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Stronger maternal social bonds and higher rank are associated with accelerated infant maturation in Kinda baboons --Manuscript Draft--

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Abstract:	<p>Social relationships are critical components of health and fitness for humans and other animals. For female-philopatric species, affiliative relationships among females (kin and non-kin alike) can influence components of fitness that include individual survival, interbirth interval, and offspring survival. Affiliative relationships with males have attracted somewhat less attention, with most studies focusing on female-male relationships as adaptations for infanticide avoidance. Here, we use eight years of behavioral data on Kinda baboons (<i>Papio kindae</i>) to assess whether maternal social relationships—both among females and between females and males—affect infant survival, interbirth interval, and the pace of infant development. Kinda baboons are an ideal system for these analyses because males and females form strong relationships outside of the periovulatory period and in the absence of obvious infanticide threat. We calculated social metrics that reflected dominance status, total social integration, and social bond strength and paired these metrics with data on offspring survival, interbirth interval (IBI) duration, and infant behavioral maturation. Neither dominance rank nor sociality had a significant effect on interbirth interval or survival, but higher rank and stronger affiliative relationships between a female and her top female and top male social partners predicted more rapid infant behavioral maturation. These results suggest that maternal dominance and sociality may confer advantages related to infant development and independence that ultimately may permit females to more quickly invest in subsequent offspring, and point to advantages of relationships with males outside of lowering infanticide threat.</p>

Stronger maternal social relationships and higher rank are associated with accelerated infant maturation in Kinda baboons

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Highlights

- Kinda baboon female–male bonds persist outside of fertility or infanticide threat.
- Kinda social bonds did not affect interbirth interval or infant survival and growth.
- Dominance and affiliative bonds predicted more rapid infant development.
- Top-partner bonds were the strongest predictors of infant development.
- Strong maternal bonds with females and males enhance infant development in Kindas.

1 **Stronger maternal social bonds and higher rank are associated with accelerated infant**
2 **maturation in Kinda baboons**

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20 animals. For female-philopatric species, affiliative relationships among females (kin and non-kin
21 alike) can influence components of fitness that include individual survival, interbirth interval, and
22 offspring survival. Affiliative relationships with males have attracted somewhat less attention, with
23 most studies focusing on female-male relationships as adaptations for infanticide avoidance. Here, we
24 use eight years of behavioral data on Kinda baboons (*Papio kindae*) to assess whether maternal social
25 relationships—both among females and between females and males—affect infant survival, interbirth
26 interval, and the pace of infant development. Kinda baboons are an ideal system for these analyses
27 because males and females form strong relationships outside of the periovulatory period and in the
28 absence of obvious infanticide threat. We calculated social metrics that reflected dominance status,
29 total social integration, and social bond strength and paired these metrics with data on offspring
30 survival, interbirth interval (IBI) duration, and infant behavioral maturation. Neither dominance rank
31 nor sociality had a significant effect on interbirth interval or survival, but higher rank and the stronger
32 affiliative relationships between a female and her top female and top male social partners predicted
33 more rapid infant behavioral maturation. These results suggest that maternal dominance and sociality
34 may confer advantages related to infant development and independence that ultimately may permit
35 females to more quickly invest in subsequent offspring, and point to advantages of relationships with
36 males outside of lowering infanticide threat.

37

38 **Introduction:**

39

40 For group-living animals, relationships with conspecifics constitute a central component of daily
41 existence and can ultimately shape reproductive fitness. Group-living is widespread among vertebrates
42 despite its numerous costs [1], suggesting that the benefits of group-living (e.g., predation avoidance,
43 mate availability) outweigh its costs (e.g., increased competition for food and mates) [2,3]. For the
44 philopatric sex, the establishment of dominance hierarchies through repeated competitive interactions
45 provides structure for navigating the costs of group-living by determining individual access to
46 resources within the group environment. Many social mammals exhibit female philopatry, in which
47 females remain in their natal groups throughout their lives while natal males disperse prior to or upon
48 reproductive maturity [4]. In such species, females thus regularly engage in dyadic interactions with
49 other females, and the outcomes of agonistic encounters within these interactions can be
50 operationalized to describe dominance rank across a population over time [5]. Dominance rank has
51 been linked to increased reproductive fitness in numerous mammals, with females of higher ranks
52 exhibiting, for example, higher fecundity, longer reproductive lifespan, heavier offspring, and
53 increased infant survival [6–11]. High-ranking females are also expected to be in better physiological
54 condition, which may allow them to better nourish and earlier wean their infants relative to lower
55 ranking females [12], and may enable them to regain condition more quickly and thus shorten the
56 duration of sexual cycling before conception. In recent years, interest in the impact of non-agonistic
57 social interactions on fitness has grown [13,14].

58
59 Social relationships in group-living mammals are fundamental to health, with lower social integration
60 or weaker social bonds associated with increased rates of disease and mortality likelihood [15,16].
61 ‘Social relationships’ can be operationalized in a number of ways that each reflect a certain component
62 of the social environment [14]. A metric that tabulates all affiliative interactions with group-mates will
63 reflect overall social integration, for example, while a metric that tabulates affiliative interactions
64 across only top social partners will reflect the strength of the most important social bonds [17–20].
65 These metrics reflect tightly interconnected dimensions of sociality that may each play a distinct role
66 in the lives of individuals in a particular social system. The past two decades have seen increasing
67 interest in understanding the role of social relationships in shaping female fitness across mammals;
68 mounting evidence points to a robust association between social integration or social bond strength
69 and infant survival or birth rates in dolphins [21], feral horses [22], bighorn sheep [23], white-faced
70 capuchins [17], yellow baboons [24], and chacma baboons [20,24,25] and suggests that the adaptive
71 value of sociality enjoys wide taxonomic breadth among social species.

72
73 Much of the growing research on the connection between sociality and fitness has been conducted in
74 primates because of their high level of gregariousness and the existence of long-term field sites that
75 allow for the observation of social behaviors over generations. In cercopithecine primates, affiliative
76 interactions typically include grooming and the maintenance of close spatial proximity [26–33]. For
77 female philopatric primates, relationships with other females constitute the majority of their
78 interactions and have been shown to be important predictors of reproductive success in multiple
79 species. Females with stronger social bonds (i.e., higher composite indices reflecting proportions of

80 spatial proximity, grooming given, and grooming received) have higher survival and infant survival in
81 yellow baboons (*Papio cynocephalus*) and chacma baboons (*P. ursinus*) [20,24,34,35], and female
82 chacma baboons with greater social network connectedness have higher infant survival [36]. Other
83 studies that have examined social bonds (often called ‘primary associations’ or ‘friendships’) between
84 females and males have found certain benefits for females, such as reduced harassment of mother and
85 offspring from other group members [37] and potential infanticide prevention by unrelated males [30].
86 In olive, chacma, and yellow baboons, these female-male primary associations generally begin during
87 gestation and last through lactation, and are positively associated with the likelihood that the male
88 primary associate is the sire of the offspring [38–40]. These relationships are considered to be related
89 to parenting effort, rather than mating effort, as they have been observed to terminate at offspring
90 death [30].

91
92 Here, we assess the impact of maternal social relationships on offspring survival, interbirth interval,
93 and infant behavioral maturation in Kinda baboons (*P. kindae*). Kinda baboons inhabit miombo
94 woodland habitat across Zambia, Angola, the Democratic Republic of Congo, and extreme
95 southwestern Tanzania, and were considered a subspecies of yellow baboons until recently being
96 recognized as a distinct phylogenetic species [41–44]. While Kinda baboons share some
97 characteristics with other baboon species, including large multi-female/multi-male groups and a
98 polygynandrous mating system, they differ significantly in certain morphological and social domains
99 that suggest a role of sexual selection in their evolution that diverges from that of other baboons.
100 Overall, Kinda baboons are smaller, less prognathic, and less sexually dimorphic than other baboon
101 species [41,42,45,46]. Kinda males have larger relative testis size and lower agonism rates than other
102 baboons, and exhibit bottom-entry immigration and succession-based dominance acquisition that
103 altogether suggest stronger indirect than direct male competition [41,47]. In line with this dominance
104 acquisition strategy, infanticide (observed or inferred) and infanticide attempts have never been
105 observed in this species. Kinda females exhibit a higher degree of seasonal breeding than females of
106 other baboon species, exhibit lower agonism and aggression with other females than reported for
107 chacma and yellow baboons (unpublished data; [41], [48], [49]), and maintain affiliative relationships
108 between females and males even outside of the periovulatory window [44] in which most female-male
109 relationships in other baboons are concentrated.

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111 Together with extended affiliative periods and low female-male agonism, the ostensible lack of
112 infanticide threat suggests an unusual—relative to most other baboon species—pattern of social
113 affiliation in Kindas. This pattern raises the question of how relationships with males benefit females
114 and how these benefits might differ from those of social relationships among females. We draw on
115 eight years of data collection on Kinda baboon behavior and sociality in Kasanka National Park,
116 Zambia, to assess potential fitness consequences of this behavioral phenotype in Kinda baboons.
117 Affiliative and agonistic relationships may contribute to overall female reproductive success by
118 ensuring maternal and/or infant access to resources or mitigating threats from conspecifics. If females
119 with higher dominance rank or more robust social relationships with either sex are able to better

120 nourish themselves and/or their offspring or better protect offspring from aggression, these females
121 may be expected to have lower infant mortality, experience a more rapid return to cycling and
122 conception following a birth, and have more rapidly developing offspring. Higher infant survival
123 would increase the number of successful offspring, shorter interbirth intervals would facilitate a
124 greater number of lifetime offspring, and more rapid infant behavioral maturation would permit
125 females to divest earlier from energetic allocation in one offspring towards earlier resumption of
126 cycling with the potential to increase the number of lifetime offspring. Here, we assess the impact of
127 maternal dominance rank, overall social integration, and social bond strength on these three
128 variables—infant survival, interbirth interval, and the pace of infant behavioral maturation. We assess
129 maternal social metrics with other females and with males to evaluate the potential benefits of each
130 type of relationship in Kinda baboons.

131

132 **Methods and Materials**

133

134 All data were collected from Kinda baboons inhabiting Kasanka National Park, Zambia (12° 35' 21"
135 S, 30° 15' 09" E; elevation 1,160m). The Kasanka Baboon Project has collected continuous behavioral
136 and life history data on a single social group of ~75 individuals since 2011. Individuals are
137 individually recognizable by the field team and are followed throughout their time in the study group.
138 All data collection procedures were noninvasive, approved by the Animal Studies Committee of
139 Washington University (assurance #A-3381-01), and adhered to local laws and regulations in Zambia.
140 This research conforms to the International Primatological Society Code of Best Practices for Field
141 Primatology.

142

143 *Behavioral data collection*

144

145 Observational data were collected with 10-minute focal sampling on all adults. For the present study,
146 we focused on grooming and proximity data, which were recorded on 2-minute intervals within the
147 10-minute focal samples. We extracted infant proximity data from maternal focals, in which infant
148 proximity to mother was recorded six times across a focal sample. Infant proximity was recorded as
149 'ventral clinging', 'dorsal clinging', '0-2 meters (from mother)', '2-6 meters', '> 6 meters', or 'out of
150 view' (Table S1). *Ad libitum* data were collected on births, deaths, immigrations, and displacements.
151 Displacements are defined here as instances in which one individual enters within a one-meter radius
152 of another individual, with the latter individual ultimately moving away from the former individual.
153 Because displacements involve non-escalation of a dyadic interaction, they are commonly understood
154 to reflect dominance relationships [50]. In total, we analyzed 10,094 focal data samples (7,193 focals
155 from 38 females; 1,643 focals from 20 males), representing over 1,500 hours of data collection
156 between April 2012 and September 2019. Survival analyses presented here include 29 adult females
157 that gave birth within the study period and 82 infants born to those 29 females, and infant behavioral
158 analyses include data from 21 infants of 14 mothers for which we had sufficient data on infant-mother
159 proximity to evaluate the impact of social metrics on infant behavioral maturation. Specifically, we

160 excluded infants from our analysis if data collection on those infants did not span at least the period
161 from 3 months to 10 months of age. We additionally excluded infants for which at least half of all
162 ‘infant-months’ did not meet a threshold of having 10 or more infant behavioral observations.

163

164 *Dominance rank*

165

166 Social hierarchies are a product of dyadic interactions and are most commonly inferred using the Elo
167 rating system, which constructs relative ranks using the outcomes of dyadic social interactions [50].
168 We inferred dominance hierarchies among adult female baboons using displacement data (described
169 above). We first calculated Elo ratings for females based on female-female displacements using the
170 function `elo.seq` from the package ‘EloRating’ [51] in the statistical platform *R* [52], as well as a
171 presence matrix documenting each female’s tenure in the group. We calculated a stability index to
172 assess rank stability over the entire study period. Because stability scores were > 0.99 , we averaged
173 the Elo ratings of females across the study period to assign each a ‘lifetime’ Elo rating, after excluding
174 the first year of scores to allow for burn-in. Assigning a lifetime Elo rating allowed us to minimize any
175 noise that would be introduced by minor fluctuations that did not produce changes in dominance
176 relationships while retaining the essential information about dominance rank and facilitating the
177 integration of Elo rating in subsequent models.

178

179 *Social phenotype*

180

181 We calculated two related measures of social bond strength for adult females across each year in our
182 analysis. Our first measure—which we refer to as the individual sociality index (ISI)—focused on the
183 strength of a female’s overall social bonds with females (ISI-F) or males (ISI-M) compared to all other
184 females. Our second measure—which we refer to as the top-partner individual sociality index (TSI)—
185 focused on the strength of a female’s strongest social bond with females (TSI-F) or males (TSI-M)
186 compared to the strongest social bonds of all other females. Both measures were based on the
187 composite sociality index of Silk *et al.* [24,34], which combines information from grooming (both
188 given and received) and proximity interactions into a single index of social bond strength that can be
189 summarized at the level of individuals [24,34] or dyads [53]. For both measures, we followed Smuts
190 [27] in summarizing proximity interactions using the composite proximity measure (“C score”), which
191 tabulates time spent between 0-2 meters and time spent between 2-6 meters, with the former given
192 four times the weight of the latter. The C score has the advantage of incorporating more information
193 from more distal proximity interactions while giving higher priority to interactions in closer physical
194 proximity.

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196 To incorporate all available information over a given year, we included grooming and proximity
197 interactions that were recorded as part of either a female’s focal samples or those of her social
198 partners. Thus, to control for differing sampling effort among individuals, we first calculated C scores
199 and grooming scores on a dyadic basis as follows:

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$$C_{ij} = \frac{C_{0-2m} + 0.25(C_{2-6m})}{C_{0-2m} + C_{2-6m}}$$
$$G_{ij} = \frac{G_{i \rightarrow j} + G_{j \rightarrow i}}{G_{i \rightarrow j} + G_{j \rightarrow i}}$$

where C_{ij} and G_{ij} represent the proximity C scores and grooming scores, respectively, for the dyad comprising individuals i and j , p represents the total number of observations of individuals i and j in a given proximity bin (0–2m or 2–6m), g represents the total number of grooming observations in a given direction ($i \rightarrow j$ or $j \rightarrow i$), and T represents the total focal sample observation time for an individual.

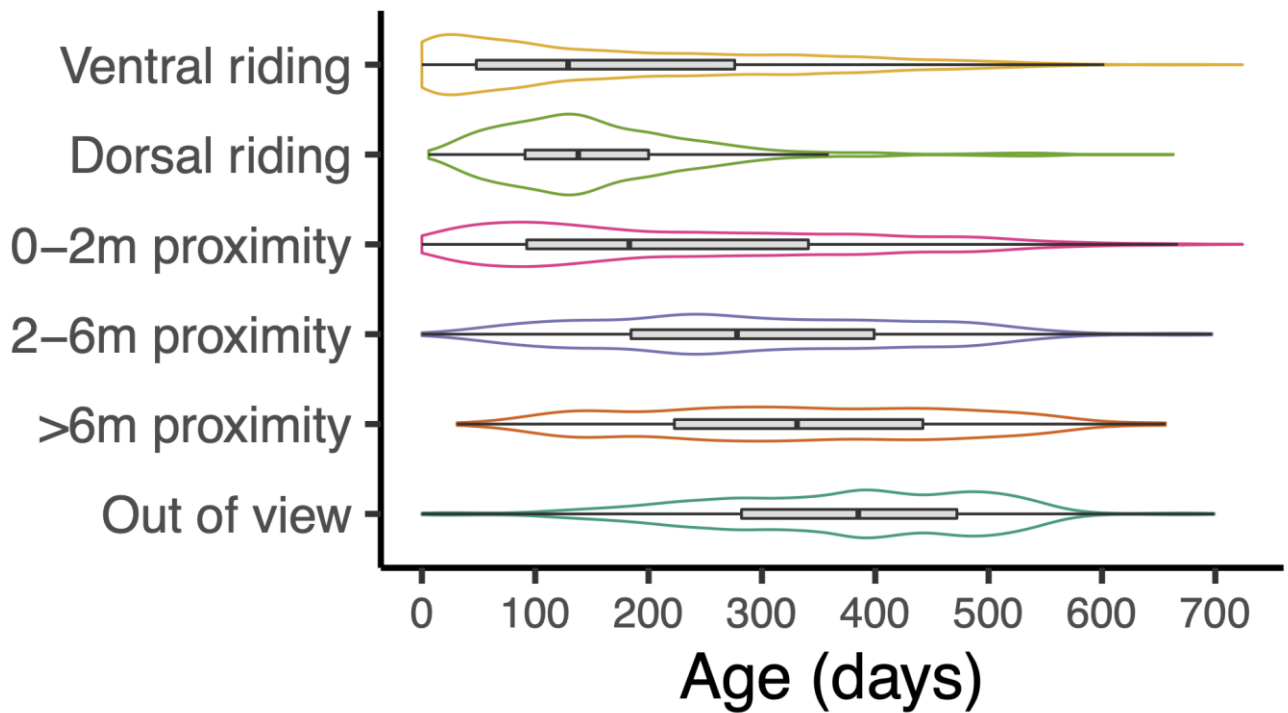
The resulting scores represent the relative strength of proximity and grooming interactions for a given dyad in a given year, controlling for differences in the combined sampling effort of dyads. To summarize these interactions at the level of an individual, we summed all dyadic proximity C scores and grooming scores for a given female, z-scored each measure across all females, and then computed individual-level averages of the two measures to derive ISI. Our ISI is an adjusted form of the composite sociality index [24,34], modified to standardize not only the mean across individuals, but also the standard deviation. For each female, we calculated ISI separately for social interactions with females and with males. To ensure comparability across years, we z-scored both versions of ISI for downstream analyses.

Because of the differentiated nature of female Kinda baboon relationships, particularly with males, we also calculated a measure of each female’s relationship with her top female or male partner, which we refer to as TSI. While females are more likely to have one top male partner than one top female partner, we included top partner relationships with both sexes to account for the possibility of cryptic female-female bond strength. We estimated TSI first by calculating C_{ij} and G_{ij} for each dyad as described above. Instead of summing these scores across individuals, we calculated composite sociality scores at the dyadic level—sometimes referred to as the “dyadic sociality index” (DSI) [53]—by z-scoring C_{ij} and G_{ij} (thus adjusting for the mean and standard deviation across all dyads), then averaging the two on a dyad-wise basis. We then assigned a TSI for each female as her highest DSI with other females (henceforth: TSI-F) or with males (TSI-M). As with ISI, we z-scored the final per-year TSI values to ensure comparability across the duration of our study.

As expected, we observed high correlations between ISI and TSI metrics for the corresponding sexes (i.e., Spearman’s rho = 0.94 between ISI-M and TSI-M; Spearman’s rho = 0.83 between ISI-F and TSI-F). Other pairwise comparisons between sociality metrics (including Elo rank) were low to moderate (Spearman’s rho: 0.10–0.43; Supplementary Figure. S1).

Infant behavioral development

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 239 We operationalize and assess infant behavioral development as the frequency of increasingly distant
 240 proximity to mother. The categories representing infant behavioral development (as defined above)
 241 represent a developmental trajectory from most dependent (i.e., ventral clinging) to most independent
 242 (i.e., out of view) with age (Figure. 1). While ‘out of view’ is not typically considered a distinct
 243 behavior and does not necessarily imply a relatively large distance from mother (for instance, an infant
 244 could be obstructed by foliage or another baboon), we found that in practice the proportion of ‘out of
 245 view’ observations increased similarly to observations in the higher distance category, providing
 246 useful information for our behavioral maturation assessment. To assess the frequency of more
 247 independent behaviors relative to more dependent behaviors, rather than an approach that would assess
 248 each behavior on its own, we tabulated the number of independent behaviors (‘> 6 meters’ and ‘out of
 249 view’) and dependent behaviors (‘ventral clinging’, ‘dorsal clinging’, ‘0-2 meters (from mother)’, ‘2-6
 250 meters’) on the level of the month for each infant. These ‘infant-months’ were excluded if there were
 251 fewer than 10 observations for a given infant-mother pair in that month.
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254
 255 **Figure 1.** Violin plots of each behavior over time show that more dependent behaviors (i.e., ventral
 256 and dorsal riding) are concentrated at the beginning of the lifespan, while more independent behaviors
 257 (i.e., greater than 6 meters away from the mother or out of view of the observer watching the mother)
 258 are more heavily concentrated in later stages of infancy.

259
 260 *Interbirth Interval*
 261

262 We calculated interbirth intervals (IBIs) as the number of days between consecutive births for each
263 adult female. IBIs were only included in downstream analyses if they began and ended with live births
264 [54] and if the infant associated with the initial birth survived to the following birth in order to avoid
265 potentially confounding effects of infant loss on IBI length.

266

267 *Statistical Analyses*

268

269 *Survival*

270

271 We used Cox proportional hazards models with random effects to assess the relationship between
272 maternal dominance or sociality and infant survival to two years of age while accommodating right-
273 censored data. This approach permits the assessment of survival to a given point without knowing the
274 true duration of infant survival, such that infants under two years of age still alive at the conclusion of
275 the study period are included as alive until the end date of the study period. We first modeled the
276 probability of mortality for infants as a function of maternal Elo rating, ISI-F, TSI-F, and infant sex,
277 with birth year and maternal ID included as random effects, using the ‘survival’ and ‘coxme’ packages
278 in the R statistical computing environment [55]. We then modeled the probability of infant mortality
279 as a function of maternal Elo rating, ISI-M, TSI-M, and infant sex, using the same random effects as
280 the first model. This approach permitted us to evaluate the within-sex sociality metrics and between-
281 sex sociality metrics separately. We adjusted for multiple testing with a Bonferroni correction.

282

283 *Interbirth Interval*

284

285 We again used Cox proportional hazards models with random effects to assess the relationship
286 between maternal dominance or sociality and IBI length. We first modeled within-sex (female-female
287 relationships) effects, assessing the relative timing of next birth as a function of maternal Elo rating,
288 ISI-F, TSI-F, and infant sex, including birth year and maternal ID as random effects. We then modeled
289 between-sex (female-male relationships) effects, assessing the relative timing of next birth as a
290 function of maternal Elo rating, ISI-M, TSI-M, and infant sex, with the same random effects as the
291 prior model. We accounted for multiple testing with a Bonferroni correction.

292

293 *Infant Behavioral Maturation*

294

295 We modeled the frequency of independent behaviors relative to dependent behaviors with generalized
296 linear mixed models using the ‘lme4’ package in R [56]. We first assessed within-sex effects by
297 modeling the frequency of independent behaviors as a function of the interaction between infant age
298 (in months), infant sex, and (1) maternal Elo rating (calculated as detailed above), (2) ISI-F, and (3)
299 TSI-F, with infant and maternal ID as random effects. We then assessed between-sex effects by
300 modeling the frequency of dependent behaviors as a function of the interaction between infant age (in
301 months), infant sex, and (1) maternal Elo rating (calculated as detailed above), (2) scaled ISI-M, and

302 (3) scaled TSI-M, with the same random effects as included in the prior model. For both models, we
 303 fit a binomial distribution and set the model intercept to 0. We fixed the model intercept because all
 304 paths to independence begin at zero (i.e., infants are fully dependent) and also because this allowed us
 305 to directly compare effect estimates on rates of behavioral maturation using slopes from our model
 306 without needing to factor in differing intercepts among infants. Our effect estimates and statistical
 307 support values were similar when running models without fixed intercepts; therefore, we report only
 308 results from our models with fixed intercepts, as these are more readily interpretable.

309

310 **Results**

311

312 *1. Survival*

313

314 Of the 81 infants included in the survival analyses, 14 died before reaching two years of age and the
 315 remaining 68 survived until two years of age (~17% mortality rate). Survival analysis revealed no
 316 significant impact of maternal Elo rating, ISIs, or TSIs on the likelihood of survival to two years of
 317 age.

318

Model	Covariate	Coefficient	Std. error	p-value	Bonferroni- value
1.1: Within-sex	Elo	0.001	0.001	0.301	
	Within-sex ISI (std)	-0.66	0.535	0.220	
	Within-sex TSI (std)	-0.034	0.434	0.940	
	Infant sex (M)	-0.396	0.681	0.560	
1.2 Between-sex	Elo	0.001	0.001	0.220	
	Between-sex ISI (std)	0.718	0.986	0.470	
	Between-sex TSI (std)	-1.524	1.12	0.170	
	Infant sex (M)	-0.349	0.635	0.580	

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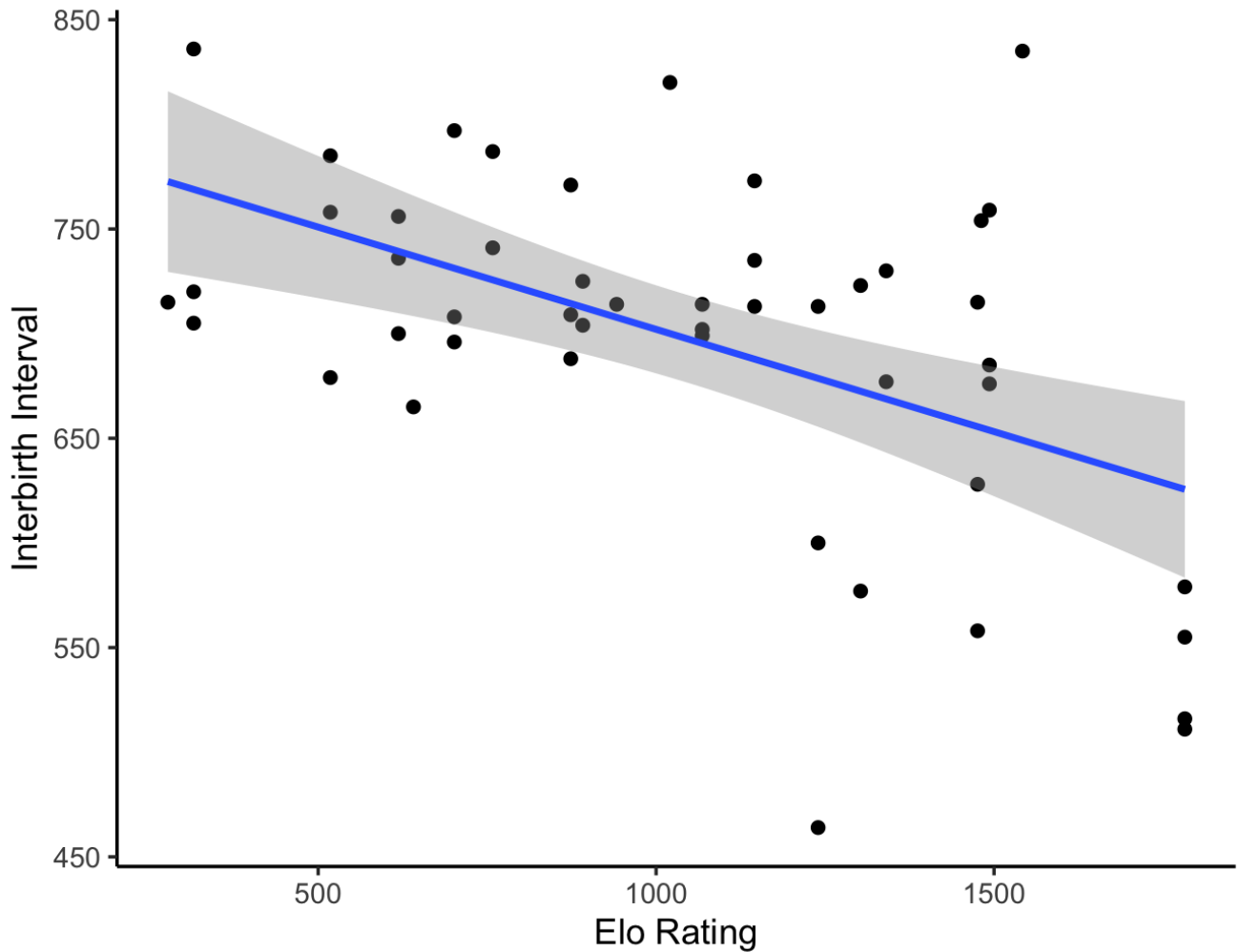
320 **Table 1: Survival analysis results.** Model results are presented for the effects of Elo rating, infant
 321 sex, and within-sex sociality metrics (Model 1.1) or between-sex sociality metrics (Model 1.2) on
 322 infant survival.

323

324 *2. Interbirth Interval*

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326 No maternal sociality metric was significantly associated with shorter IBIs after controlling for
 327 maternal ID and birth year and correcting for multiple testing (Figures S2-5). Elo rating trended
 328 towards significance in each of the models ($p = 0.054$, $p = 0.085$) prior to Bonferroni correction
 329 (Figure 2).
 330
 331



332
 333 **Figure 2. Interbirth interval (IBI) by maternal Elo rating.** Interbirth interval duration is plotted by
 334 an averaged ‘lifetime’ Elo rating due to high rank stability in Kinda baboons.
 335

Model	Covariate	Coefficient	Std. error	p-value	Bonferroni-adjusted p-value
2.1: Within-sex	Elo rating	0.001	0.001	0.054	0.108
	Within-sex ISI (std)	-0.054	0.356	0.88	1.76

	Within-sex TSI (std)	-0.019	0.287	0.95	1.9
	Infant sex (M)	0.145	0.386	0.71	1.42
2.2: Between-sex	Elo rating	0.001	0.001	0.085	0.17
	Between-sex ISI (std)	-0.253	0.388	0.52	1.04
	Between-sex TSI (std)	0.435	0.448	0.33	0.66
	Infant sex (M)	0.227	0.373	0.54	1.08

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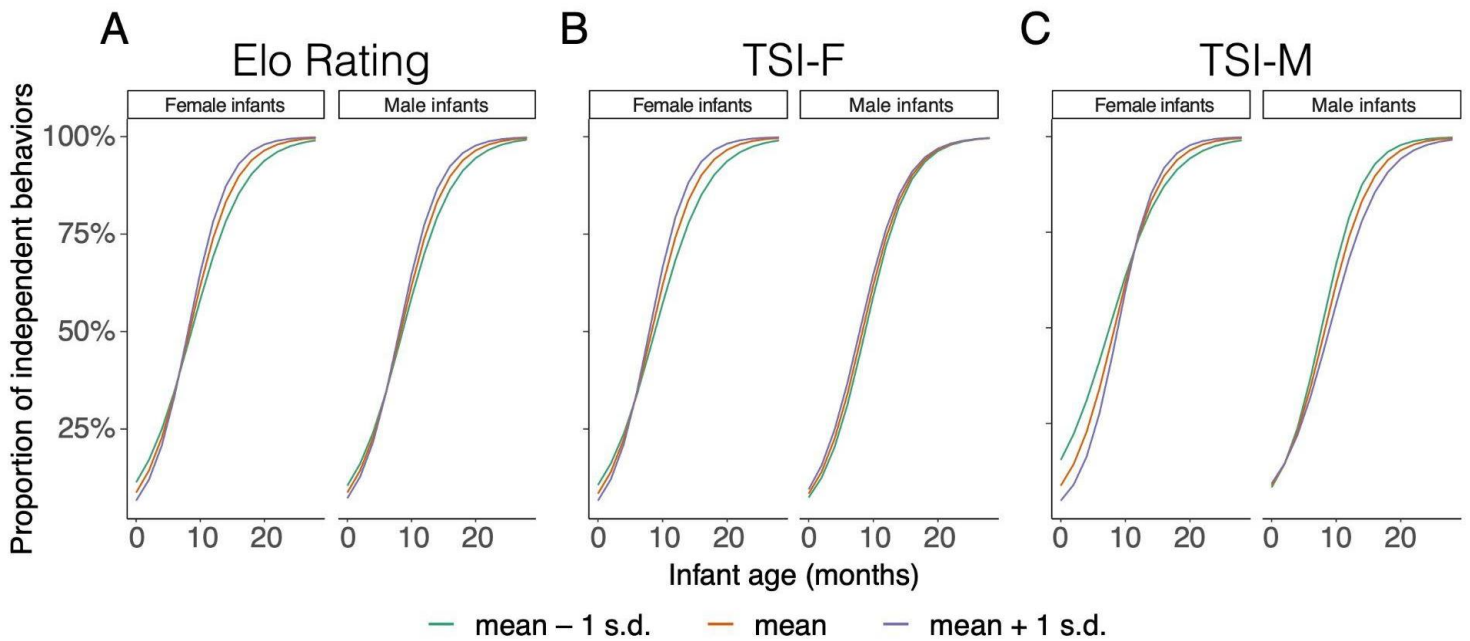
337 **Table 2: Interbirth interval.** Model results are presented for analyses of interbirth interval duration
338 as a function of (Model 2.1) Elo rating, within-sex sociality scores (ISI-F, TSI-F), and infant sex, and
339 (Model 2.2) Elo rating, between-sex sociality scores (ISI-M, TSI-M), and infant sex. P-values and
340 Bonferroni-adjusted p-values are presented.

341

342 3. *Infant behavioral maturation*

343

344 Our analysis of infant maturation in both within- and between- sex models revealed a significant
345 positive effect of the interaction between maternal Elo rating and infant age ($p = 0.021$; $p < 0.001$,
346 respectively) such that infants of higher-ranking mothers displayed higher frequencies of independent
347 behaviors more quickly than did infants of lower ranking mothers (Figure 3). Similarly, in both
348 models, there was a significant positive effect of the interaction between TSI and age, such that infants
349 of mothers with higher TSIs both with females and with males displayed higher frequencies of
350 independent behaviors more quickly than did infants of mothers with lower TSIs with either sex ($p =$
351 0.015 ; $p = 0.017$, respectively). The effect of the interaction between TSI and age was significantly
352 lower for male infants than for female infants in both the within- and between- sex models ($p = 0.054$
353 and $p = 0.011$, respectively), suggesting that male infants of mothers with stronger relationships with
354 both sexes displayed higher frequencies of independent behaviors more quickly than female infants.
355 Individual sociality indices (i.e., overall social integration) were not significantly associated with any
356 differences in infant behavioral maturation.



358
 359 **Figure 3.** Predicted values of the proportion of independent behaviors by infant age as a function of
 360 maternal social phenotype. Predicted values are derived from the within-sex model (Elo rating, ISI-F,
 361 TSI-F) and the between-sex model (Elo rating, ISI-M, TSI-M) and visualized here for significant
 362 interactions: Elo rating in the within-sex model, TSI-F, and TSI-M (all others can be found in Figure
 363 S6). Red lines denote the mean value (e.g., average Elo rating, TSI-F, or TSI-M), while purple lines
 364 denote the mean plus one standard deviation (e.g., high Elo rating, TSI-F, or TSI-M) and green lines
 365 denote the mean minus one standard deviation (e.g., low Elo rating, TSI-F, or TSI-M). For example,
 366 the steeper purple slope for female infants in (A) indicates a higher predicted proportion of
 367 independent behaviors at younger ages for infants of females with higher Elo ratings. Lower density of
 368 observations for females at younger ages may contribute to crossing slopes for female infants.
 369

Model	Covariate	Estimate	Std. error	p value	Adjusted p value
3.1: Within-sex	Elo rating	-0.014	0.125	0.909	1.817
	Infant age	1.563	0.034	<0.001	<0.001*
	TSI-F	0.121	0.077	0.114	0.228
	ISI-F	-0.103	0.068	0.132	0.264
	Elo rating:infant age	0.120	0.047	0.010	0.021*

	Infant age:TSI-F	0.248	0.093	0.007	0.015*
	Infant age:ISI-F	0.081	0.081	0.315	0.631
	Elo rating: infant age: infant sex (F)	0.005	0.07	0.940	1.880
	Infant age: infant sex (M): TSI-F	-0.258	0.117	0.027	0.054*
	Infant age: infant sex (M): ISI-F	-0.041	0.105	0.706	1.411
3.2:					
Between-sex	Elo rating	0.072	0.123	0.560	1.120
	Infant age	1.532	0.033	<0.001	<0.001*
	TSI-M	-0.175	0.087	0.046	0.091
	ISI-M	0.037	0.085	0.666	1.331
	Elo rating:infant age	0.178	0.043	<0.001	<0.001*
	Infant age:TSI-M	0.305	0.116	0.009	0.017
	Infant age:ISI-M	-0.193	0.119	0.106	0.212
	Elo rating: infant age: infant sex (F)	0.060	0.064	0.346	0.691
	Infant age: infant sex (M): TSI-M	-0.460	0.166	0.006	0.011*
	Infant age: infant sex (M): ISI-M	0.263	0.166	0.113	0.227

370
371 **Table 3: Infant behavioral maturation.** Model results are presented for analyses of infant behavioral
372 development as a function of Elo rating, infant age, and infant sex, Elo ranking, and (Model 3.1)
373 within-sex sociality scores (ISI-F and TSI-F) or (Model 3.2) between-sex sociality scores (ISI-M and
374 TSI-M). Interaction effects were run between infant age, sex, Elo rank, and sociality scores.

375
376 **Discussion**

377
378 Our analyses suggest that dominance rank and affiliative relationships in Kinda baboons carry benefits
379 for infant behavioral maturation, which may contribute to female reproductive success by ultimately
380 increasing the speed at which a female can resume investment in her own condition. If a higher-ranked
381 or more socially integrated female is able to conceive more quickly than a lower-ranked or more
382 socially peripheral female, then this may be reflected in her lifetime reproductive output. None of the

383 social metrics was associated with differences in infant survival or IBI length, but maternal top-partner
384 sociality indices, both among females and between females and males, were strong predictors of more
385 rapid infant behavioral maturation. Our results demonstrate that stronger relationships with males play
386 an important role in infant behavioral maturation and demonstrate the importance of the top maternal
387 social bonds (with both female and males) and of maternal dominance rank for Kinda baboons. These
388 results suggest that there may be benefits associated with being high-ranking and having strong
389 primary social bonds that take the form of faster infant maturation as opposed to increased infant
390 survival rates or IBI length.

391

392 *Social phenotype and infant survival*

393

394 We observed low infant mortality in Kinda baboons (~17%), relative to the 38% mortality (to one year
395 of age) reported for chacma baboons in Botswana's Okavango Delta ([11], the 33% mortality (to
396 mother's next conception) reported for yellow baboons in Kenya's Amboseli National Park [57], and
397 the 47% mortality (to one year) reported for olive baboons in Nigeria's Gashaka-Gumti National Park
398 [58]. This comparatively low infant mortality rate might be related to the low rates of agonism and
399 aggression—including infanticide—observed in this population, and thus might represent a characteristic
400 of the species. Alternatively, the low mortality rate could also be linked to low observed predator
401 abundance within the small confines of Kasanka National Park (390km²). Future studies should assess
402 predator abundance and compare infant mortality across Kinda baboons in different areas in order to
403 determine whether low infant mortality is an idiosyncrasy of the Kasanka National Park population or
404 whether it is a greater pattern across Kinda populations.

405

406 Neither dominance rank nor affiliative relationship strength affected infant survival, which may be a
407 function of the low observed infant mortality rate. While dominance rank and body condition have
408 been shown to be tightly linked in multiple mammalian species [7,59], such reproductive benefits
409 might only appear in times of resource shortage, when dominance rank would become key to
410 maintaining a sufficient energy balance [60]. Similarly, the benefits of maternal social relationships
411 might only be detectable in the context of high predation, limited resources, or high levels of social
412 stress, all of which have been proposed to explain the relationship between stronger affiliative female-
413 female relationships and infant survival in yellow and chacma baboons [20]. Thus, one possibility as
414 to why we did not observe the predicted relationship here is because this population of Kinda baboons
415 likely faces low predation pressure and may not have experienced a drought that would have been
416 severe enough to restrict fruit availability (the majority of the Kinda baboon diet [61]). Continued
417 longitudinal data collection in this population and comparisons with other populations of Kinda
418 baboons will be able to refine our understanding of the lack of observed relationship between infant
419 survival and dominance rank or affiliative social relationships.

420

421 *Social phenotype and interbirth interval*

422

423 We found no significant association between Elo rating or any of the affiliative metrics and interbirth
424 interval, which is a critical component of overall lifetime reproductive success for many mammalian
425 females [54,62]. The interbirth interval itself is the product of trade-offs between investment in current
426 offspring, maternal physiological condition, and next offspring [63], and higher dominance rank may
427 confer benefits that facilitate a more beneficial trade-off. Among primates, little is known about
428 potential effects of maternal affiliative relationships on interbirth interval, but higher rank has been
429 observed to be associated with shorter lactation duration [54,64], suggesting that higher-ranking
430 females are able to wean their infants [12], and shorter duration of sexual cycling following
431 weaning [65,66], suggesting that these females are better able to regain condition and conceive earlier
432 than lower ranking females.

433
434 While dominance rank did not meet the threshold we set for statistical significance in our models
435 following adjustment for multiple testing, the association between higher dominance rank and shorter
436 IBI trended toward significance in both models prior to correction (Figure 2). As we continue data
437 collection in this population, we will be able to assess with a greater sample size whether higher
438 dominance confers an advantage in female Kinda baboons and, if so, whether this permits them to
439 accelerate weaning or to resume sexual cycling more rapidly (or a combination of the two).
440 Alternatively, there may be less flexibility in the interbirth interval of Kinda baboons compared to
441 other baboon taxa. This may be connected to their greater birth seasonality, which appears to be tied to
442 high levels of climatic and plant seasonality in Kasanka National Park [41]. In wild spotted hyenas
443 (*Crocuta crocuta*) and captive plains zebra (*Equus burchelli*), for example, the shorter interbirth
444 intervals of higher-ranking females are associated with duration of sexual cycling as opposed to
445 lactation duration [67,68]. Among primates, shorter interbirth intervals for higher-ranking females
446 have been tied to lactation duration [54,64] as well as duration of sexual cycling [65,66]. Further work
447 is needed to identify which components of the interbirth interval may contribute to this pattern.

448 449 *Social phenotype and infant behavioral maturation*

450
451 Our analyses demonstrate an association between maternal social phenotype and infant behavioral
452 development, point to a greater importance of top-partner affiliations relative to overall social
453 integration, and show that relationships with both conspecific females and males contribute to the
454 effect on infant behavioral development in Kinda baboons. Maternal dominance is well-known to
455 contribute to offspring development and success in multiple species, and a growing body of evidence
456 points to strong effects of sociality on health and survival as well as an adaptive role of sociality in
457 mammals [13,22] and baboons in particular [13,20,24]. For example, higher maternal dominance rank
458 is associated with higher weight for age and faster growth in chacma baboon offspring [69], earlier age
459 at reproduction for yellow baboon offspring [70], earlier age at reproduction and faster growth in
460 dispersing spotted hyena offspring [71], and higher overall lifetime reproductive success in red deer
461 offspring [72]. In Kinda baboons, maternal dominance rank is associated with infant behavioral
462 maturation, such that higher-ranking females have infants that exhibit higher frequencies of

463 independent behaviors at earlier ages. This may mean that higher-ranking females are able to wean
464 their offspring earlier based on greater access to resources or to higher quality resources, which would
465 potentially result in the earlier onset of independent behaviors. Alternatively, the infants of higher-
466 ranking mothers might engage in more independent behaviors earlier because they face less aggression
467 from conspecifics. In both cases, the earlier independence exhibited by infants of higher-ranking
468 females might permit those females to regain condition, resume cycling, and conceive earlier, thereby
469 contributing to lifetime reproductive success.

470
471 In addition to dominance rank, stronger maternal affiliative relationships with both female and male
472 top partners were significantly associated with more rapid attainment of infant independence in Kinda
473 baboons. The observed association between female-female affiliative relationship strength and the
474 pace of infant behavioral development is consistent with existing data on the benefits of female-female
475 sociality in primates [20,22,24]. For both within-sex and between-sex models, top-partner bond
476 strength significantly predicted higher rates of independent behavior for a given infant age, while
477 overall social affiliation did not. This may situate Kinda baboons behaviorally closer to chacma
478 baboons, in which the strength of the strongest bonds is associated with fitness benefits [20,34], than
479 to yellow baboons, in which overall social integration is associated with fitness benefits [14,35].
480 Female-female affiliative relationship strength might share certain benefits with dominance rank that
481 contribute to the association between both of these metrics and the pace of infant behavioral
482 maturation. Specifically, Kinda baboon mothers with more robust social bonds may face lower
483 aggressive or non-aggressive infant interference from other females with the potential for infant injury
484 [73] and are thus less invested in maintaining close proximity to their infants throughout infant
485 development, or, conversely, may be able to leverage those bonds to recruit allo-caring from other
486 females or males.

487
488 The adaptive significance of female-male relationships in primates is suggested to take the shape of
489 infanticide avoidance or harassment mitigation for females and joint parental care for males
490 [14,30,74,75]. In Assamese macaques, for example, females that form close bonds with a male receive
491 less harassment from that male [14,76], and in yellow baboons, females and their dependent offspring
492 received less harassment from other group mates if the female had a close association with a male
493 (regardless of whether that male was the sire of the offspring) [37]. However, the lack of effect of
494 female-male affiliative relationships on infant survival in our study suggests that the benefit of these
495 friendships for females is not rooted in protective benefits for infants or infanticide avoidance for
496 Kinda baboons. In addition, Kinda males groom females outside of the periovulatory period and more
497 than any other baboon species [44] and exhibit low overall rates of aggression (unpublished data) that
498 align them behaviorally with Guinea baboons (*P. papio*) [77]. Altogether, this suggests that, while
499 social buffering may be a component of female-male relationships, it may not hinge on aggression of
500 male origin. Rather, the strength of maternal relationships with males may be seen through an adaptive
501 lens as a mechanism that not only ensures the safety of infants but actively contributes to their
502 development.

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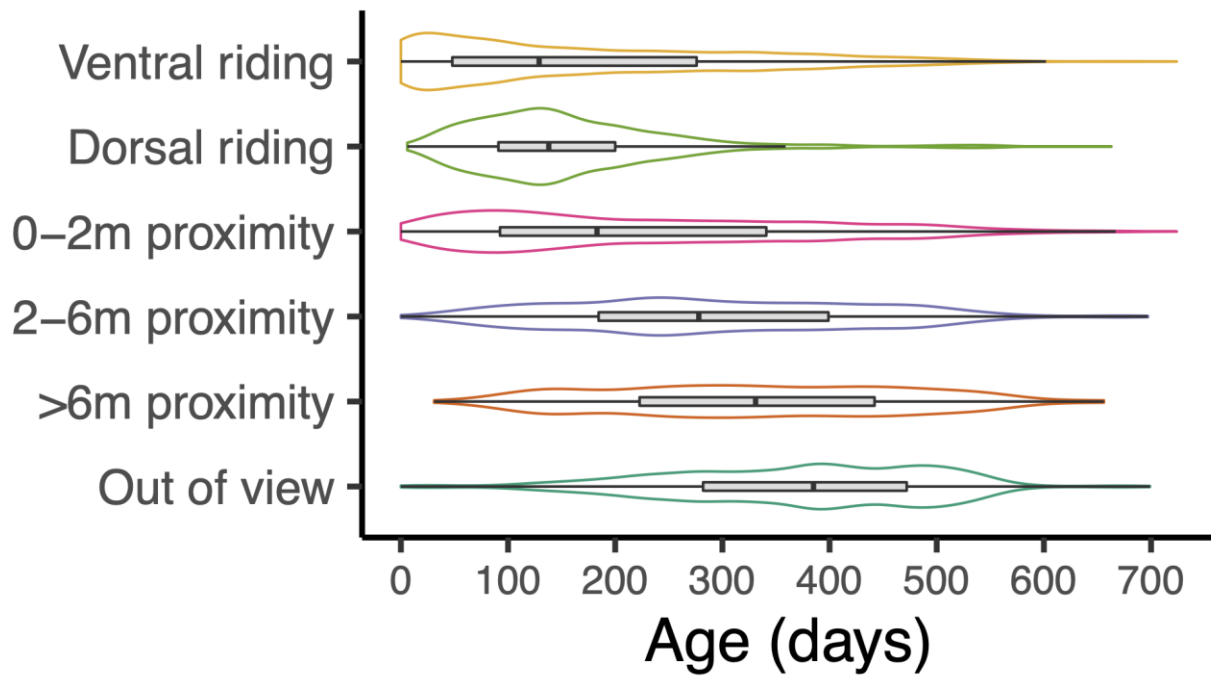


Fig. 1

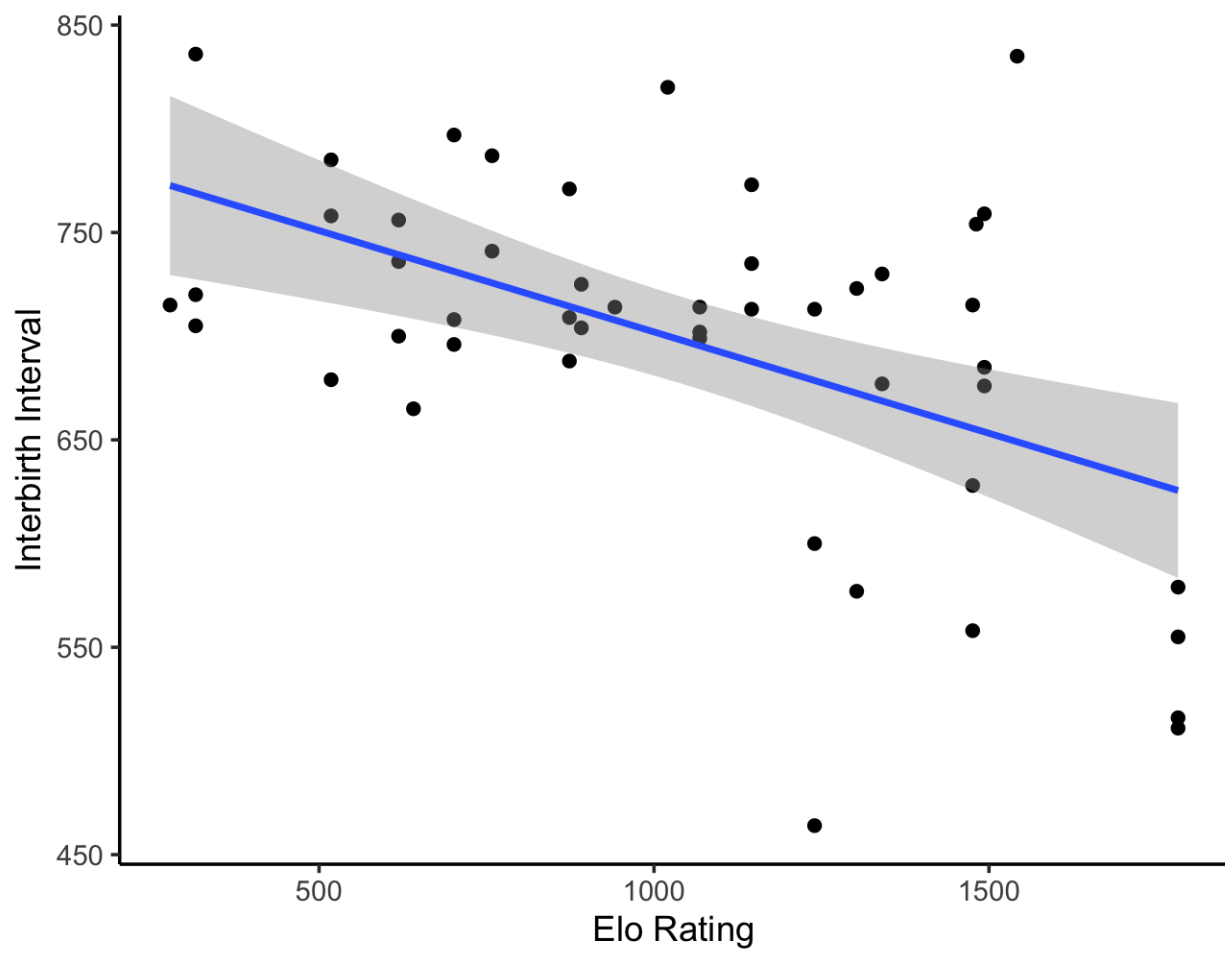


Fig. 2

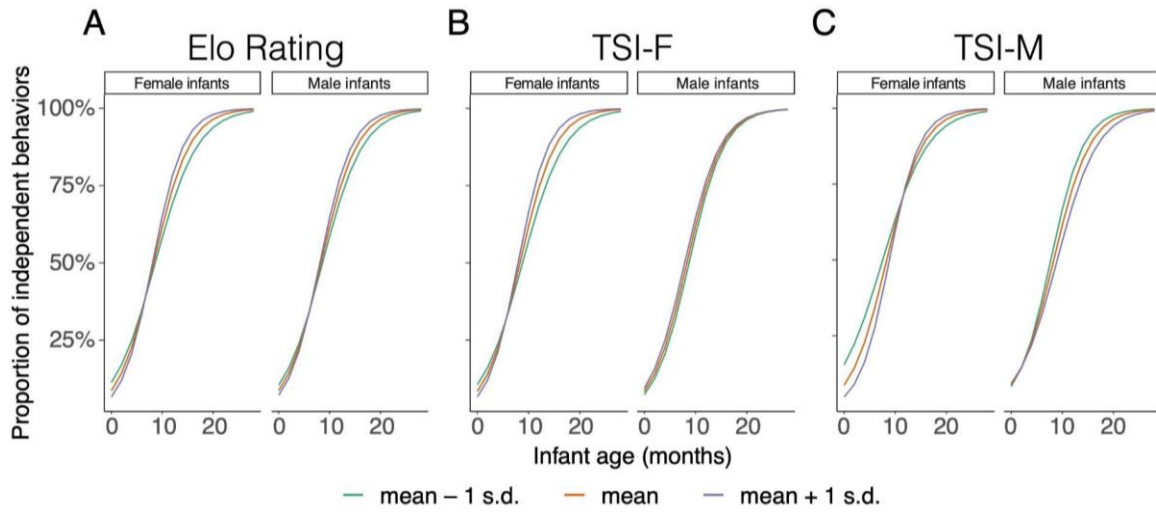


Fig. 3

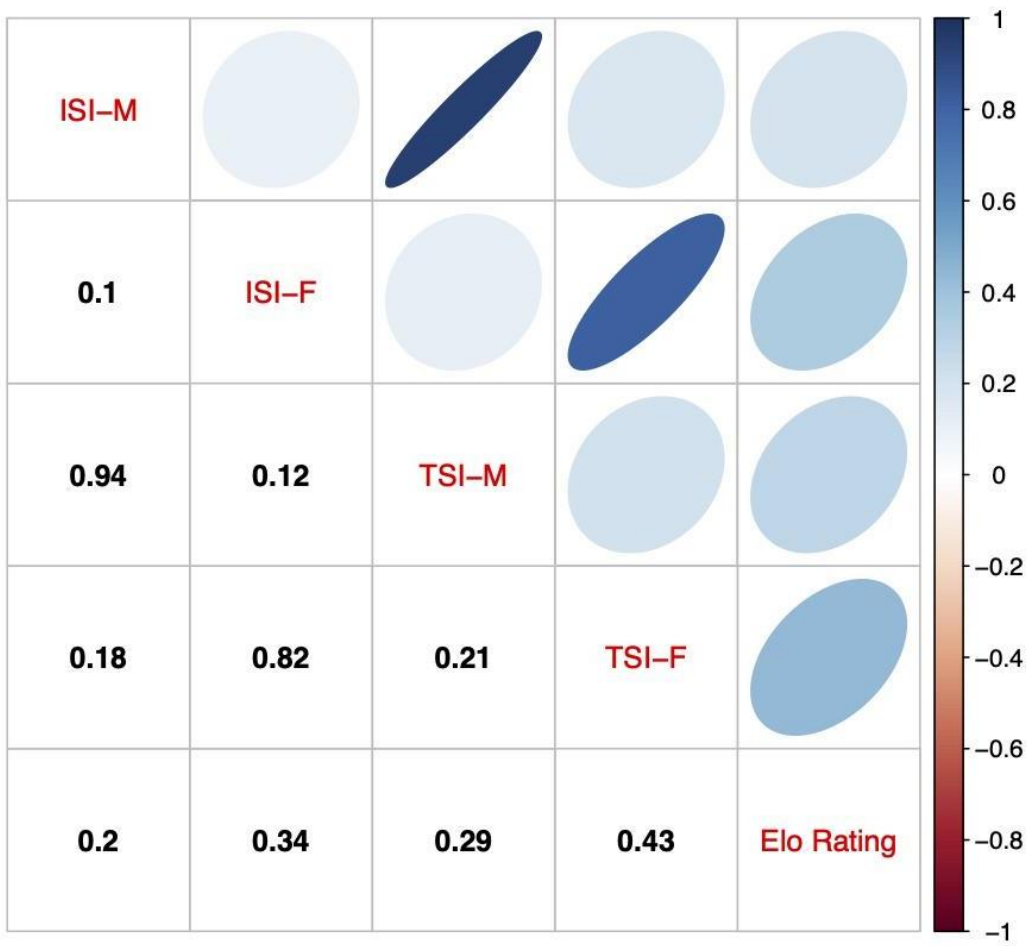


Fig. A1

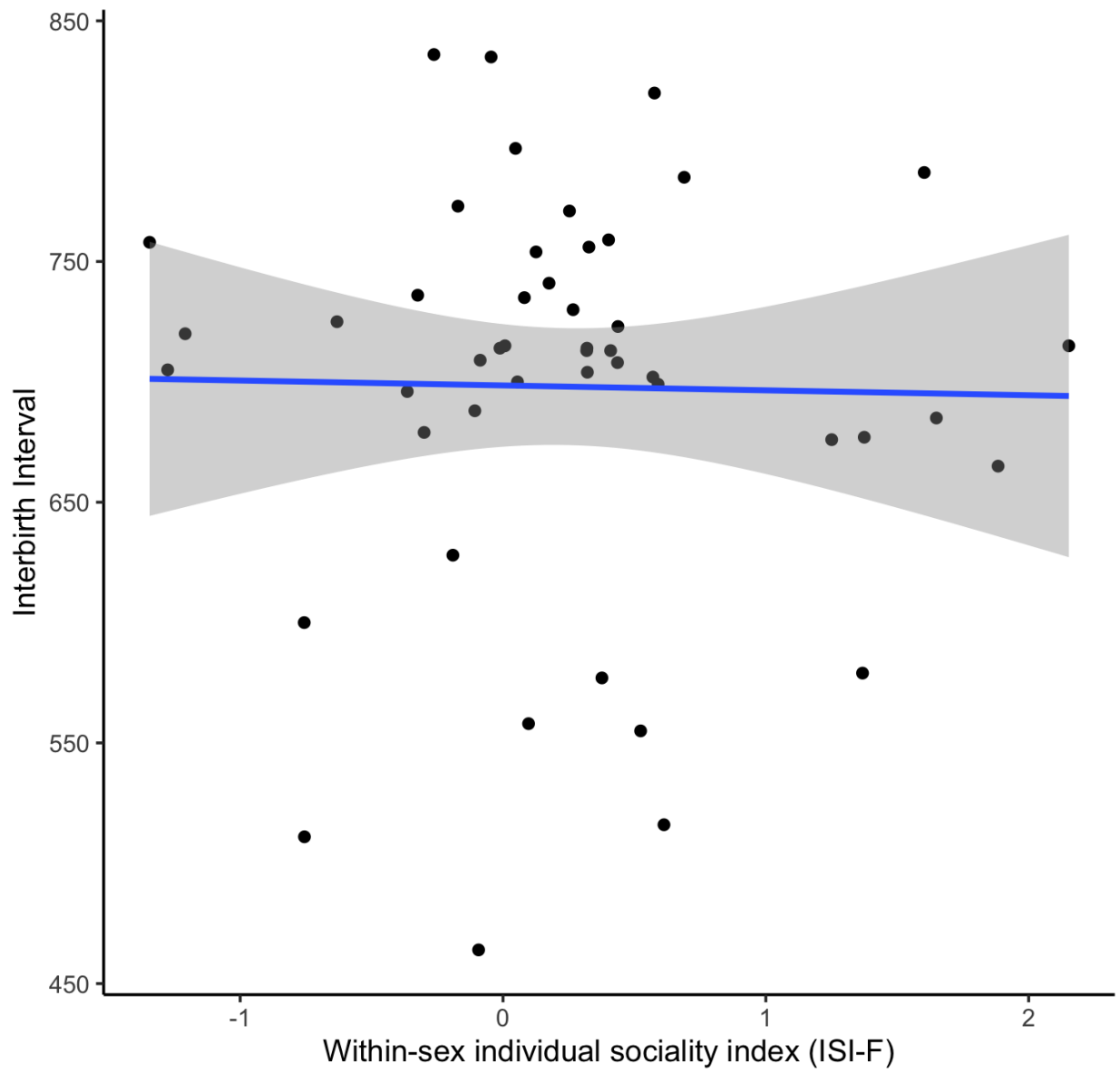


Fig. A2

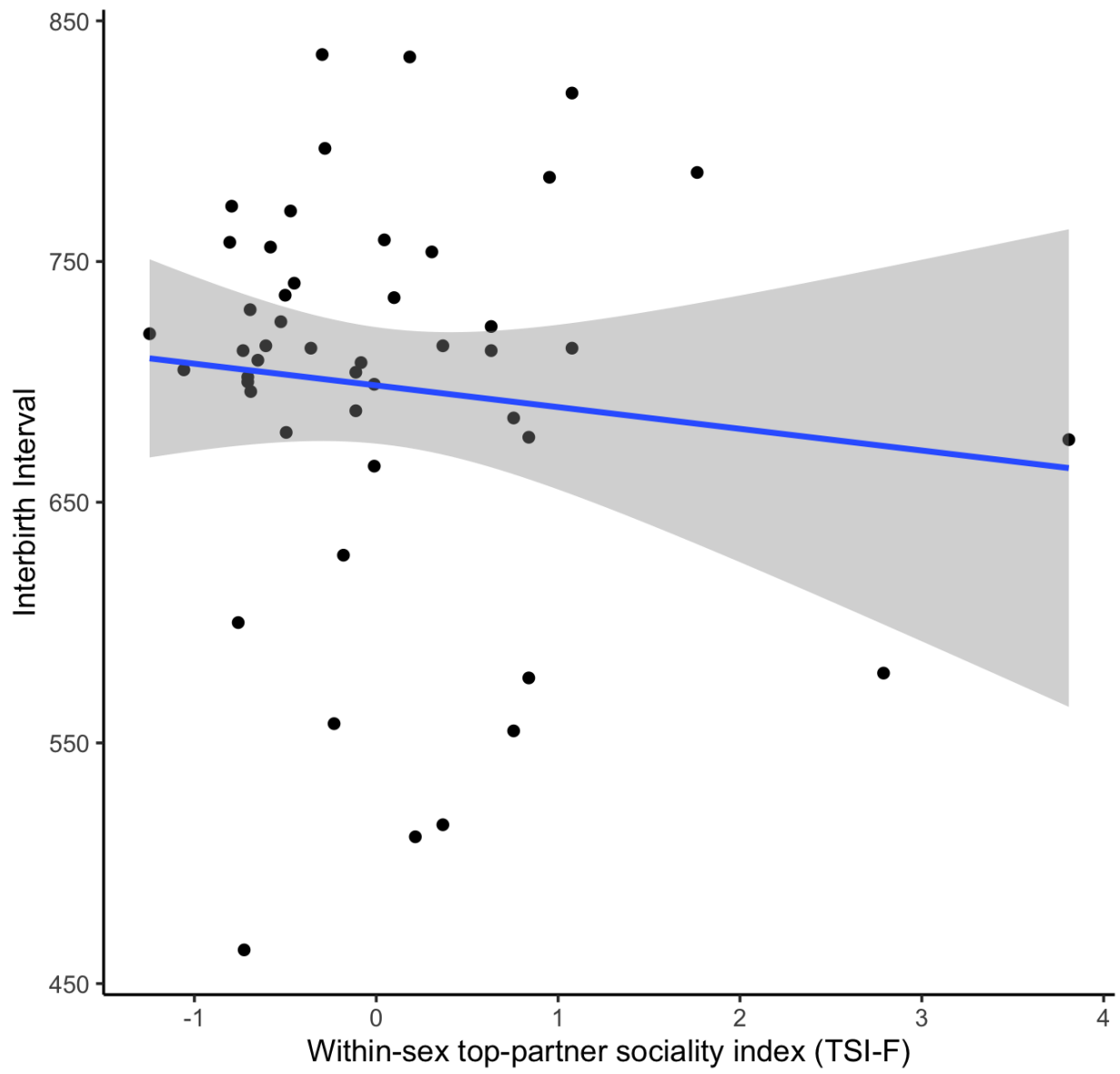


Fig. A3

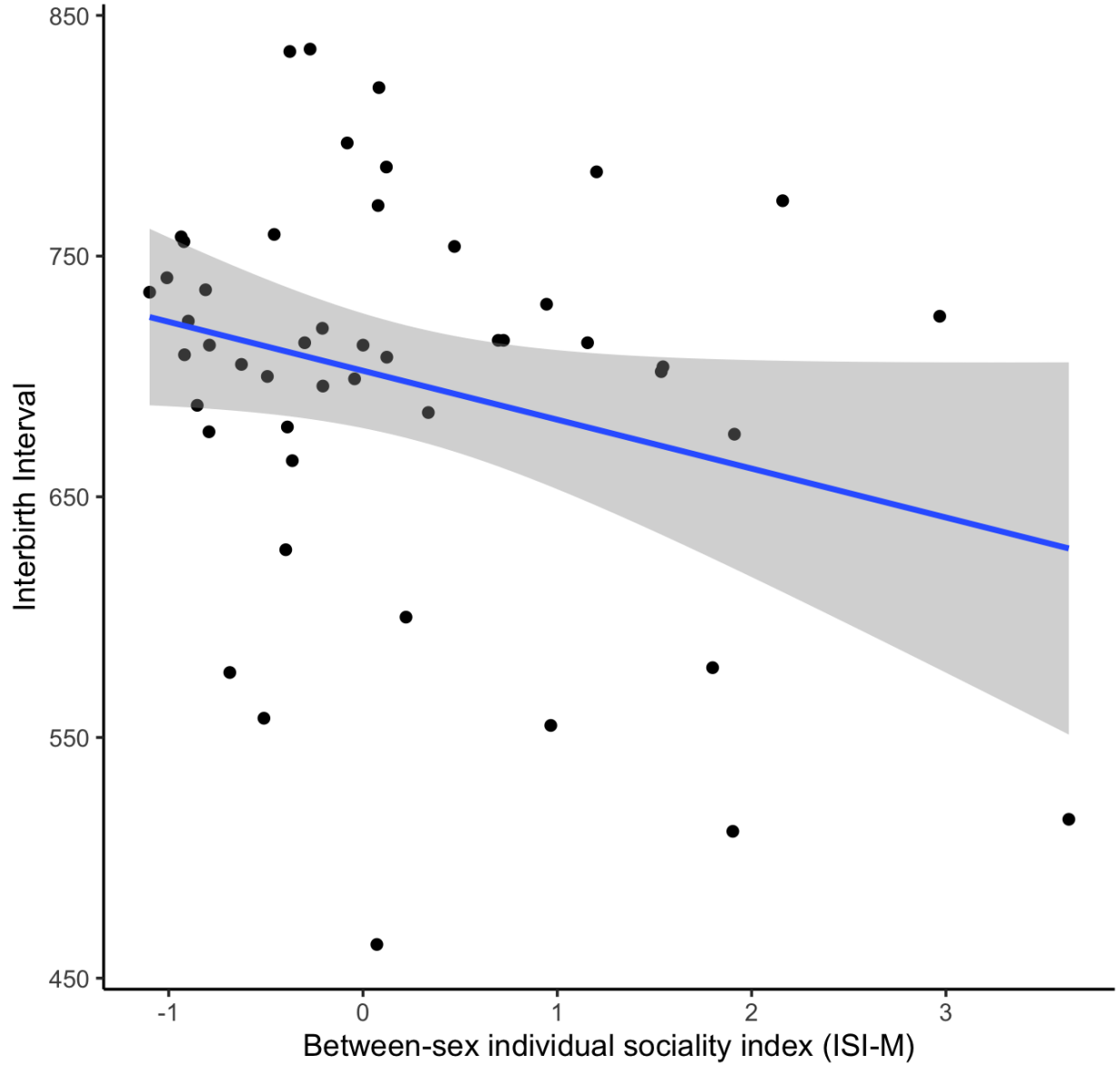


Fig. A4

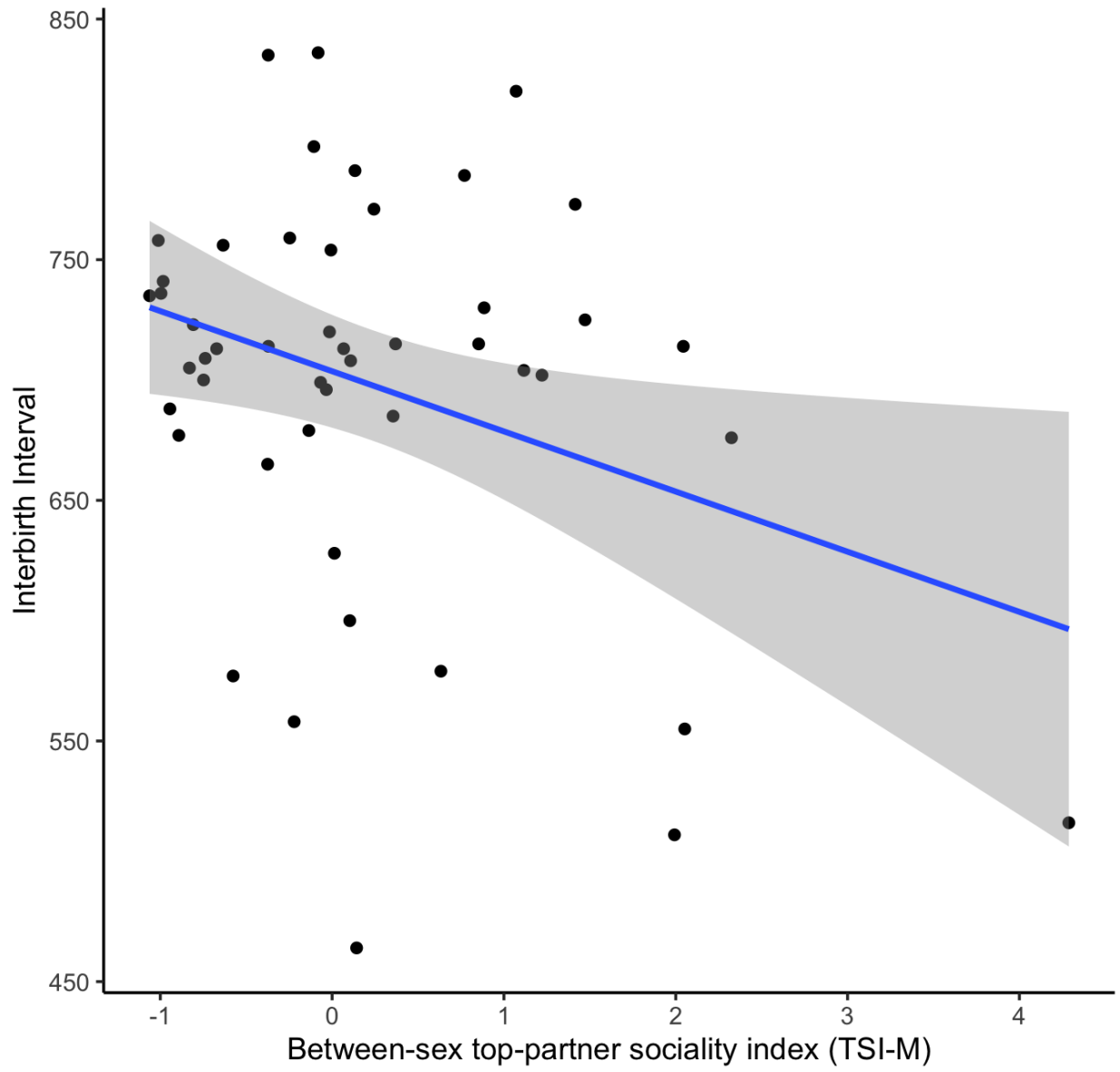


Fig. A5

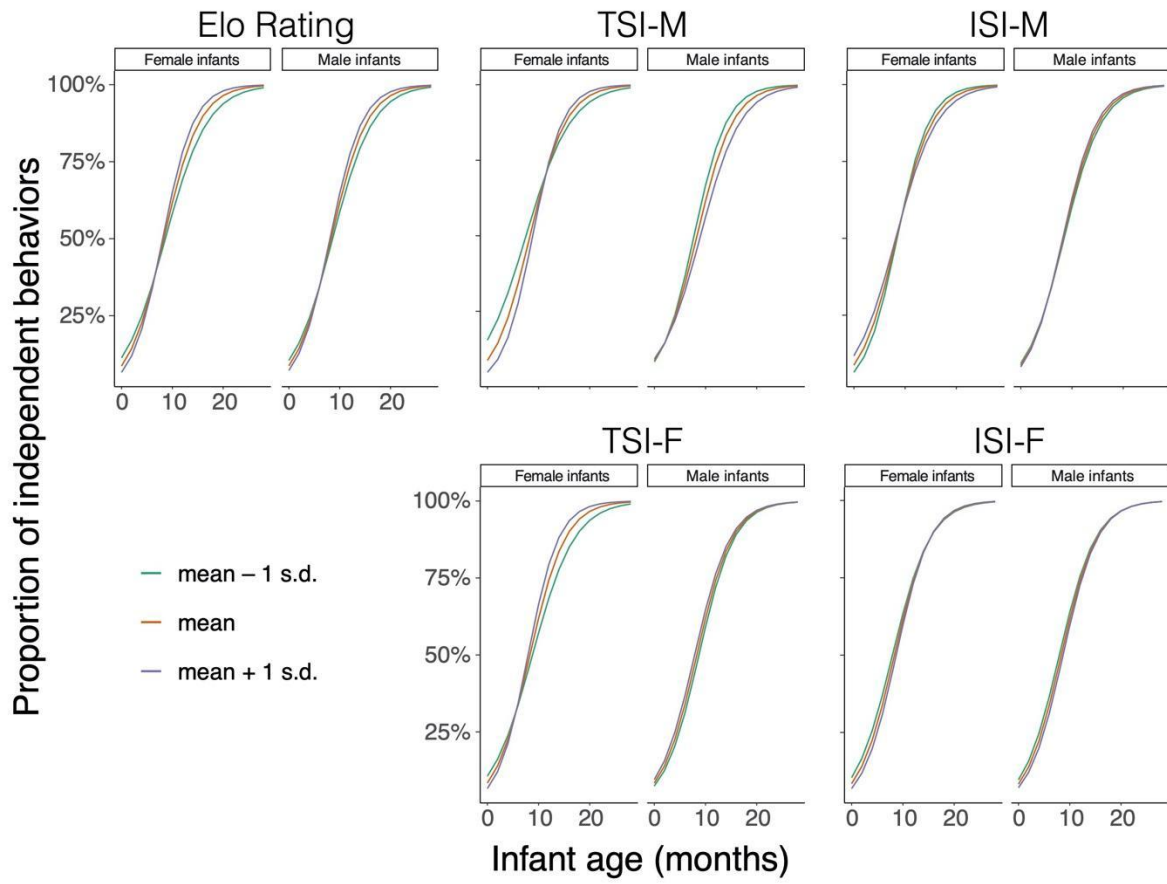


Fig. A6