 to a greater beneficial influence of high SCI on survival and more negative slopes correspond to a  
406 greater detrimental influence of high SCI on survival.

407

408

## 409 **DISCUSSION**

### 410 **MATERNAL SOCIALITY AND INFANT SURVIVAL**

411 We found no strong evidence that maternal sociality is causally associated with improved infant  
412 survival in our infant-wise analysis. We instead found that apparent relationships between maternal  
413 sociality and infant survival are more parsimoniously explained by infant-dependent and  
414 reproductive state-dependent trends in a mother's social behavior. As a result, the direction of the  
415 relationship between maternal social behavior and infant survival changes depending on the time  
416 interval maternal sociality is captured over.

417

418 Our results further suggest that infant-dependent and reproductive state-dependent  
419 differences in maternal social behavior can generate a spurious positive relationship between  
420 maternal social relationships and infant survival not only in the first six months of an infant's life,  
421 but even in the seven to 12 months following a birth. Specifically, Fig. 3C and Fig. 3G demonstrate  
422 that the distribution of effect sizes from analyses with randomized SCI-F and SCI-M data do not  
423 center on zero, indicating that removing data for the first 100 days following a birth (as in Silk et  
424 al., 2009) would not be enough to completely eliminate the effect of this confound in our  
425 population. Furthermore, controlling for this confound not only effects conclusions from infant-  
426 wise analyses, but also strongly attenuates the original effect reported in Silk et al. (2003a), which  
427 used the lifetime estimates of maternal sociality and infant survival (Fig. 4). Notably, when tested  
428 separately as predictors of relative infant survival in Silk et al. (2003a), proportion of time being  
429 groomed was the only one of the three social components of CSI that was a significant predictor  
430 of survival on its own (i.e., time spent grooming and spent in proximity to others are not significant  
431 predictors), suggesting that the amount of time mothers spend being groomed by others drives the  
432 relationship between CSI and infant survival. This further supports the idea that infants and certain  
433 reproductive states (e.g., sexual cycling) attracting social attention (expressed as directed  
434 grooming) contribute to the original result.

435

436           After accounting for variation in individual behavior driven by reproductive state and  
437 infants, our analyses with data from the Randomization of SCI Values analysis produced some  
438 limited evidence that more social mothers may experience higher infant mortality (Fig. 3C and  
439 3G). A negative association between infant survival and maternal sociality captured over certain  
440 time periods could have multiple, non-mutually exclusive explanations. High levels of maternal  
441 social interactions could result in increased exposure to pathogens (May, 1983; Nunn, 2012),  
442 increased stress (Pearson et al., 2015), reduced time spent feeding (Altmann, 1980), or increased  
443 vulnerability to fatal kidnappings or infanticide (Kleindorfer & Wasser, 2004; Shopland &  
444 Altmann, 1987; Kalbitzer et al., 2017). Furthermore, a high frequency of social interactions  
445 between mothers and other females can result in rough handling of infants by other females, which  
446 in turn is associated with signs of distress in infants in Amboseli (Nguyen et al., 2009), and with  
447 lower survival in several other nonhuman primate populations (Silk 1980; Kleindorfer & Wasser  
448 2004). On the other hand, maternal sociality may be negatively associated with infant survival if  
449 less healthy mothers or infants attract more social attention, for example, if kin and other close  
450 social partners intensify efforts to help support mothers when risk of offspring mortality appears  
451 heightened. In this case, maternal social bonds would not contribute directly to infant survival, but  
452 rather unhealthy mothers and infants would receive more social attention.

453

454           Notably, a potentially harmful effect of higher maternal sociality on infant survival was  
455 only supported over some time intervals used in our analyses. Analyses from our Randomization  
456 of Time Intervals approach did not support an effect of SCI on infant survival in either direction.  
457 Moreover, when SCI-F was measured over pregnancy and SCI-M was measured over the six  
458 months following a birth, the results of our Randomization of SCI Values were suggestive in the  
459 opposite direction: high SCI may be associated with slightly higher survival (although we could  
460 not rule out that these effects could be explained by a confound; Fig. 3A and 3F). The direction of  
461 these results with SCI-F are consistent with findings in Blersch et al. (2023) who found a positive  
462 relationship between maternal social connectedness and infant survival when measuring social  
463 relationships during pregnancy in an attempt to avoid the confound of infant attractiveness.  
464 Importantly, such a result could also be explained by reverse causality if, for example, mothers  
465 tend to socialize more when they are healthier (and thus more likely to birth a healthy infant).

466 Regardless, given that we show maternal sociality has a neutral and occasionally even negative  
467 relationship with infant survival when quantified over other time periods, this suggests that  
468 mothers being more social does not provide universal fitness benefits for infants overall, at least  
469 in our population.

470

471 Furthermore, according to the results of our matrix projection model, any negative or  
472 positive effects of maternal sociality on infant survival are unlikely to shape maternal social  
473 behavior if maternal social relationships are linked to improved adult female survival. Specifically,  
474 even if maternal sociality directly affects both adult and infant outcomes, the survival benefits or  
475 costs that a mother experiences from being social outweigh the benefits or costs experienced by  
476 her infants. In other words, selection should not act to reduce sociality in baboon females if it  
477 improves their own survival, even if those social relationships pose potential risks to their infants.  
478 Consistent with adult survival having an outsized effect on fitness, findings suggest longevity is  
479 more important than fecundity for lifetime reproductive success in the Amboseli baboons (McLean  
480 et al., 2019).

481

482

### 483 **CONCLUSIONS**

484 We have shown that the manner in which a female baboon's social interactions are affected by her  
485 reproductive state and whether she has a live infant can lead to the erroneous inference that  
486 maternal sociality improves infant survival. Specifically, the manner in which a female's social  
487 behavior changes depending upon her reproductive state and infant status generates a correlation  
488 between maternal sociality and infant survival that varies in both direction and magnitude  
489 depending on when sociality is measured relative to an infant's birth or death (Fig. 3). Correcting  
490 for reproductive state and infant-related variation in maternal sociality can attenuate, eliminate, or  
491 even reverse the direction of maternal sociality-infant survival correlations. We believe that this  
492 confound is the best explanation for previous results reported from our study system, where high  
493 levels of maternal sociality were interpreted as a driver of enhanced infant survival (Silk et al.,  
494 2003a).

495

496 Taken together our results provide no strong support for a positive effect of maternal  
497 sociality on infant survival after accounting for this confound. In fact, the most compelling  
498 evidence for an association between maternal sociality and offspring survival was found in the  
499 seven to twelve months following birth where maternal sociality may be associated with poor  
500 infant survival in the Amboseli baboon population. This evidence that more social mothers may  
501 experience poor infant survival is suggestive rather than definitive: the strength of the relationship  
502 between high maternal sociality and poor infant survival varies across the time periods in which  
503 we measured maternal sociality (Fig. 3). Importantly, female state-dependent patterns of social  
504 interaction occur in other primate species (e.g., Gumert, 2007; Proctor et al., 2011; Tiddi et al.,  
505 2010), suggesting that our findings may generalize to other analyses. Consequently, our results  
506 mandate a closer scrutiny of the causal pathways linking maternal social behavior and infant  
507 survival in other nonhuman primate populations.

508

509

## 510 **METHODS**

511

### 512 ESTIMATING THE RELATIONSHIP BETWEEN INFANT SURVIVAL AND MATERNAL 513 SOCIALITY, MEASURED OVER DIFFERENT TIME INTERVALS

514 *Study system and subjects.* Data for this analysis come from a long-term study of baboons (*Papio*  
515 *cynocephalus* and *P. anubis*) in the Amboseli basin of southern Kenya. This population has been  
516 under continuous observation since 1971 (Alberts & Altmann, 2012). All study subjects in our  
517 data set were live infants born into study groups between July of 1983 (when behavioral data began  
518 being collected systematically and consistently in our population) and December of 2020.

519

520 *Maternal sociality.* We quantified SCI (our measure of maternal sociality) in four six-  
521 month time intervals: (i) pregnancy, (ii) the fixed six-month window after the infant's live birth  
522 (regardless of whether and when the infant died), (iii) the fixed six-month window beginning seven  
523 months after any infant's live birth (regardless of whether and when the infant died), and (iv) a  
524 'shifting time window' that represents the six months prior to each infant's death or – if it survived  
525 – its first birthday. Maternal SCI with females (SCI-F) and with males (SCI-M) were calculated  
526 separately for each time interval using grooming data collected during "representative interaction

527 sampling” (see Supplementary Methods) by averaging the residuals from two linear regressions:  
528 (i) log grooms given by the focal individual to other groupmates, regressed on log observer effort  
529 (i.e., the number of focal follows per adult female in the group divided by the number of days the  
530 female of interest was present in the group; see extended description in Supplementary Methods);  
531 and (ii) log grooms received by the focal individual, regressed on log observer effort (Archie et  
532 al., 2014). These values were z-scored within population and year and used as our final measure  
533 of SCI.

534

535 *Testing the relationship between SCI and infant survival.* We tested whether SCI-F or SCI-  
536 M predicted infant survival in separate models using binomial GLMs implemented with the glm  
537 function from R. Each model included one maternal social measure (SCI-F or SCI-M) measured  
538 over one of four time intervals. The outcome was scored according to whether the infant died (1)  
539 or survived (0). Given that the purpose of our analysis was to interrogate the previously reported  
540 linear effects of maternal sociality on infant survival and that no explicit hypotheses exist to  
541 support a non-linear relationship between sociality and infant survival, we did not explore the  
542 possibility of non-linear relationships in our analyses.

543

544 Several variables are already known or suspected to influence offspring survival in this  
545 population (Silk et al., 2003a; Zippel et al., 2021). To control for the possible influence of these  
546 variables on infant survival, we also measured them over the time intervals of interest and included  
547 them as additional fixed effects in our GLMs. These additional fixed effects were i) the relative  
548 proportion of adult females a given mother outranked in her group, ii) maternal age, (iii) maternal  
549 age squared, (iv) whether the infant of interest was the mother’s first birth (1=true; 0=false), and  
550 (v) group size. In models with SCI-M we also included the absolute proportion of days over the  
551 six-month time interval in which the mother was experiencing menstrual cycling as a fixed effect,  
552 to control for the ephemeral social relationships that arise between adult males and females when  
553 females are sexually cycling (Rowell, 1968; Seyfarth, 1978). In all models, continuous fixed  
554 effects were scaled by subtracting the mean and dividing by the standard deviation to ensure model  
555 convergence. We initially used mixed models including the random effects of maternal identity,  
556 hydrological year, and group identity in addition to fixed effects. However, these variables  
557 explained little to no variance leading to issues of singular fit and thus uninterpretable results.

558 These terms were therefore dropped from all final analyses. Analyses of residuals with DHARMA  
559 (Hartig, 2017) indicated acceptable model fits.

560

#### 561 **DATA AVAILABILITY STATEMENT**

562 Data and code will be made available on Zenodo upon publication.

563

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589 **REFERENCES:**

- 590 Alberts, S. C., & Altmann, J. (2012). The Amboseli Baboon Research Project: 40 years of  
591 continuity and change. In Kappeler, P. M. and Watts, D. P. (Eds.), *Long-term field studies*  
592 *of primates* (pp. 261-287). Springer, Berlin, Heidelberg.
- 593 Altmann, J. (1980). *Baboon mothers and infants*. Harvard University Press, Cambridge.
- 594 Altmann, J., Altmann, S. A., Hausfater, G., & McCuskey, S. A. (1977). Life history of yellow  
595 baboons: physical development, reproductive parameters, and infant mortality. *Primates*,  
596 18, 315-330.
- 597 Archie, E. A., Tung, J., Clark, M., Altmann, J., & Alberts, S. C. (2014). Social affiliation matters:  
598 both same-sex and opposite-sex relationships predict survival in wild female baboons.  
599 *Proceedings of the Royal Society B: Biological Sciences*, 281, 20141261.
- 600 Baniel, A., Cowlshaw, G., & Huchard, E. (2016). Stability and strength of male-female  
601 associations in a promiscuous primate society. *Behavioral Ecology and Sociobiology*, 70,  
602 761-775.
- 603 Barrett, L., Henzi, P., & Rendall, D. (2007). Social brains, simple minds: does social complexity  
604 really require cognitive complexity? *Philosophical Transactions of the Royal Society B:*  
605 *Biological Sciences*, 362, 561-575.
- 606 Blersch, R. A., Bonnell, T. R., Clarke, M., Dostie, M. J., Lucas, M., Jarrett, J., ... & Henzi, S. P.  
607 (2023). Maternal social position and survival to weaning in arid-country vervet monkeys.  
608 *American Journal of Biological Anthropology*, 181, 3-9.
- 609 Brent, L. J., Ruiz-Lambides, A., & Platt, M. L. (2017). Family network size and survival across  
610 the lifespan of female macaques. *Proceedings of the Royal Society B: Biological Sciences*,  
611 284, 20170515.
- 612 Burkart, J. M. (2017). Evolution and consequences of sociality. In Call, J., Burghardt, G. M.,  
613 Pepperberg, I. M., Snowdon, C. T., & Zentall, T. (Eds.), *Oxford Handbook of Comparative*  
614 *Psychology* (pp. 257-271). Oxford University Press, Oxford.



- 615 Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females  
616 increase reproductive success in feral horses. *Proceedings of the National Academy of*  
617 *Sciences*, 106, 13850-13853.
- 618 Campos, F. A., Villavicencio, F., Archie, E. A., Colchero, F., & Alberts, S. C. (2020). Social  
619 bonds, social status and survival in wild baboons: a tale of two sexes. *Philosophical*  
620 *Transactions of the Royal Society B*, 375, 20190621.
- 621 Dunayer, E. S., & Berman, C. M. (2018). Infant handling among primates. *International Journal*  
622 *of Comparative Psychology*, 31.
- 623 Ellis, S., Snyder-Mackler, N., Ruiz-Lambides, A., Platt, M. L., & Brent, L. J. (2019).  
624 Deconstructing sociality: the types of social connections that predict longevity in a group-  
625 living primate. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20191991.
- 626 Frère, C. H., Krützen, M., Mann, J., Connor, R. C., Bejder, L., & Sherwin, W. B. (2010). Social  
627 and genetic interactions drive fitness variation in a free-living dolphin population.  
628 *Proceedings of the National Academy of Sciences*, 107, 19949-19954.
- 629 Gesquiere, L. R., Altmann, J., Archie, E. A., & Alberts, S. C. (2018). Interbirth intervals in wild  
630 baboons: Environmental predictors and hormonal correlates. *American Journal of Physical*  
631 *Anthropology*, 166, 107-126.
- 632 Gumert, M. D. (2007). Grooming and infant handling interchange in *Macaca fascicularis*: the  
633 relationship between infant supply and grooming payment. *International Journal of*  
634 *Primatology*, 28, 1059-1074.
- 635 Hartig, F. (2017). DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression  
636 models. R package version 0.3.0. <https://cran.r-project.org/web/packages/DHARMA>.
- 637 Kalbitzer, U., Bergstrom, M. L., Carnegie, S. D., Wikberg, E. C., Kawamura, S., Campos, F. A.,  
638 ... & Fedigan, L. M. (2017). Female sociality and sexual conflict shape offspring survival  
639 in a Neotropical primate. *Proceedings of the National Academy of Sciences*, 114, 1892-  
640 1897.

- 641 Kappeler, P. M., Cremer, S., & Nunn, C. L. (2015). Sociality and health: impacts of sociality on  
642 disease susceptibility and transmission in animal and human societies. *Philosophical*  
643 *Transactions of the Royal Society B: Biological Sciences*, 370, 20140116.
- 644 Kleindorfer, S., & Wasser, S. K. (2004). Infant handling and mortality in yellow baboons (*Papio*  
645 *cynocephalus*): evidence for female reproductive competition? *Behavioral Ecology and*  
646 *Sociobiology*, 56, 328-337.
- 647 Krause, J., & Ruxton, G. D. (2002). *Living in Groups*. Oxford University Press, Oxford.
- 648 Lange, E. C., Zeng, S., Campos, F. A., Li, F., Tung, J., Archie, E. A., & Alberts, S. C. (2023).  
649 Early life adversity and adult social relationships have independent effects on survival in a  
650 wild primate. *Science Advances*, 9, eade7172.
- 651 May, R. M. (1983). Parasitic infections as regulators of animal populations: the dynamic  
652 relationship between parasites and their host populations offers clues to the etiology and  
653 control of infectious disease. *American Scientist*, 71, 36-45.
- 654 McFarland, R., Murphy, D., Lusseau, D., Henzi, S. P., Parker, J. L., Pollet, T. V., & Barrett, L.  
655 (2017). The ‘strength of weak ties’ among female baboons: fitness-related benefits of social  
656 bonds. *Animal Behaviour*, 126, 101-106.
- 657 McLean, E. M., Archie, E. A., & Alberts, S. C. (2019). Lifetime fitness in wild female baboons:  
658 trade-offs and individual heterogeneity in quality. *The American Naturalist*, 194, 745-759.
- 659 Nguyen, N., Van Horn, R. C., Alberts, S. C., & Altmann, J. (2009). “Friendships” between new  
660 mothers and adult males: adaptive benefits and determinants in wild baboons (*Papio*  
661 *cynocephalus*). *Behavioral Ecology and Sociobiology*, 63, 1331-1344.
- 662 Nunn, C. L. (2012). Primate disease ecology in comparative and theoretical perspective. *American*  
663 *Journal of Primatology*, 74, 497-509.
- 664 Pearson, B. L., Reeder, D. M., & Judge, P. G. (2015). Crowding increases salivary cortisol but not  
665 self-directed behavior in captive baboons. *American Journal of Primatology*, 77, 462-467.

- 666 Proctor, D. P., Lambeth, S. P., Schapiro, S. J., & Brosnan, S. F. (2011). Male chimpanzees'  
667 grooming rates vary by female age, parity, and fertility status. *American Journal of*  
668 *Primatology*, 73, 989-996.
- 669 Ranta, E., Rita, H., & Lindstrom, K. (1993). Competition versus cooperation: success of  
670 individuals foraging alone and in groups. *The American Naturalist*, 142, 42-58.
- 671 Rowell, T. E. (1968). Grooming by adult baboons in relation to reproductive cycles. *Animal*  
672 *Behaviour*, 16, 585-588.
- 673 Schneider-Crease, I. A., Weyher, A. H., Mubemba, B., Kamilar, J. M., Petersdorf, M., & Chiou,  
674 K. L. (2022). Stronger maternal social bonds and higher rank are associated with  
675 accelerated infant maturation in Kinda baboons. *Animal Behaviour*, 189, 47-57.
- 676 Seyfarth, R. M. (1976). Social relationships among adult female baboons. *Animal Behaviour*, 24,  
677 917-938.
- 678 Seyfarth, R. M. (1978). Social relationships among adult male and female baboons. I. Behaviour  
679 during sexual consortship. *Behaviour*, 64, 204-226.
- 680 Shopland, J. M., & Altmann, J. (1987). Fatal intragroup kidnapping in yellow baboons. *American*  
681 *Journal of Primatology*, 13, 61-65.
- 682 Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical*  
683 *Transactions of the Royal Society B*, 362, 539-559.
- 684 Silk, J. B., Alberts, S. C., & Altmann, J. (2003a). Social bonds of female baboons enhance infant  
685 survival. *Science*, 302, 1231-1234.
- 686 Silk, J. B., Altmann, J., & Alberts, S. C. (2006). Social relationships among adult female baboons  
687 (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and*  
688 *Sociobiology*, 61, 183-195.
- 689 Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., ... &  
690 Cheney, D. L. (2009). The benefits of social capital: close social bonds among female  
691 baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological*  
692 *Sciences*, 276, 3099-3104.

- 693 Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., ... &  
694 Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female  
695 baboons. *Current Biology*, 20, 1359-1361.
- 696 Silk, J., Cheney, D., & Seyfarth, R. (2013). A practical guide to the study of social relationships.  
697 *Evolutionary Anthropology: Issues, News, and Reviews*, 22, 213-225.
- 698 Silk, J. B., Rendall, D., Cheney, D. L., & Seyfarth, R. M. (2003b). Natal attraction in adult female  
699 baboons (*Papio cynocephalus ursinus*) in the Moremi Reserve, Botswana. *Ethology*, 109,  
700 627-644.
- 701 Small, M. F. (1982). A comparison of mother and nonmother behaviors during birth season in two  
702 species of captive macaques. *Folia Primatologica*, 38, 99-107.
- 703 Snyder-Mackler, N., Burger, J. R., Gaydosh, L., Belsky, D. W., Noppert, G. A., Campos, F. A., ...  
704 & Tung, J. (2020). Social determinants of health and survival in humans and other animals.  
705 *Science*, 368, eaax9553.
- 706 Sterck, E. H., Watts, D. P., & Van Schaik, C. P. (1997). The evolution of female social  
707 relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, 41, 291-309.
- 708 Tiddi, B., Aureli, F., & Schino, G. (2010). Grooming for infant handling in tufted capuchin  
709 monkeys: a reappraisal of the primate infant market. *Animal Behaviour*, 79, 1115-1123.
- 710 Vander Wal, E., Festa-Bianchet, M., Réale, D., Coltman, D. W., & Pelletier, F. (2015). Sex-based  
711 differences in the adaptive value of social behavior contrasted against morphology and  
712 environment. *Ecology*, 96, 631-641.
- 713 Vilgalys, T. P., Fogel, A. S., Anderson, J. A., Mututua, R. S., Warutere, J. K., Siodi, I. L. I., ... &  
714 Tung, J. (2022). Selection against admixture and gene regulatory divergence in a long-term  
715 primate field study. *Science*, 377, 635-641.
- 716 Wenzel, J. W., & Pickering, J. (1991). Cooperative foraging, productivity, and the central limit  
717 theorem. *Proceedings of the National Academy of Sciences*, 88, 36-38.

- 718 Wright, J., Berg, E., De Kort, S. R., Khazin, V., & Maklakov, A. A. (2001). Safe selfish sentinels  
719 in a cooperative bird. *Journal of Animal Ecology*, 70, 1070-1079.
- 720 Zippel, M. N., Altmann, J., Campos, F. A., Cords, M., Fedigan, L. M., Lawler, R. R., ... & Alberts,  
721 S. C. (2021). Maternal death and offspring fitness in multiple wild primates. *Proceedings*  
722 *of the National Academy of Sciences*, 118, e2015317118.
- 723 Zippel, M. N., Grady, J. H., Gordon, J. B., Chow, L. D., Archie, E. A., Altmann, J., & Alberts, S.  
724 C. (2017). Conditional fetal and infant killing by male baboons. *Proceedings of the Royal*  
725 *Society B: Biological Sciences*, 284, 20162561.