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# 1 **Birth timing generates reproductive trade-offs in a non-seasonal** 2 **breeding primate**

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13

## 14 **ABSTRACT**

15 The evolutionary benefits of reproductive seasonality are often measured by a single fitness  
16 component, namely offspring survival. Yet different fitness components may be maximised by  
17 dissimilar birth timings. This may generate fitness trade-offs that could be critical to  
18 understanding variation in reproductive timing across individuals, populations and species.  
19 Here, we use long-term demographic and behavioural data from wild chacma baboons (*Papio*  
20 *ursinus*) living in a seasonal environment to test the adaptive significance of seasonal variation  
21 in birth frequencies. We identify two distinct optimal birth timings in the annual cycle, located  
22 4-months apart, which maximize offspring survival or minimize maternal interbirth intervals  
23 (IBIs), by respectively matching the annual food peak with late or early weaning. Observed  
24 births are the most frequent between these optima, supporting an adaptive trade-off between  
25 current and future reproduction. Furthermore, infants born closer to the optimal timing

26 favouring maternal IBIs (instead of offspring survival) throw more tantrums, a typical  
27 manifestation of mother-offspring conflict. Maternal trade-offs over birth timing, which extend  
28 into mother-offspring conflict after birth, may commonly occur in long-lived species where  
29 development from birth to independence spans multiple seasons. Our findings therefore open  
30 new avenues to understanding the evolution of breeding phenology in long-lived animals,  
31 including humans.

32

## 33 **MAIN TEXT**

### 34 **Introduction**

35 Empirical studies investigating variation in reproductive timing have mostly focused on fast-  
36 lived seasonal breeders, whose development from birth to independence generally occurs  
37 within the most productive season [1]. In long-lived mammals, the reproductive cycle from  
38 birth to weaning cannot similarly be squeezed into one annual food peak, and consequently,  
39 females must choose which stage(s) of the reproductive cycle to synchronize with one or more  
40 food peak(s). For example, female mammals could match the annual food peak to coincide with  
41 either late-weaning or mid-lactation (two critical stages that require readily accessible food),  
42 but usually not both. The reproductive timing strategy is likely to depend on how females trade-  
43 off the survival of their offspring (mortality risks tend to peak at the end of weaning) [2–4] with  
44 their own reproductive costs (energetic demands tend to peak around mid-lactation) [5,6].  
45 Whether such reproductive timing strategies can vary within populations is largely unknown.  
46 In addition, while evolutionary trade-offs between offspring quality and quantity have been  
47 described both within and across species through associations between birth spacing and infant  
48 growth and survival [7,8], the existence of maternal trade-offs over birth timing have only been  
49 suggested theoretically [3] and never tested empirically in mammals (but for birds, see *Fulica*  
50 *atra*: [9]).

51           Here, we investigate variation in maternal reproductive success and mother-offspring  
52 relationships associated with variable birth timings in the annual cycle of wild chacma baboons  
53 (*Papio ursinus*) living in a seasonal semi-arid savannah (Tsaobis, Namibia). Baboons are  
54 African primates distributed across a wide latitudinal range and a classic model for  
55 understanding how early humans adapted to seasonal savannahs [10,11]. In particular, baboons  
56 typically breed year-round [12] and are therefore considered non-seasonal breeders, though the  
57 distribution of births shows moderate seasonality (i.e. varies along the annual cycle) in some  
58 species and populations [13–15]. In addition, infant baboons, like many young primates  
59 including human toddlers, commonly perform tantrums, a manifestation of mother-offspring  
60 conflict [16,17]. Using a combination of detailed long-term life-history and behavioural data  
61 collected over 15 years (2005-2019), we first characterize the reproductive and environmental  
62 seasonality of the Tsaobis baboons. Second, we quantify the consequences of birth timing on  
63 two components of female fitness: offspring survival and maternal inter-birth intervals (IBIs)  
64 and seek to identify two distinct birth timing optima. We further test whether individual females  
65 may vary in their birth timing strategies, and specifically individual traits predict whether a  
66 female is more likely to give birth around one or the other optimum. In particular, dominance  
67 rank and parity can affect various aspects of individual reproductive performance, including  
68 offspring survival and IBI [18–20], and may influence birth timing strategies accordingly.  
69 Similarly, mothers conceiving close to the optimal timing that alleviates the energetic costs of  
70 lactation may subsequently favour male over female embryos, which are more costly to produce  
71 in sexually dimorphic mammals [18,21]. Third, we investigate if maternal care can mitigate the  
72 costs of suboptimal birth timing for offspring, and whether infants born and weaned during  
73 suboptimal periods had higher tantrum frequencies.

74

## 75 **Materials and methods**

76 **Study population**

77 Three habituated groups (named J, L and M) of wild chacma baboons were followed between  
78 2005 and 2019: J and L since 2005, and M, a fission group from J, since 2016. They live in a  
79 desert-edge population at Tsaobis Nature Park (22°23S, 15°44'50E) in Namibia, in a seasonal  
80 and arid environment [22]. Water is always available through the presence of both natural seeps  
81 and artificial water points for wildlife and livestock. A field team was present each year, mainly  
82 during winter (between May to October), for a variable number of months (mean = 4.5, range:  
83 1.9-7.9), that collected daily demographic and behavioural data, as well as GPS locations, while  
84 following the groups on foot. All individuals, including infants, are individually recognizable  
85 thanks to small ear markings performed during capture and/or other distinctive features.

86

87 **Ethical Note.** Our research procedures were evaluated and approved by the Ethics Committee  
88 of the Zoological Society of London and the Ministry of Environment and Tourism, Namibia  
89 (MET Research/Collecting Permits 886/2005, 1039/2006, 1186/2007, 1302/2008, 1379/2009,  
90 1486/2010, 1486/2011, 1696/2012, 1786/2013, 1892/2014, 2009/2015, 2147/2016, 2303/2017,  
91 RPIV00392018/2019), and adhered to the ASAB/ABS Guidelines for the Treatment of Animals  
92 in Behavioural Research and Teaching.

93

94 **Environmental data**

95 In order to describe the relationship between reproductive and environmental seasonality, we  
96 characterize two aspects of environmental seasonality at Tsaobis: rainfall and vegetation cover  
97 (an index of food availability).

98 Daily rainfall in a  $0.25 \times 0.25$  degree grid cell resolution (corresponding to  $28 \times 28$  km  
99 at this latitude) was extracted using satellite data sensors from the Giovanni NASA website  
100 (product TRMM 3B42) [23]. We computed a rectangular geographic area that encompasses the

101 global ranging area of the Tsaobis baboons, using GPS locations collected by observers every  
102 30 min when following the study groups. We used the minimal and maximal latitude and  
103 longitude recorded between 2005 and 2019. Monthly cumulative rainfall (summed across daily  
104 values) were computed between 2005 and 2019.

105 We used the Normalized Difference Vegetation Index (NDVI) as an index of food  
106 availability. NDVI is obtained from the red:near-infrared reflectance ratio, with  $NDVI = (NIR -$   
107  $RED) / (NIR + RED)$ , where NIR and RED are the amounts of respectively near-infrared and red  
108 light, reflected by the vegetation and captured by satellites [24]. NDVI thus produces a  
109 quantitative index of primary productivity with higher values corresponding to a higher degree  
110 of vegetation cover [25]. It has previously been used as an indicator of habitat quality for the  
111 Tsaobis baboons [26] and other baboon populations [27]. We further confirmed that temporal  
112 variation in NDVI reflected temporal variation in rainfall: mean cumulative rainfall over the  
113 past three months explained between 60-72% of the NDVI variation (Appendix 1). To index  
114 food availability using NDVI, we first computed 100% isopleth home ranges for each group  
115 using kernel density estimates with the `adehabitatHR` package ('`kernelUD`' function) [28],  
116 based on the daily 30-min GPS locations from 2005-2019 (from 2016-2019 for M group). We  
117 obtained one home range per group for the entire study period. We then extracted the mean  
118 NDVI per 16 day-period on a 500 m  $\times$  500 m resolution (these 16-days windows are imposed  
119 by the resolution of the NASA datasets) across these periods using data provided by NASA  
120 (MODIS13A1 product) [25] within these home ranges. Daily NDVI was computed by linear  
121 interpolation and then averaged to obtain a monthly value. In contrast to rainfall, NDVI was  
122 measured with greater resolution and for each group separately because baboons finely adjust  
123 their ranging behaviour in relation to food availability [29].

124

125 **Individual data**

126 A female was considered adult when she reached menarche. The reproductive state of each  
127 adult female was monitored daily. A female could be: (i) pregnant (assessed by the paracallosal  
128 skin turning red and absence of cycles over the following months), with the exact start date of  
129 pregnancy being determined *post hoc* following infant birth, and encompassing 190 days (mean  
130 gestation length in this population,  $n = 13$  pregnancies where both conception and birth were  
131 observed, range: 181-200 days,  $SD = 5$ ) between conception and birth; (ii) lactating, as long as  
132 the female did not resume cycling after an infant birth; (iii) cycling, including both swollen  
133 females in oestrus (i.e., sexually receptive with a perineal swelling) and non-swollen females  
134 at other stages of their cycle. Conceptive cycles were established based on the beginning of a  
135 pregnancy and were usually confirmed by a birth. The first post-partum cycle (i.e. cycle  
136 resumption) is the first cycle following an infant's birth, when the female resumes cycling after  
137 lactation. The exact date of the cycle resumption corresponds to the first day of oestrus of the  
138 first post-partum cycle, i.e. the first day when a sexual swelling is recorded. The dates of these  
139 reproductive events (conceptions, births and cycling resumptions) were either known with  
140 accuracy when recorded by field observers, or estimated in the absence of observers using the  
141 methods detailed in Appendix 2 and Table S1.

142 Female parity was known from life history records and defined as primiparous (between  
143 the birth of her first and second infant) or multiparous (after the birth of her second infant).  
144 Parity of adult females at the start of the study was assessed using both the presence of older  
145 offspring based on a combination of behavioural and genetic data [30], alongside female age  
146 estimated using teeth eruption patterns [31].

147 Female social rank was established annually for each group using *ad libitum* and focal  
148 observations of agonistic interactions between adult females: supplants, displacements, attacks,  
149 chases and threats (Huchard and Cowlshaw 2011). We computed a linear hierarchy using  
150 Matman 1.1.4 (Noldus Information Technology, 2013) and then converted to a relative rank to

151 control for group size (i.e. the number of adult females in the group). Each female was thus  
152 assigned one rank per year, ranging from 0 (lowest ranking) to 1 (highest ranking).

153

#### 154 **Fitness data**

155 We tested the influence of birth timing in the annual cycle on two fitness measures, namely  
156 offspring mortality before weaning and the duration of the maternal interbirth interval. For each  
157 infant born between 1<sup>st</sup> January 2005 and 1<sup>st</sup> August 2018, we investigated whether it died  
158 (yes/no) before weaning. The weaning age was identified as 550 days on the basis of the  
159 maximum length of post-partum anoestrus (n = 33 cases for which both birth and cycle  
160 resumption were known with accuracy, see also Appendix 3) and presumably reflected the  
161 upper threshold of weaning age in our population [33,34]. Death was recorded when a corpse  
162 was observed or when the infant had been missing in the group for five consecutive days.  
163 Infants born later than August 2018 were not considered as their survival outcome was  
164 unknown. Four infants that disappeared between consecutive field seasons were omitted  
165 because we could not establish whether the age of death was before or after 550 days.

166 We defined interbirth intervals (IBI) as the number of days between two consecutive  
167 live births of the same female. We only considered IBIs for which the first infant reached  
168 weaning [18], i.e. survived until 550 days old. We discarded other IBIs as females resumed  
169 cycling rapidly after their infant's death when unweaned (median=21 days, range=9-51, n=9  
170 observed death), and their IBIs would have been shortened regardless of environmental  
171 seasonality.

172

#### 173 **Behavioural observations**

174 In order to characterize variation in maternal care and in mother-offspring conflict, we used  
175 three behavioural indicators: suckling, infant carrying and tantrum frequencies. We also used



176 these behavioural data, along with life history data, to assign different developmental stages,  
177 including the different stages of weaning and the peak of lactation after an infant's birth (see  
178 Appendix 3). Field observers collected a total of 1185 hours of focal observation [35] of 20 (in  
179 2017, 2018 and 2019) or 60 (in 2006) minutes long on 69 infants (mean  $\pm$  SD = 17.1  $\pm$  7.8  
180 hours of observations per infants, range = 6.3–34.6) (see Appendix 4 for more details).

181

### 182 Maternal care during weaning

183 Maternal care was quantified through two measures: suckling frequency and infant carrying  
184 frequency, which represent the two main energetic costs of maternal care before weaning  
185 [5,36]. First, for each scan observation (taken every 5 min), we considered whether the infant  
186 was suckling (1) or not (0) to investigate the effect of birth timing on variation in suckling  
187 frequency. Here, suckling was recorded when the focal individual had its mouth on its mother  
188 nipple, and we therefore could not distinguish comfort (when a juvenile suckles for reassurance,  
189 without any milk transfer [37]) from nutritive suckling. We considered only infants aged 2- to  
190 18-months-old for this analysis (Figure S1), using 11687 scans from 55 infants. The birth date  
191 uncertainty for these 55 infants ranged from 0 to 130 days (with a median birth date uncertainty  
192 of 16 days) and was taken into account in subsequent models (see Appendix 5).

193 Second, for each scan observation during which an infant was travelling, we determined  
194 whether the infant was carried by its mother (1) or travelled on its own (0). This variable  
195 allowed us to monitor the gradual decrease from full maternal dependence to full independence  
196 during travelling. We considered infants aged from 2 to 12 months old for this analysis (Figure  
197 S1), using 924 scans from 35 infants.

198

### 199 Mother-infant conflicts during weaning

200 We considered infant tantrums as a behavioural measure of mother-offspring conflict, reflecting  
201 when an infant's request to access resources from its mother was not initially satisfied [16]. We  
202 considered only infants aged 2 to 18 months old for this analysis (Figure S1), using 2221 focal  
203 observations from 55 infants. During each focal observation, we determined if a tantrum  
204 occurred (1) or not (0), based on a range of distinctive offspring vocalizations (gecks, moans  
205 and loud screams) and behaviours (frenzied behaviour when infants hurl themselves to the  
206 ground, sometimes accompanied by rapidly rotating their tail) that were recorded on a  
207 continuous basis and are characteristic of baboon tantrums [38,39]. A tantrum was considered  
208 to occur when at least two of these behaviours or vocalizations were recorded, separated by at  
209 least 30 seconds (isolated complaints, and complaints that lasted fewer than 30 seconds, were  
210 thus not considered as tantrums here). Tantrums were usually caused by maternal refusal of  
211 access to the nipple or to carrying and more rarely by maternal absence.

212

### 213 **Statistical analysis**

#### 214 Characterization of the environmental and reproductive seasonality of the Tsaobis baboons

215 First, to assess the strength and direction of reproductive seasonality, we used a Rayleigh test,  
216 from circular statistics, which characterizes the deviation of circular data from a uniform  
217 distribution, via the direction ( $\mu$ ) and length ( $R$ ) of the mean vector summing all observed  
218 events across the annual cycle ( $R=0$  when the event is evenly distributed, and  $R=1$  when all  
219 events are synchronized, i.e. occurs the same day) [40]. Our sample comprised 241 conceptions,  
220 215 births and 171 cycle resumptions which occurred between 2005 and 2019. Uncertainties in  
221 those dates were taken into account in all subsequent analyses using 1000 randomized  
222 reproductive events for each variable (Appendix 5).

223

#### 224 Birth timing effects on two fitness traits, and individual effects on birth timing

225 To quantify the effect of birth timing on the probability of offspring mortality before weaning  
226 (Model 1), we ran a generalized linear mixed model (GLMM) with a binomial error structure.  
227 We then ran a linear mixed model (LMM, Model 2), testing the effect of birth timing on IBIs.

228 In both models, we used a sine term to describe the timing of an infant's birth in the  
229 annual cycle (see Appendix 6 for more details on this procedure) [26]. We included as random  
230 effects year of infant birth and identity of the mother to control for repeated observations. We  
231 also included maternal parity, rank (in the birth year of the focal infant) and infant sex as fixed  
232 effects, because maternal parity and rank often affect reproductive traits in primates, including  
233 baboons [18,41], while infant sex can affect both the mother's subsequent interbirth interval  
234 [42] and the probability of infant survival in sexually dimorphic primates [43]. We also control  
235 for group identity as a fixed effect in both models, as data were collected from only three groups  
236 in this study [44].

237 We investigated the individual determinants of female reproductive decisions over birth  
238 timing, based on 215 births from 62 females. Our two response variables were the deviations,  
239 in days, from the birth timing that minimises offspring survival (December 15<sup>th</sup>) in Model 3  
240 and maternal IBIs (September 1<sup>st</sup>) in Model 4 (Table S2). For both Models 3 and 4, we tested  
241 the influence of infant sex, female parity and rank (as fixed effects) on the proximity of birth to  
242 the optimal timing for offspring survival (Model 3) or for maternal IBI (Model 4). We also  
243 controlled for the identity of the mother and birth year as random effects, in order to take into  
244 account the between-year environmental variation likely to affect birth timings. We included  
245 group identity as fixed effects (as there was only three levels for this factor [44]). We tested the  
246 significance of maternal identity using a likelihood-ratio test (LRT), comparing the model with  
247 and without this random effect.

248

249 Birth timing effects on maternal care and tantrum probability

250 We ran three GLMMs with a binomial error structure to test the effect of birth timing on the  
251 probability of suckling (Model 5), infant carrying (Model 6), and tantrums (Model 7). Models  
252 5 and 6 are scan-based data: during a scan observation, the infant is suckling (yes/no, Model  
253 5), and during a travelling scan observation, the infant is carried by its mother (yes/no, Model  
254 6). Model 7 is based on the entire focal observation as tantrum events are relatively rare: during  
255 a focal observation, the infant throws a tantrum (yes/no).

256 In order to investigate the potential effect of birth timing on maternal care and tantrum  
257 probability, we used a sine wave term for infant birth date as a fixed effect (Appendix 6). We  
258 included, as random effects, the identity of the infant (Models 5-7) to control for repeated  
259 observations. We also added the focal observation as a random effect for Models 5-6. We  
260 controlled for group identity and year of observation as fixed effects in all models, as there were  
261 less than five levels for both factors [44]. In all models, we included maternal parity, rank (in  
262 the year of birth of the focal infant) and infant sex as fixed effects. Such parameters are likely  
263 to affect reproductive performances as well as the probabilities of maternal care and mother-  
264 offspring conflict [39,43]. For Model 7, we also controlled for the duration of focal observation  
265 as a fixed effect.

266 For Models 5-7, we further controlled for the effects of infant age, which modulates the  
267 amount of maternal care and probability of tantrums throughout early development [16,43]. We  
268 considered four different possibilities for the form of the relationship between infant age and  
269 the response variable, using a regression thin plate spline (general additive model), a simple  
270 linear effect, and a polynomial regression (of 2 or 3 degrees), respectively [45]. To determine  
271 the best fit, we ran these different preliminary models with no other fixed effect but including  
272 all random effects (and the duration of focal observation for Model 7), and selected the model  
273 minimizing the AIC. The age effect was linear for suckling and infant carrying probabilities  
274 (Model 5 and 6), and a second-degree polynomial for tantrum probability (Model 7).

275           Lastly, mothers might be expected to invest more, and similarly infants might be  
276 expected to have more requests for maternal care, during the lean season, irrespective of the  
277 developmental trajectory of the infant, i.e. regardless of its age and birth timing (whether it was  
278 born in the optimal period or not). Therefore, we also investigated the potential effect of  
279 seasonality by assessing the influence of the observation date on suckling, infant carrying and  
280 tantrum probabilities (see Appendix 7 for more details). We did not include in the same model  
281 observation date and birth date, as they give redundant information (observation date is, by  
282 definition, the sum of birth date and infant's age, and infant's age is already included as a fixed  
283 effect). We present our models of birth date effects in the main text (Models 5-7, see also Table  
284 S3), and our models of observation date effects in the Supporting Information (Models 5bis-  
285 7bis, Table S4).

286           The structure of each model, with the different fixed and random effects included,  
287 alongside sample size, is summarised in Table S5.

288

## 289 Statistical methods

290 All statistical analyses were conducted in R version 3.5.0 [46]. For the Rayleigh test, we used  
291 the function 'r.test' from the R package 'CircStats' [47]. To run mixed models, we used 'lmer'  
292 (for LMMs) or 'glmer' (for binomial GLMMs) function on the lme4 package [48]. To run  
293 general additive mixed models (GAMMs) when investigating the best age effects on suckling,  
294 infant carrying and tantrum probabilities, we used the 'gam' function of the 'mgcv' package  
295 [45]. All quantitative fixed effects were z-transformed to facilitate model convergence. When  
296 we obtained singular fits, we confirmed the results by running the same models with a Bayesian  
297 approach, using the 'bglmer' and 'blmer' functions of the 'blme' package [49]. To diagnose the  
298 presence of multicollinearity, we calculated the variance inflation factor for each predictor in  
299 each full model using the 'vif' function of the R 'car' package [50]. These were lower than 2.5

300 in all cases. To assess the strength of the fixed effects in each model, we used the Wald chi-  
301 square tests with associated P-values computed with the ‘Anova’ function of the R package  
302 ‘car’ [50], and calculated the 95% Wald level confidence intervals. We further checked the  
303 distribution of residuals with ‘qqPlot’ function of the car package for LMMs [50], and with  
304 ‘simulateResiduals’ from DHARMA package for binomial GLMMs [51].

305

## 306 **Results**

### 307 **1. Characterization of the environmental and reproductive seasonality of the Tsaobis** 308 **baboons**

309 Environmental seasonality was pronounced at Tsaobis (Figure 1A). Mean annual rainfall was  
310 low and variable (mean  $\pm$  SD = 192  $\pm$  143mm), falling mostly between January and April  
311 (Figure 1A). Seasonal variation in NDVI, a satellite-based proxy of primary productivity,  
312 followed a similar, but slightly lagged pattern, to rainfall (Figure 1A). The highest birth  
313 frequency occurred in October-November (i.e. 28.4% of annual births), preceding the peak in  
314 rainfall (February) and NDVI (March-April, Figure 1A).

315 Conceptions, births and cycle resumptions occurred throughout the year (Figure S2),  
316 indicating an absence of a strict breeding season. We used circular statistics to test whether  
317 moderate seasonality may still occur, computing respectively the mean annual angle ( $\mu$ ) and  
318 Rayleigh tests (R and p-values) for the annual distribution of 241 conceptions, 215 births and  
319 171 cycle resumptions recorded between 2005-2019. The frequency of conceptions and births  
320 showed slight seasonal variations, which reached statistical significance for conceptions only  
321 (conceptions:  $\mu$  = May 12, R=0.13, p=0.02; births:  $\mu$ = November 18, R=0.09, p=0.17; cycle  
322 resumptions:  $\mu$ = December 4, R=0.08, p=0.36, Figure S2).

323

### 324 **2. Birth timing effects on two fitness traits, and individual effects on birth timing**

325 We considered two indicators of maternal fitness. First, we assessed whether or not infants  
326 survived until weaning (550 days). In our sample, 39 infants out of 195 (i.e. 20%) died before  
327 weaning, at a median age of 74 days (range 1-284 days, n=17 known dates of death). Second,  
328 we gathered 120 IBIs from 43 adult females, ranging from 397 to 1132 days with a mean of  
329 678 days (SD=128).

330 Birth timing influenced these two indicators of maternal fitness. First, birth timing  
331 affected offspring survival (Table S6): infants born between November 15<sup>th</sup> and January 1<sup>st</sup>  
332 were the most likely to survive until weaning (Table S2), indicating an optimal birth timing for  
333 offspring survival in the annual cycle (Figure 2A). Infants born in July 15<sup>th</sup> were 66% more  
334 likely to die before being weaned than the infants born in December 15<sup>th</sup> (Table S6). Second,  
335 the duration of maternal IBI was influenced by the timing of the birth opening the IBI (Table  
336 S6): females giving birth between August 1<sup>st</sup> and September 15<sup>th</sup> had the shortest IBIs (Table  
337 S2), indicating another different optimal birth timing for maternal reproductive pace in the  
338 annual cycle (Figure 2B). Females giving birth in September 1<sup>st</sup> had IBIs 73 days shorter than  
339 females giving birth in March 1<sup>st</sup>.

340 We then wondered whether some females might be more likely to time their births to  
341 maximise current over future reproduction, or vice versa. However, we failed to detect any  
342 significant variance associated with maternal identity on the deviation between observed birth  
343 and the optimal birth timing maximizing offspring survival (LRT=0.66, p=0.42) versus  
344 maternal IBI (LRT=0.00, p=0.98). This suggests that females did not consistently give birth in  
345 one timing over the other across successive births. Moreover, female parity, rank and infant sex  
346 did not influence the proximity of birth timing in relation to each optimum (Table 1).

347

### 348 **3. Birth timing effects on maternal care and tantrum probability**

349 In order to test whether maternal care may compensate for the costs of suboptimal birth timings  
350 in offspring, we investigated the effects of birth timing on the frequency of suckling and infant  
351 carrying. We did not find any effect of infant birth date on patterns of maternal care (Table S3).  
352 Further analyses revealed that mothers increase maternal care in the dryer winter months, but  
353 such compensation occurs regardless of an infant's birth date (Appendix 7, Table S4).

354 We also investigated whether infants born in suboptimal timings may beg for maternal  
355 care more frequently, looking at tantrum frequencies. We found that infants born near the  
356 maternal IBI optimal timing, i.e. between August 1<sup>st</sup> and October 1<sup>st</sup> (Table S2), were more  
357 likely to exhibit tantrums than other infants (Table S3, Figure 3). Observation date did not affect  
358 tantrum frequencies, meaning that such an effect was independent of the season of observation  
359 (Table S4).

360

## 361 **Discussion**

362 We identify two distinct optimal birth timings in the annual cycle, respectively favouring  
363 current reproduction (offspring survival) and future reproduction (maternal reproductive pace).  
364 These are separated by four months, and the highest birth frequency occurs between these  
365 optima, indicating that mothers balance current and future reproduction, though closer to the  
366 optimal birth timing favouring offspring survival. Several reasons might explain why offspring  
367 survival might be prioritized over maternal reproductive pace. First, lifespan and offspring  
368 survival are the primary components of female lifetime reproductive success in long-lived  
369 species such as baboons, while reproductive pace may be less important [52]. Second, shorter  
370 IBIs might compromise infant survival independently of the effect of birth timing, and are thus  
371 not necessarily adaptive [7]. Finally, the effect size of birth timing is greater on offspring  
372 survival than on maternal IBIs in our population.



373 More broadly, these results further our understanding of the evolution of vertebrate  
374 reproductive timing in several ways. First, trade-offs over birth timing may be widespread in  
375 long-lived species with slow life histories, for which development from birth to independence  
376 spans several months, therefore exceeding the length of the most productive season. In such  
377 cases, different stage(s) of the reproductive cycle may be synchronized with one or more  
378 seasonal food peaks, with the specific pattern dependent on the trade-offs females make among  
379 different fitness components [53]. Such variation could account for empirical cases where the  
380 observed birth peak fails to coincide with the birth timing expected on the basis of a single  
381 fitness measure. For example, in humans from pre-industrial Finland, births did not concentrate  
382 in the months with the highest infant survival expectations [54]. More generally, such trade-  
383 offs may contribute to explain the partial or total lack of breeding seasonality observed in some  
384 large mammals [55], such as social primates including apes [15] and humans [56,57].

385 Second, while different species synchronize different stages of their reproductive cycle  
386 with the seasonal food peak [1,2,58,59], this study reveals variations in breeding timing within  
387 the same population. However, while mothers experience a trade-off between reproductive pace  
388 and offspring survival in their birth timing, it is not clear if particular individuals consistently  
389 favour certain strategies, as we did not detect any inter-individual effects of female identity,  
390 parity or rank on parturition timing. Instead, intra-individual factors, such as maternal  
391 reproductive history, may constrain the evolution of such individually-based specializations, if  
392 only because the duration of IBIs - 22 months on average but with extensive variation - prevents  
393 females from giving birth every two years at the same period of the year. In addition, birth  
394 timings may be affected by many external factors beyond female control, such as male  
395 reproductive strategies. In addition, the costs of waiting for the next optimal timing may often  
396 outweigh the costs of giving birth at suboptimal timings.

397 Third, this study underlines the importance of weaning to understand the evolution of  
398 mammalian reproductive schedules. Late-weaning is most critical for infants, as they must learn  
399 to ensure their own provisioning. Matching that stage, which occurs between 12 and 18 months  
400 of age in this population, with the most productive season may substantially enhance infant  
401 survival (Figure 1B) [43,60,61]. Moreover, the peak of lactation, which is the most  
402 energetically-costly reproductive stage for mothers [3,43], typically coincides with the onset of  
403 weaning, occurring around 6 months after birth in this population. Matching lactation peak with  
404 abundant resources can alleviate the costs of reproduction and help to accelerate the transition  
405 to feeding independence by granting infants access to a wealth of weaning foods (Figure 1B)  
406 [43]. It may contribute to explain the shorter interbirth intervals associated with this birth  
407 timing. Such patterns may be very general. In the lemur radiation, for instance, despite a variety  
408 of life-histories, ecologies and societies, and the fact that different species mate and give birth  
409 at different times of year, all species synchronize weaning with the food peak [60]. Our  
410 understanding of the ultimate causes of mammalian reproductive seasonality may gain from  
411 granting more consideration to the dynamics and consequences of weaning, which may have  
412 been underappreciated in comparison to the energetic costs of pregnancy and lactation [1,2,4].

413 Fourth, our results show that the trade-off over birth timing faced by mothers may  
414 subsequently translate into mother-offspring conflict after birth. Although mothers adjust  
415 maternal care seasonally, they do so regardless of the offspring's age. Offspring born at  
416 suboptimal periods face the dry season in a critical developmental window (i.e., the end of  
417 weaning), and maternal care is insufficient to buffer them entirely from the adverse  
418 consequences that lead to higher mortality. Consequently, baboon infants respond by throwing  
419 more tantrums, which may be an honest signal of need [38,62], just as children do in similar  
420 situations [63]. More generally, these results shed light on the potential influence of  
421 environmental fluctuations, and specifically seasonality, on mother-offspring conflicts over

422 maternal care. While the literature focusing on optimal birth spacing has mainly examined  
423 trade-offs between current and future reproduction for an implicitly stable level of resources  
424 [7,64], such a stability may rarely be encountered by mothers in the wild, who typically face  
425 extensive, but partly predictable, fluctuations in food availability. Taking into account the  
426 intensity and predictability of resource fluctuations may largely re-draw the landscape of  
427 strategic decisions available to mothers confronted with trade-offs between current and future  
428 reproduction in natural environments [65,66].

429         Our findings open new perspectives to understand the evolutionary drivers of vertebrate  
430 reproductive seasonality, by revealing the occurrence of a maternal trade-off between current  
431 and future reproduction over birth timing, extended by mother-offspring conflict during  
432 weaning. Such a trade-off may commonly occur in organisms with a slow reproductive pace,  
433 and future studies on such taxa should investigate the consequences of reproductive timing on  
434 several fitness components. Indeed, multiple optimal birth timings in the annual cycle may  
435 generate a bimodal birth peak or an extended birth season. Evolutionary trade-offs over birth  
436 timing may therefore account for unexplained variation in the reproductive timing of long-lived  
437 vertebrates, including the evolution of non-seasonal breeding in humans and other species.

438

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454

## 455 REFERENCES

- 456 1. Bronson FH. 2009 Climate change and seasonal reproduction in mammals. *Philos.*  
457 *Trans. R. Soc. B Biol. Sci.* **364**, 3331–3340. (doi:10.1098/rstb.2009.0140)
- 458 2. Brockman DK, van Schaik C. 2005 Seasonality and reproductive function. In  
459 *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human*  
460 *Primates* (ed Cambridge University Press), pp. 269–305.
- 461 3. van Schaik CP, van Noordwijk MA. 1985 Interannual variability in fruit abundance  
462 and the reproductive seasonality in Sumatran Long-tailed macaques (*Macaca*  
463 *fascicularis*). *J. Zool., Lond.* **206**, 533–549. (doi:10.1111/j.1469-7998.1985.tb03557.x)
- 464 4. Janson C, Verdolin J. 2005 Seasonality of primate births in relation to climate. In  
465 *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human*  
466 *Primates*, pp. 307–350. Cambridge: Cambridge University Press.  
467 (doi:10.1017/cbo9780511542343.012)
- 468 5. Lee PC. 1996 The meanings of weaning: growth, lactation, and life history. *Evol.*  
469 *Anthropol.* **5**, 87–98. (doi:https://doi.org/10.1002/(SICI)1520-6505(1996)5:3<87::AID-  
470 EVAN4>3.0.CO;2-T)
- 471 6. Emery Thompson M. 2013 Comparative reproductive energetics of human and

- 472 nonhuman primates. *Annu. Rev. Anthropol.* **42**, 287–304. (doi:10.1146/annurev-anthro-  
473 092412-155530)
- 474 7. Lee SD, Ruiz-Lambides A V., Higham JP. 2019 Higher offspring mortality with short  
475 interbirth intervals in free-ranging rhesus macaques. *Proc. Natl. Acad. Sci.* **116**, 1–6.  
476 (doi:10.1073/pnas.1817148116)
- 477 8. Bateson P. 1994 The dynamics of parent-offspring relationships in mammals. *Trends*  
478 *Ecol. Evol.* **10**, 399–403. (doi:10.1016/0169-5347(94)90066-3)
- 479 9. Brinkhof MWG, Cavé AJ, Daan S, Perdeck AC. 2002 Timing of current reproduction  
480 directly affects future reproductive output in european coots. *Evolution (N. Y.)*. **56**, 400–  
481 411.
- 482 10. Fischer J *et al.* 2019 The Natural History of Model Organisms: Insights into the  
483 evolution of social systems and species from baboon studies. *Elife* **1960**, 1–16.
- 484 11. Barrett L, Henzi SP. 2008 Baboons. *Curr. Biol.* **18**, 404–406.  
485 (doi:10.1016/j.cub.2008.02.074)
- 486 12. Swedell L. 2011 African papionins: diversity of social organization and ecological  
487 flexibility. In *Primates in perspective*, pp. 241–277. Oxford: Oxford University Press.
- 488 13. Cheney DL *et al.* 2004 Factors affecting reproduction and mortality among baboons in  
489 the Okavango Delta, Botswana. *Int. J. Primatol.* **25**, 401–428. (doi:10.1016-  
490 0291/04/0400-0401/0)
- 491 14. Lycett JE, Weingrill T, Henzi SP. 1999 Birth patterns in the Drakensberg Mountain  
492 baboons (*Papio cynocephalus ursinus*). *S. Afr. J. Sci.* **95**, 354–356.
- 493 15. Campos FA *et al.* 2017 Does climate variability influence the demography of wild  
494 primates? Evidence from long-term life-history data in seven species. *Glob. Chang.*  
495 *Biol.* **23**, 1–15. (doi:10.1111/gcb.13754)
- 496 16. Maestriperi D. 2002 Parent–offspring conflict in primates. *Int. J. Primatol.* **23**, 923–

- 497 951. (doi:10.1023/A:1015537201184)
- 498 17. Trivers RL. 1972 Parental Investment and Sexual Selection. In *Sexual Selection and*  
499 *the Descent of Man 1871-1971* (ed Harvard University), pp. 136–207.  
500 (doi:10.1002/ajpa.1330400226)
- 501 18. Gesquiere LR, Altmann J, Archie EA, Alberts SC. 2017 Interbirth intervals in wild  
502 baboons: Environmental predictors and hormonal correlates. *Am. J. Phys. Anthropol.*  
503 **166**, 107–126. (doi:10.1002/ajpa.23407)
- 504 19. Bulger J, Hamilton WJ. 1987 Rank and density correlates of inclusive fitness measures  
505 in a natural chacma baboon (*Papio ursinus*) troop. *Int. J. Primatol.* **8**, 635–650.  
506 (doi:10.1007/BF02735781)
- 507 20. Packer C, Collins DA, Sindimwo A, Goodall J. 1995 Reproductive constraints on  
508 aggressive competition in female baboons. *Nature* **373**, 60–63. (doi:10.1038/373060a0)
- 509 21. Lonsdorf E V. 2017 Sex differences in nonhuman primate behavioral development. *J.*  
510 *Neurosci. Res.* **95**, 213–221. (doi:10.1002/jnr.23862)
- 511 22. Cowlshaw G, Davies JG. 1997 Flora of the Pro-Namib Desert Swakop River  
512 catchment, Namibia: community classification and implications for desert vegetation  
513 sampling. *J. Arid Environ.* **36**, 271–290. (doi:10.1016/0140-1963/97/020271)
- 514 23. Huffman GJ, Bolvin DT, Nelkin EJ, Adler RF. 2016 TRMM (TMPA) Precipitation L3  
515 1 day 0.25 degree x 0.25 degree V7.
- 516 24. Pettorelli N, Vik JO, Mysterud A, Gaillard JM, Tucker CJ, Stenseth NC. 2005 Using  
517 the satellite-derived NDVI to assess ecological responses to environmental change.  
518 *Trends Ecol. Evol.* (doi:10.1016/j.tree.2005.05.011)
- 519 25. Didan K, Barreto Munoz A, Solano R, Huete A. 2015 MOD13A1 MODIS/Terra  
520 Vegetation Indices 16-Day L3 Global 500m SIN Grid V006 [Data set].  
521 (doi:https://doi.org/10.5067/MODIS/MOD13A1.006)

- 522 26. Dezeure J, Dagorrette J, Baniel A, Carter AJ, Cowlshaw G, Marshall HH, Martina C,  
523 Raby CL, Huchard E. 2021 Developmental transitions in body color in chacma baboon  
524 infants: Implications to estimate age and developmental pace. *Am. J. Phys. Anthropol.*  
525 **174**, 89–102. (doi:10.1002/ajpa.24118)
- 526 27. Zinner D, Pei Aez F, Torkler F. 2001 Distribution and habitat associations of baboons  
527 (*Papio hamadryas*) in central Eritrea. *Int. J. Primatol.* **22**, 397–413.
- 528 28. Calenge C. 2006 The package ‘adehabitat’ for the R software: A tool for the analysis of  
529 space and habitat use by animals. *Ecol. Modell.* **197**, 516–519.  
530 (doi:10.1016/j.ecolmodel.2006.03.017)
- 531 29. Bronikowski AM, Altmann J. 1996 Foraging in a variable environment: weather  
532 patterns and the behavioral ecology of baboons. *Behav Ecol Sociobiol* **39**, 11–25.
- 533 30. Huchard E, Knapp L, Wang J, Raymond M, Cowlshaw G. 2010 MHC , mate choice  
534 and heterozygote advantage in a wild social primate. *Mol. Ecol.* , 2545–2561.  
535 (doi:10.1111/j.1365-294X.2010.04644.x)
- 536 31. Huchard E, Courtiol A, Benavides JA, Knapp LA, Raymond M, Cowlshaw G. 2009  
537 Can fertility signals lead to quality signals? Insights from the evolution of primate  
538 sexual swellings. *Proc. R. Soc. B Biol. Sci.* **276**, 1889–1897.  
539 (doi:10.1098/rspb.2008.1923)
- 540 32. Huchard E, Cowlshaw G. 2011 Female – female aggression around mating : an extra  
541 cost of sociality in a multimale primate society. *Behav. Ecol.* **22**, 1003–1011.  
542 (doi:10.1093/beheco/arr083)
- 543 33. Borries C, Lu A, Ossi-Lupo K, Larney E, Koenig A. 2014 The meaning of weaning in  
544 wild Phayre’s leaf monkeys: Last nipple contact, survival, and independence. *Am. J.*  
545 *Phys. Anthropol.* **154**, 291–301. (doi:10.1002/ajpa.22511)
- 546 34. Saltzman W, Tardif SD, Rutherford JN. 2011 Hormones and Reproductive Cycles in

- 547 Primates. In *Hormones and reproduction of vertebrates* (eds Norris DO, Lopez K), pp.  
548 1–40. New York: NY Academic Press.
- 549 35. Altmann J. 1974 Observational Study of Behavior: Sampling Methods. *Behaviour* **49**,  
550 227–267.
- 551 36. Altmann J, Samuels A. 1992 Costs of maternal care: infant-carrying in baboons. *Behav.*  
552 *Ecol. Sociobiol.* **29**, 391–398. (doi:10.1007/BF00170168)
- 553 37. Bădescu I. 2018 The attainment of independence from the mother in primate infants  
554 and its implications for the evolution of cooperative breeding in hominins. In *The*  
555 *talking species : perspectives on the evolutionary, neuronal and cultural foundations of*  
556 *language* (eds EM Luef, MM Marin), pp. 169–194. Uni-Press Graz.
- 557 38. Barrett L, Henzi PS. 2000 Are baboon infants Sir Phillip Sydney’s offspring? *Ethology*  
558 **106**, 645–658. (doi:10.1046/j.1439-0310.2000.00577.x)
- 559 39. Nicolson N. 1982 Weaning and the Development of Independence in Olive Baboons.  
560 Harvard University, Cambridge, Massachusetts. (doi:10.13140/RG.2.1.4000.9761)
- 561 40. Batschelet E. 1981 *Circular Statistics in Biology (Mathematics in Biology)*. Academic  
562 Press.
- 563 41. Altmann J, Alberts SC. 2005 Growth rates in a wild primate population: ecological  
564 influences and maternal effects. *Behav. Ecol. Sociobiol.* **57**, 490–501.  
565 (doi:10.1007/s00265-004-0870-x)
- 566 42. Bercovitch FB, Berard JD. 1993 Behavioral Ecology and Sociobiology Life history  
567 costs and consequences of rapid reproductive maturation in female rhesus macaques.  
568 *Behav Ecol Sociobiol* **32**, 103–109.
- 569 43. Altmann J. 1980 *Baboon Mothers and Infants*. The University of Chicago Press.
- 570 44. Harrison XA, Donaldson L, Eugenia Correa-Cano M, Evans J, Fisher DN, Goodwin C,  
571 Robinson B, Hodgson DJ, Inger R. 2017 Best practice in mixed effects modelling and



- 572 multi-model inference in ecology. *PeerJ Open Access*  
573 (doi:10.7287/peerj.preprints.3113v1)
- 574 45. Wood SN. 2003 Thin plate regression splines. *J. R. Stat. Soc. Stat. Methodol. Ser. B* **65**,  
575 95–114.
- 576 46. R Core Team. 2019 R: A language and environment for statistical computing.
- 577 47. Agostinelli C, Lund U. 2018 Package ‘CircStats’: Circular Statistics, from ‘Topics in  
578 Circular Statistics’.
- 579 48. Bates D, Mächler M, Bolker BM, Walker SC. 2015 Fitting linear mixed-effects models  
580 using lme4. *J. Stat. Softw.* **67**. (doi:10.18637/jss.v067.i01)
- 581 49. Dorie V. 2015 blme: Bayesian Linear Mixed-Effects models.
- 582 50. Fox J *et al.* 2019 Companion to Applied Regression.
- 583 51. Hartig F. 2020 Package ‘DHARMA’: Residual Diagnostics for Hierarchical (Multi-  
584 Level / Mixed) Regression Models.
- 585 52. Weibel CJ, Tung J, Alberts SC, Archie EA. 2020 Accelerated reproduction is not an  
586 adaptive response to early-life adversity in wild baboons. *PNAS* **117**, 24909–24919.  
587 (doi:10.1073/pnas.2004018117/-/DCSupplemental)
- 588 53. Jones TM *et al.* 2020 Parental benefits and offspring costs reflect parent-offspring  
589 conflict over the age of fledging among songbirds. *PNAS* **117**, 30539–30546.  
590 (doi:10.1073/pnas.2008955117)
- 591 54. Lummaa V, Lemmetyinen R, Haukioja E, Pikkola M. 1998 Seasonality of births in  
592 *Homo sapiens* in pre-industrial Finland: maximisation of offspring survivorship? *J.*  
593 *Evol. Biol.* **11**, 147–157. (doi:10.1046/j.1420-9101.1998.11020147.x)
- 594 55. Bronson FH. 1989 *Mammalian Reproductive Biology*. Chicago: The University of  
595 Chicago Press.
- 596 56. Bronson FH. 1995 Seasonal variations in human reproduction: environmental factors.

- 597 *Q. Rev. Biol.* **70**, 55.
- 598 57. Ellison PT, Valeggia CR, Sherry DS. 2005 Human Birth Seasonality. In *Seasonality in*  
599 *Primates: Studies of Living and Extinct Human and Non-Human Primates*, pp. 379–  
600 399. Cambridge: Cambridge University Press.
- 601 58. Stouffer PC, Johnson EI, Bierregaard RO. 2013 Breeding seasonality in central  
602 Amazonian rainforest birds. *Auk* **130**, 529–540. (doi:10.1525/auk.2013.12179)
- 603 59. Sinclair ARE, Mduma SAR, Arcese P. 2000 What determines phenology and  
604 synchrony of ungulate breeding in Serengeti? *Ecology* **81**, 2100–2111.  
605 (doi:10.1890/0012-9658(2000)081[2100:WDPASO]2.0.CO;2)
- 606 60. Wright PC. 1999 Lemur Traits and Madagascar Ecology: Coping With an Island  
607 Environment. *Yearb. Phys. Anthropol.* **42**, 31–72. (doi:10.1002/(sici)1096-  
608 8644(1999)110:29+<31::aid-ajpa3>3.0.co;2-0)
- 609 61. Barrett L, Henzi SP, Lycett JE. 2006 Whose Life Is It Anyway? Maternal Investment,  
610 Developmental Trajectories, and Life History Strategies in Baboons. In *Reproduction*  
611 *and Fitness in Baboons: Behavioral, Ecological, and Life History Perspectives*, pp.  
612 199–224.
- 613 62. Lummaa V, Vuorisalo T, Barr RG, Lehtonen L. 1998 Why Cry? Adaptive Significance  
614 of Intensive Crying in Human Infants. *Evol. Hum. Behav.* **19**, 193–202.
- 615 63. Fouts HN, Hewlett BS, Lamb ME. 2005 Parent-Offspring weaning conflicts among the  
616 Bofi farmers and foragers of Central Africa. *Curr. Anthropol.* **46**, 29–50.
- 617 64. Fotso JC, Cleland J, Mberu B, Mutua M, Elungata P. 2013 Birth spacing and child  
618 mortality: An analysis of prospective data from the nairobi urban health and  
619 demographic surveillance system. *J. Biosoc. Sci.* **45**, 779–798.  
620 (doi:10.1017/S0021932012000570)
- 621 65. Ljungström G, Francis TB, Mangel M, Jørgensen C. 2019 Parent-offspring conflict

622 over reproductive timing: Ecological dynamics far away and at other times may explain  
623 spawning variability in Pacific herring. *ICES J. Mar. Sci.* **76**, 559–572.  
624 (doi:10.1093/icesjms/fsy106)

625 66. de Villemereuil P *et al.* 2020 Fluctuating optimum and temporally variable selection on  
626 breeding date in birds and mammals. *PNAS* , 1–10. (doi:10.1073/pnas.2009003117/-  
627 /DCSupplemental.y)

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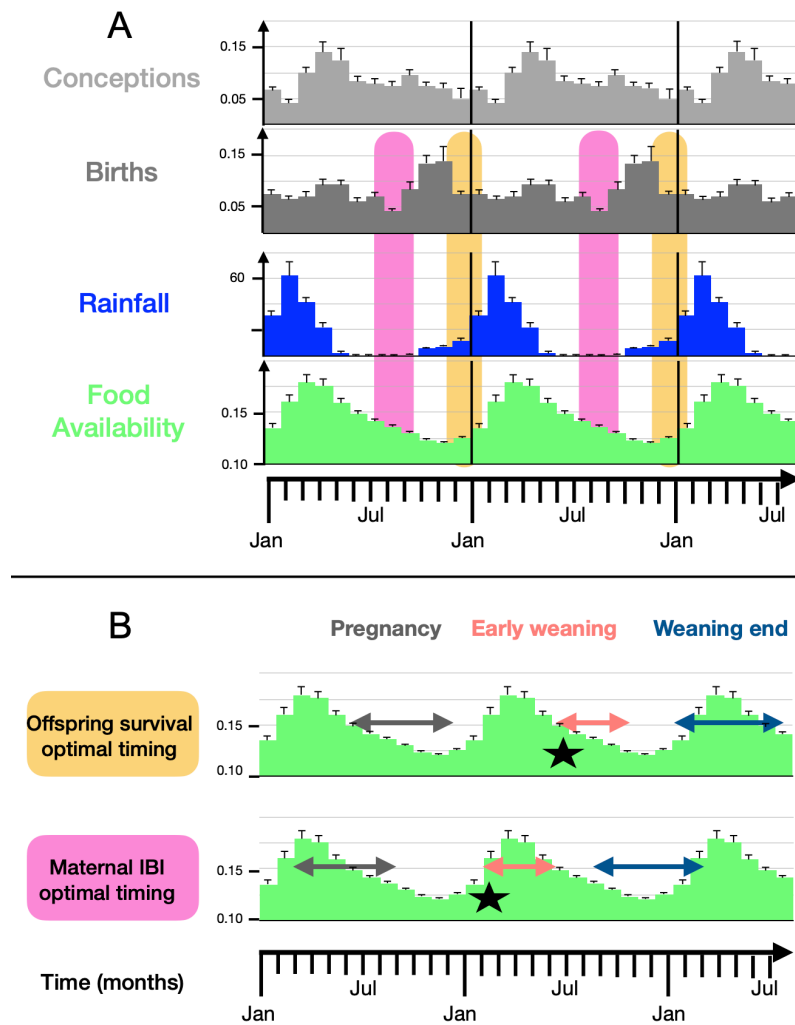
630 **TABLES**

631 **Table 1:** Predictors of female reproductive timing.

632 Estimates, confidence intervals,  $X^2$  statistics and P-values of the predictors of the two linear mixed models (Models  
 633 3 and 4). The response variables are respectively the deviation from the offspring survival optimal birth timing,  
 634 i.e. from December 15<sup>th</sup> (Model 3), and the deviation from the maternal IBI optimal birth timing, i.e. from  
 635 September 1<sup>st</sup> (Model 4), in days, based on 215 births from 62 females. Female identity and year of infant birth are  
 636 included as random effects. For categorical predictors, the tested category is indicated between parentheses.

Fixed effect	Estimate	IC		$X^2$	P-value	
		Lower	Upper			
<b>Model 3: Deviation from the offspring survival optimal birth timing</b>						
Infant sex	(Male)	5.91	-7.42	19.23	0.76	0.385
Female parity	(Primiparous)	-12.77	-30.02	4.47	2.11	0.147
Female rank		2.59	-4.82	10.00	0.47	0.493
Group	(L)	5.16	-10.37	20.69	1.33	0.515
	(M)	-12.66	-44.70	19.39		
<b>Model 4: Deviation from the maternal IBI optimal birth timing</b>						
Infant sex	(Male)	-3.19	-16.46	10.08	0.22	0.7637
Female parity	(Primiparous)	9.67	-7.49	26.82	1.22	0.269
Female rank		-3.41	-10.75	3.92	0.83	0.362
Group	(L)	10.67	-4.70	26.04	1.92	0.382
	(M)	0.93	-30.91	32.78		

637



639

640 **Figure 1:** Tsaobis baboons' reproductive timings in relation with environmental seasonality.

641 In Panel A, we plotted the proportion of conceptions (N=241, in light grey) and births (N=215, in dark grey)

642 recorded in 2005-2019 per month (Jan for January, Jul for July). We plotted the mean monthly cumulative rainfall

643 (in mm) per month in blue and the mean NDVI value per month in green between 2005 and 2019. We represented

644 the standard errors associated with vertical black segments. The pink and orange squares in the background

645 represent respectively the maternal IBI and the offspring survival optimal birth timings. In Panel B, we aimed to

646 represent the different phases of the female reproductive cycle, when the birth date occurs within the offspring

647 survival (December 15<sup>th</sup>) or maternal IBI (September 1<sup>st</sup>) optimal timing, according to seasonal variation of NDVI.

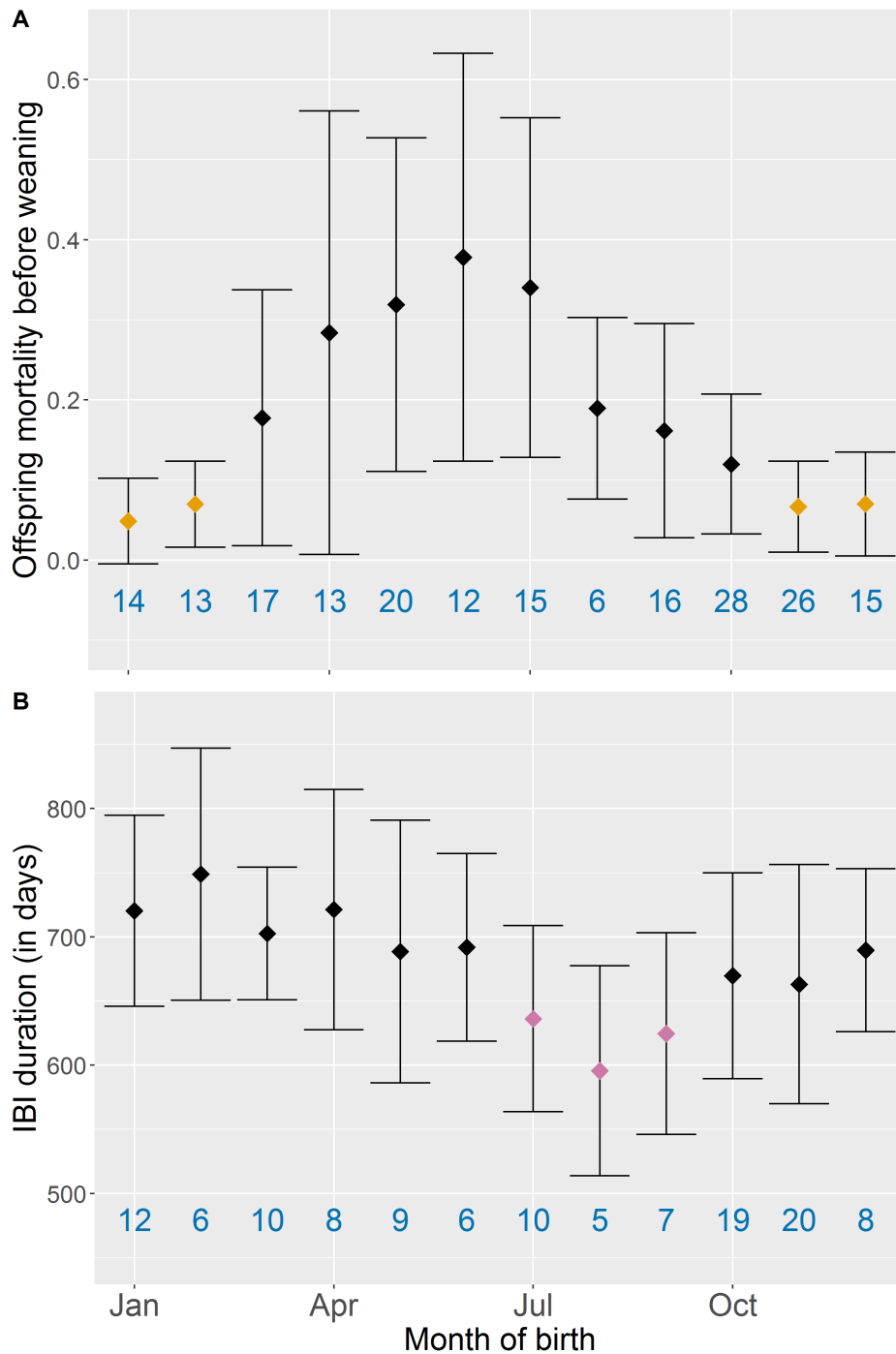
648 The green bar plot in the background indicates the mean NDVI per month (see y-axis). Pregnancy, indicated with

649 grey arrows, occurs the 6 months prior a birth. Early-weaning, indicated with salmon-colour arrows, occurs from

650 6 to 9 months after a birth. Lactation peak, indicated with black stars, occur around 6 months after a birth. Weaning

651 end, indicated with blue arrows, occurs from 12 to 18 months after a birth (see Appendix 3 for the characterization

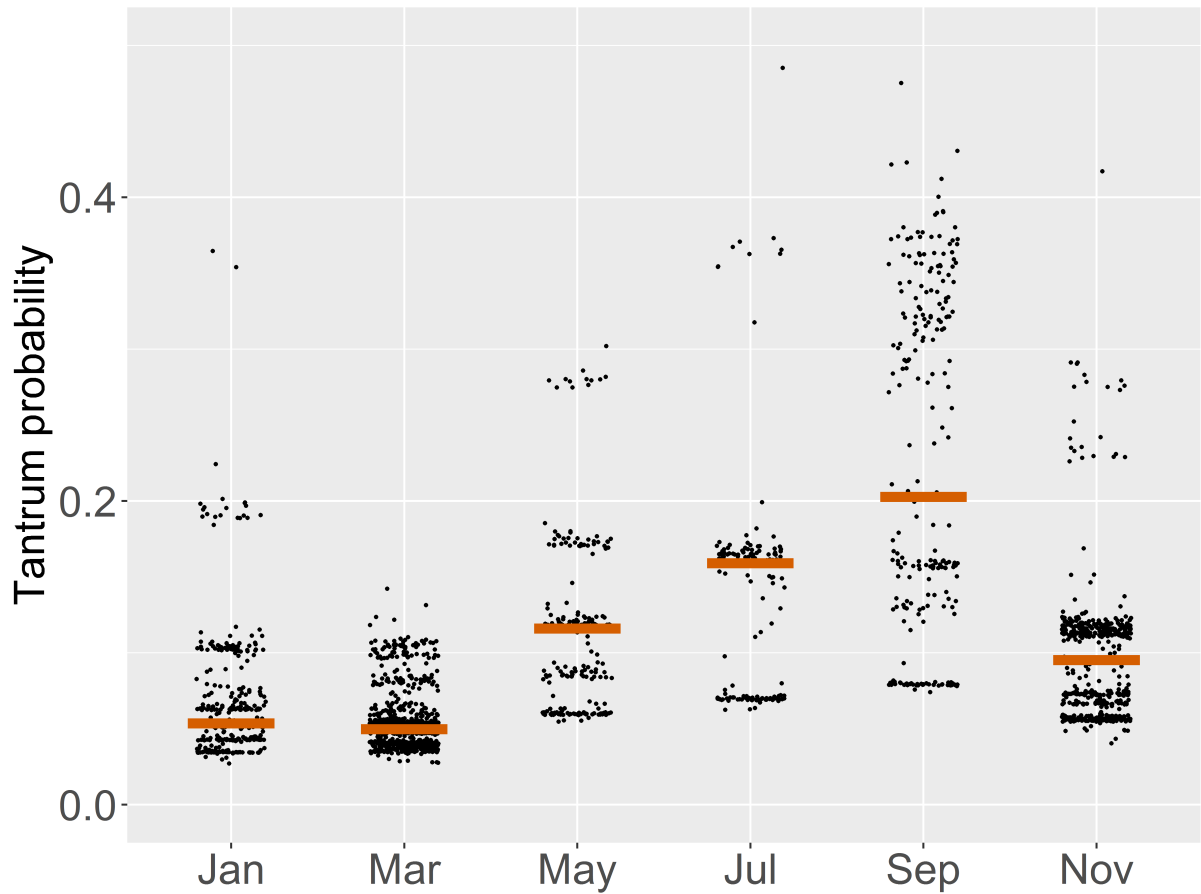
652 of these different reproductive stages).



653

654 **Figure 2:** Distinct optimal birth timings for current and future reproduction.

655 We plotted the predicted values of the full models (Model 1 looking at offspring mortality in panel A, and Model  
 656 2 looking at IBIs in panel B) according to the month of infant birth (Jan for January, Apr for April, etc.). The  
 657 number of births observed for each month is indicated in blue below the bar. The dots represent the mean values,  
 658 while the vertical black bars represent its standard deviations. The offspring survival optimal birth timing is  
 659 identified as the period minimizing offspring mortality, i.e. from November to February, and indicated with orange  
 660 dots (Panel A). The maternal IBI optimal birth timing is identified as the period minimizing maternal interbirth  
 661 interval, i.e. from July to September, and indicated with pink dots (Panel B).



662

663 **Figure 3:** Influence of birth timing on tantrum probability.

664 Predicted values of tantrum probability (Model 7) at weaning (age 12 months), according to infants' birth month,

665 based on 2221 focal observations from 55 infants. For graphical reasons, and given the low sample size of infants

666 observed for some birth months, we pooled infants born in 2 consecutive months, so that Jan indicates infants born

667 in both January and February, Mar in both March and April, etc. The brown horizontal bars indicate the median

668 values of fitted values for each birth month category.

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673  
674 **Supporting Information for:**  
675 **Birth timing generates reproductive trade-offs in a non-seasonal**  
676 **breeding primate**

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719 SUPPLEMENTARY TEXT

720 **Appendix 1.** Correlations between rainfall and NDVI at Tsaobis

721 In order to estimate the correlation between monthly rainfall and NDVI at Tsaobis, we used a  
722 moving window approach. We expected that the cumulative rainfall over the preceding months,  
723 rather than the rainfall during the current month, would be the best predictor of monthly NDVI.  
724 First, we identified the time window maximizing the correlation between rainfall and NDVI  
725 variation, testing periods covering 0 to 6 month(s) prior to the current month using an AIC-  
726 based selection procedure, and a univariate linear model containing only the fixed effect of  
727 interest (cumulative rainfall over variable periods) and three response variables, namely the  
728 monthly NDVI values associated with the home ranges of all three study groups. For these three  
729 groups, the time window minimizing the model AIC was cumulative rainfall over the preceding  
730 three months. The adjusted value of the model  $R^2$  measures the proportion of NDVI variance  
731 explained by variation in cumulative rainfall over the past three months.

732

733 **Appendix 2.** Estimations of the dates of conceptions, births and cycle resumptions

734 We characterized the reproductive seasonality in our population considering three main  
735 reproductive events: conceptions, births, and cycle resumptions (i.e. the end of post-partum  
736 amenorrhea).

737 1. **Births.** The dates of births, conceptions, and cycle resumptions were directly  
738 observed where possible, but otherwise estimated for those periods when no observers were  
739 present. We observed a total of 84 births. Of those, 62 were seen by observers on the exact day,  
740 and 22 were witnessed after a short absence (leading to a small uncertainty in the actual date:  
741 median=17 days, range=1-30). When the conception only was observed (n=52 births), we  
742 estimated birth dates by adding the mean gestation length (n=190 days, range: 181-200 days,

743 SD=5, n=13 pregnancies where both conception and birth were observed) to the conception date.  
744 Conception was considered to occur on the day of deturgescence (D-day) of the swelling during  
745 a conceptive cycle. This generated a total of 136 birth dates known with high accuracy. When  
746 neither conception nor birth were observed (n=56 births), the birth date was estimated using  
747 infant coloration (based on the progressive loss of natal coat and skin coloration) following a  
748 method recently described and validated in our population [1], with further refinement provided  
749 by the reproductive history of the mother (e.g., if the mother was pregnant during the last three  
750 months of a field season, then the infant was necessarily born in the three months following the  
751 end of this season given that a pregnancy lasts 190 days). Finally, when neither birth nor  
752 conception was observed, and infant colour when first seen was unknown or uninformative (i.e.,  
753 the transition from natal to adult coat had already occurred) (n=23 births), we used the  
754 reproductive state of females in the preceding field season to minimize uncertainty over birth  
755 timing. For example, if a female was cycling the last day of the preceding season, the infant was  
756 necessarily born at least 190 days after this day. In total, our sample comprised 215 births  
757 between 2005 and 2019, with a median uncertainty of 10 days (range: 0-153 days) (Table S1).

758           2. **Conceptions.** We observed 81 conceptions: 68 conceptions were witnessed  
759 (observers were present during the conceptive cycle), and 13 occurred during a short absence  
760 of observers (leading to a small uncertainty in the actual date: median=10 days, range=3-30).  
761 The exact date of conceptions was the day of swelling detumescence of the conceptive cycle  
762 (when witnessed) [2]. When the birth was observed but not the conception, the latter was  
763 estimated to occur 190 days prior to birth (n=65 conceptions). When neither conception nor  
764 birth were observed but birth occurred (i.e. no miscarriage), we estimated birth date as  
765 explained above, and inferred conception from the birth date using the mean gestation period  
766 (n=79). Finally, when pregnancy signs were seen (i.e. red paracallosal skin and an absence of  
767 cycles) but conception was not observed and there was no birth due to a miscarriage or early

768 death (occurring before an infant was recorded by observers), we estimated the date of  
769 conception using female reproductive states (n=16 conceptions). For example, if a female was  
770 seen pregnant on the first day of a field season, we knew that the conception occurred from 0-  
771 190 days prior to this date (as gestation lasts 190 days in this population). All in all, we  
772 generated a sample of 241 conceptions, with a median uncertainty of 10 days (range: 0-164  
773 days).

774           3. *Cycle resumptions*. Only cycle resumptions following a period of lactation were  
775 included in our analyses. Cycle resumptions were observed in 64 cases. In 107 other cases, a  
776 female was lactating at the end of a field season and then cycling at the beginning of the next  
777 (median days between consecutive field seasons=225, range=83-584). To reduce the  
778 uncertainty of the resumption date estimations in these cases, we calculated the minimum post-  
779 partum amenorrhea length (the time between birth and cycle resumption) (mean  $\pm$  SD = 353  $\pm$   
780 89 days, range=223-550) based on the 33 cases for which both events were known, and used  
781 this value as a minimum threshold in our estimations. We also excluded all cycle resumptions  
782 for which the uncertainty exceeded one year. Our sample thus comprised a total of 171 cycle  
783 resumptions, with a median uncertainty of 61 days (range= 0-272 days).

784

### 785 **Appendix 3.** Characterization of developmental stages: weaning and lactation peak

786 In order to understand which stage of the reproductive cycle might be timed with the seasonal  
787 food peak (Figure 1B), we needed to define the sequential behavioural stages of weaning, which  
788 is the infant's gradual transition to nutritional independence [3], along with the peak of lactation  
789 in our population. First, the onset of weaning can be defined as the period when solid foods  
790 start to account for an important part of an infant's energy intake, and is characterized by an  
791 increase in maternal refusals to accede to her offspring's suckling demands. The onset of

792 behavioural conflict between a mother and her offspring has therefore often been used as a  
793 proximate measure of the early-weaning period [3]. In our population, tantrum probabilities  
794 peak between 6 and 9 months of age (Figure S1), and we therefore used this age window to  
795 characterize ‘early-weaning’. The peak of lactation typically occurs just before the beginning  
796 of weaning [3,4], when offspring have grown larger but are still fully dependent. So we can  
797 consider that lactation peak occurs around 6 months after birth in our population. Similar ages  
798 for early-weaning and lactation peak have been found in other baboon populations [5–7], albeit  
799 weaning age and lactation durations can vary substantially between populations [8].

800         The end of weaning can be defined as the complete cessation of nursing, i.e. when  
801 offspring feed exclusively on solid foods. Looking at behavioural data, suckling frequencies  
802 decrease gradually from 2 to 18 months old, before stabilizing to ca. 2% of time from 18 to 24  
803 months old (Figure S1). In addition, the maximum length of post-partum amenorrhea (PPA),  
804 often used as a proxy for the end of weaning [3], was 550 days (i.e. 18.1 months) in this  
805 population (based on  $n = 33$  cases for which both birth and cycle resumption were known with  
806 accuracy). We therefore considered the age of 18.1 months as an upper threshold marking the  
807 end of weaning for all juveniles in our models on infant mortality and IBI (see main text).  
808 However, age at the end of weaning is highly variable between individuals, as indicated by the  
809 wide range of variation for PPA (8-18 months, mean = 12 months). To take this variation into  
810 account, we defined the ‘end of weaning’ as the age window of 12-18 months after birth for  
811 Figure 1B.

812         All in all, for Figure 1B, in order to better understand the relationship between  
813 reproductive phenology and environmental seasonality, we considered the lactation peak to  
814 occur around 6 months after birth, early-weaning between 6 and 9 months of age, and the end  
815 of weaning between 12 and 18 months of age. As a note of caution, these windows are strictly  
816 based on behavioural and life-history data, which show some limitations to evaluate the

817 dynamics of lactation [9,10]. More objective measures, such as isotopic comparisons of mother-  
818 offspring hair or faecal samples [11–14], may help to refine these estimates.

819

#### 820 **Appendix 4.** Methodology of infants' focal observations

821 Field observers collected behavioural data on infants aged between 2 and 24 months on a daily  
822 basis from dawn until dusk over four periods: from October to December 2006, from July to  
823 August 2017, from September to December 2018, and from April to July 2019. We collected a  
824 total of 1185 hours of focal observation on 69 infants across four field seasons (mean  $\pm$  SD =  
825  $17.1 \pm 7.8$  hours of observations per infants, range = 6.3–34.6), with a mean of 40.7 focal  
826 observations per individual (SD=29.4). Focal observations were spread equally across the day  
827 (divided in four 3 h-long blocks) and focal individuals were chosen randomly, and never  
828 sampled more than once within a block. Focal observations durations were 1 h in 2006 and 20  
829 min in 2017-2019, with a minimum of 10 min in all cases. We recorded the following activities  
830 on a continuous basis: suckling (when the focal individual had its mouth on its mother's nipple;  
831 we could not distinguish comfort from nutritive suckling), travelling alone, infant carrying  
832 (carried by the mother, either ventrally or dorsally) and other activities. We also collected  
833 events related to mother-offspring conflicts (see in main text). In addition, we collected scan  
834 observations every 5 minutes (n=16702 scans across 3081 focal observations), including the  
835 activity of the focal individual.

836

#### 837 **Appendix 5.** Controlling for uncertainties in the dates of conceptions, births and cycle

838 resumptions in statistical analyses

839 Dates of conceptions, births and cycle resumptions were estimated in many cases because the  
840 Tsaobis baboons are not followed year round (see Appendix 1). In addition, uncertainty in these  
841 estimations varied with the time of year, as we generally follow baboons during the cooler,

842 dryer months. In order to account for these uncertainties in our analyses, we ran a set of  
843 randomizations to evaluate the robustness of the fixed effects found to be statistically  
844 significant. For each reproductive event (conceptions, births, and cycle resumptions) for which  
845 the date was associated to some uncertainty (i.e. exact date unknown), we created an extended  
846 dataset including all possible dates of the full range of uncertainty (from the minimum to the  
847 maximum date). For example if a baboon birth date was estimated to occur between October  
848 2<sup>nd</sup> and December 23<sup>rd</sup>, we included all possible dates between October 2<sup>nd</sup> and December 23<sup>rd</sup>  
849 in this extended dataset. Using this extended dataset, we generated 1000 simulations; in each  
850 iteration, a date was randomly drawn between the minimal and maximal estimate for each  
851 reproductive event that was not known with certainty. Events known with certainty did not vary  
852 throughout such simulations.

853         These simulations were integrated in different statistical analyses slightly differently. In  
854 our characterization of reproductive seasonality, we extracted the mean  $R$ ,  $\mu$  and p-value of the  
855 Rayleigh test for the 1000 simulated datasets of cycle resumptions, conceptions and births. We  
856 indicate these mean values in the main text. We also computed the 95% level confidence  
857 intervals of these p-values: for conceptions,  $p=0.019 - 0.021$ ; for births,  $p=0.166 - 0.174$ ; for  
858 cycle resumptions,  $p=0.328 - 0.358$ .

859         In our multivariate mixed models investigating the effect of seasonal birth timing on  
860 offspring mortality before weaning (Model 1) and maternal interbirth intervals (Model 2), we  
861 controlled for the uncertainties in dates of birth which could affect both our response variables  
862 and our main fixed effect of interest (seasonal birth timing). For Model 1, we generated 1000  
863 simulations with random birth dates drawn, for each birth, between minimal and maximal birth  
864 date estimations for this particular birth, and subsequently ran 1000 mixed models, one for each  
865 simulated value of the offspring's birth date and for each survival outcome (as birth date affects  
866 an offspring's age, and therefore its estimated age at death). For Model 2, we similarly

867 generated 1000 simulations with random birth dates drawn between minimum and maximum  
868 birth date estimations for the two births defining the IBI. We subsequently ran 1000 models  
869 with randomized values for both IBI (the response variable, i.e. number of days between the  
870 first and second birth) and the birth date fixed effect. For both models, we then extracted the  
871 1000 p-values of our fixed effect ‘seasonal birth timing’ and computed the confidence intervals  
872 of these p-values (see the footnote of Table S6).

873 In our analysis of the individual determinants of birth timing (Models 3 and 4), we  
874 similarly generated 1000 simulations of birth dates drawn between minimum and maximum  
875 birth date estimations, and assessed for each of these randomly drawn births the deviation, in  
876 days, from December 15<sup>th</sup> for Model 3 and September 1<sup>st</sup> for Model 4 respectively. For both  
877 models, we then ran 1000 LMMs using these deviations as the response variable (Models 3 and  
878 4). We extracted 1000 p-values of our various fixed effects, and computed their 95% level  
879 confidence intervals. No fixed effect was close to significance, and this information was thus  
880 not added to the footnote of Table 1.

881 Finally, in our analysis investigating the effects of seasonal birth timing on maternal  
882 care and mother-offspring conflict at the behavioural level, we similarly generated 1000  
883 simulations of birth dates drawn between minimum and maximum birth date estimations. We  
884 then ran 1000 GLMMs looking at the effect of seasonal birth timing, along with other  
885 covariates, on the probabilities of suckling (Model 5), infant carrying (Model 6) and tantrums  
886 (Model 7). We extracted the 1000 resulting p-values for our fixed effect ‘seasonal birth timing’,  
887 computed their median and 95% level confidence interval, and added this information to the  
888 footnote of Table S3.

889



890 **Appendix 6.** Method used to capture birth timing effects in Models 1-2 and 5-7

891 To investigate the influence of birth timings on offspring mortality (Model 1), female IBI  
892 (Model 2), suckling probability (Model 5), infant carrying probability (Model 6) and tantrum  
893 probability (Model 7), we used a sine term that captures the timing of an infant's birth in the  
894 annual cycle. Sine waves allow the introduction of a circular variable into a multivariate model  
895 as a fixed effect: the possible effects of the date of birth are circular with a period of one year,  
896 as January 1<sup>st</sup> is equally close to December 31<sup>st</sup> than to January 2<sup>nd</sup>. This sinusoidal term was  
897 as follows:

898 
$$\sin(\text{Date of Birth} + \varphi)$$

899 The date of birth in the formula above was converted in a radian measure, so that the period,  
900 i.e. one year, equalled to  $2*\pi$ , ranging from  $2*\pi/365$  for January 1<sup>st</sup> to  $2*\pi$  for December 31<sup>st</sup>.  
901 We tested 12 different phase values  $\varphi$  ( $0, \pi/12, 2*\pi/12, 3*\pi/12, 4*\pi/12, 5*\pi/12, 6*\pi/12,$   
902  $7*\pi/12, 8*\pi/12, 9*\pi/12, 10*\pi/12, 11*\pi/12$ ), to account for different potential optimal periods  
903 for the event of interest across the year [1], as our different response variables could be  
904 minimized for different birth dates (and so tested all potential dates as minimal). For example,  
905 a phase of 0 could maximize April 1<sup>st</sup> or October 1<sup>st</sup> depending on the sign of the estimate  
906 (see Table S2). We ran sequentially these 12 multivariate models, containing all other fixed  
907 and random effects (see below), and selected the best phase as the one minimizing the Akaike  
908 Information Criterion (AIC) in this full model set: the phase of  $7*\pi/12$  was retained for  
909 offspring mortality probability,  $2*\pi/12$  for IBI,  $9*\pi/12$  for suckling, 0 for infant carrying, and  
910  $2*\pi/12$  for tantrum probabilities (Table S2).

911

912 **Appendix 7.** Seasonal effects on maternal care and tantrum probability

913 When modelling suckling, infant carrying and tantrum probabilities (Models 5-7), we further  
914 tested for seasonal effects, i.e. effects of the date of observation, on the response variable. To  
915 do so, we applied the approach used to describe the effects of birth timings, i.e. a sine term of  
916 the date of observation (in radians) was entered as a fixed effect in the multivariate model. This  
917 sinusoidal term was as follows:

918 
$$\sin(\text{Date of observation} + \varphi)$$

919 The date of observation in the formula above was converted to a radian measure, so that the  
920 period, i.e. one year, equalled  $2*\pi$ , ranging from  $2*\pi/365$  for the 1<sup>st</sup> of January to  $2*\pi$  for the  
921 31<sup>st</sup> of December. We similarly tested 12 different phase values  $\varphi$  and selected the best phase  
922 as the one minimizing the AIC of the full models 5-7 (with all random and fixed effects, except  
923 the sine term of the date of birth). We found that  $7*\pi/12$  was the best phase for suckling  
924 probability,  $3*\pi/12$  for infant carrying probability, and  $10*\pi/11$  for tantrum probability. The  
925 results of the models with observation date are presented in Table S4.

926

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934 TABLES

935 **Table S1:** Different methods used to estimate the dates of births of the 215 baboon infants born  
 936 at Tsaobis between 2005 and 2019.

937

Criteria used for estimation	Infant colour when first seen	N births estimated	Median uncertainty (days)	Range of uncertainty (days)
Birth observed in the field	Pink	62	0	0
Birth occurred during a short field break	Pink	22	17	1-30
Conception date known	/	52	10	10- 37
Infant coloration & mother's reproductive state [1]	Pink or transitional	56	61	6-151
Mother's reproductive state only	Grey or unknown	23	67	21-153
Total	/	215	30	0-153

938

939

940 **Table S2:** Identification of the best birth timing effect for Models 1-2 & 5-7:  $\Delta$ AIC (Akaike  
 941 Information Criterion) according to the phase of the sine wave term

942 In order to identify the best birth timing effect on our various indicators of fitness and maternal care, we ran 12  
 943 different models, with 12 different phases  $\varphi$  for the sine wave term of the birth date (as a fixed effect), for each  
 944 full model (Models 1-2 & 5-7). If the estimate of the sine term fixed effect is positive, then the birth date maximised  
 945 is indicated in the ‘Date maximised’ column and the one minimised is indicated in the ‘Date minimised’ column.  
 946 On the contrary, if the estimate of the sine term fixed effect is negative, then the birth date maximised is indicated  
 947 in the ‘Date minimised’ column.  $\Delta$ AIC of each model equals the AIC value of the considered model minus the  
 948 AIC value of the best model ( $\Delta$ AIC=0 for the best model, indicated in bold writing). We selected the best phase  
 949 as the one minimizing the AIC, i.e. for which  $\Delta$ AIC=0. For example, for Model 2, the best phase is  $\varphi = 2 * \pi/12$ ,  
 950 and the estimate of the sine term fixed effect is positive (Table S6), indicating that IBIs are maximised in March  
 951 1<sup>st</sup>, and minimized in September 1<sup>st</sup>. Wherever the fixed effect ‘birth date’ was significant (Model 1, 2 and 7), we  
 952 considered all phases  $\varphi$  for which  $\Delta$ AIC<2 to define the optimal time window presented in the main text (see  
 953 greyer background), for instance between August 1<sup>st</sup> and September 15<sup>th</sup> for Model 2.

Phase $\varphi$	Date maximised	Date minimised	$\Delta$ AIC				
			Mortality (Model 1)	IBI (Model 2)	Suckling (Model 5)	Infant carrying (Model 6)	Tantrum (Model 7)
0	1st April	1st October	8.26	2.16	0.67	<b>0</b>	1.15
$\pi/12$	15th March	15th September	9.42	0.72	1.13	0.17	0.34
$2*\pi/12$	1st March	1st September	9.45	<b>0</b>	1.62	0.65	<b>0</b>
$3*\pi/12$	14th February	15th August	8.12	0.33	1.96	1.29	0.39
$4*\pi/12$	1st February	1st August	5.66	1.61	1.92	1.85	1.49
$5*\pi/12$	15th January	15th July	2.91	3.36	1.46	2.16	2.94
$6*\pi/12$	1st January	1st July	0.84	5.02	0.86	2.18	4.20
$7*\pi/12$	15th December	15th June	<b>0</b>	6.16	0.37	1.93	4.84
$8*\pi/12$	1st December	1th June	0.47	6.59	0.09	1.53	4.80
$9*\pi/12$	15th November	15th May	1.99	6.29	<b>0</b>	1.05	4.20

$10*\pi/12$	1st November	1st May	4.10	5.31	0.08	0.56	3.27
$11*\pi/12$	15th October	15th April	6.34	3.84	0.32	0.17	2.19

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954

955

956

957 **Table S3:** Birth timing and other predictors of the probability of suckling, infant carrying and  
 958 tantrums

959 Estimates, confidence intervals,  $X^2$  statistics and P-values of the predictors of binomial generalized linear mixed  
 960 models of the probability of suckling (Model 5), infant carrying (Model 6) and tantrums (Model 7), including  
 961 infant's identity (and focal number for Models 5 and 6) as random effect, and focal observation time as an 'offset'  
 962 fixed effect for Model 7. These GLMMs are based on 11687 scan observations from 55 infants for Model 5, 924  
 963 scan observations from 35 infants for Model 6 and 2211 focal observations from 55 infants for Model 7. Significant  
 964 effects are indicated in bold. For relevant significant effect, we also indicated in the footnote the 95% level  
 965 confidence interval of the 1000 p-values taking into account birth date uncertainty. Infant birth date is fitted as a  
 966 sine term with a phase of  $9*\pi/12$  for suckling, 0 for infant carrying, and  $2*\pi/12$  for tantrum probabilities. For  
 967 categorical predictors, the tested category is indicated between parentheses.

Fixed Effect	Estimate	IC		$X^2$	P-value
		Lower	Upper		
<b>Model 5: Suckling</b>					
Infant birth date	-0.32	-0.76	0.13	1.97	0.16
Infant sex (Male)	-0.01	-0.73	0.73	0.00	0.99
Female parity (Primiparous)	-0.89	-2.20	0.42	1.76	0.18
Female rank	-0.09	-0.42	0.24	0.30	0.59
<b>Infant age</b>	<b>-1.66</b>	<b>-1.97</b>	<b>-1.35</b>	<b>110</b>	<b>&lt;10<sup>-4</sup></b>
<b>Group (L)</b>	<b>0.18</b>	<b>-0.53</b>	<b>0.90</b>	<b>7.79</b>	<b>0.02</b>
<b>(M)</b>	<b>1.51</b>	<b>0.36</b>	<b>2.66</b>		
<b>(2017)</b>	<b>0.21</b>	<b>-1.22</b>	<b>1.63</b>		
<b>Observation year (2018)</b>	<b>1.73</b>	<b>0.84</b>	<b>2.62</b>	<b>40.45</b>	<b>&lt;10<sup>-4</sup></b>
<b>(2019)</b>	<b>0.03</b>	<b>-0.82</b>	<b>0.88</b>		
<b>Model 6: Infant carrying</b>					
Infant birth date	0.53	-0.18	1.24	2.13	0.14
<b>Infant sex (Male)</b>	<b>-0.94</b>	<b>-1.60</b>	<b>-0.28</b>	<b>7.78</b>	<b>0.005</b>
<b>Female parity (Primiparous)</b>	<b>-1.08</b>	<b>-2.11</b>	<b>-0.05</b>	<b>4.21</b>	<b>0.040</b>
<b>Female rank</b>	<b>-0.51</b>	<b>-0.82</b>	<b>-0.19</b>	<b>10.0</b>	<b>0.002</b>
<b>Infant age</b>	<b>-1.94</b>	<b>-2.69</b>	<b>-1.20</b>	<b>26.2</b>	<b>&lt;10<sup>-4</sup></b>
Group (L)	0.01	-0.53	0.55	0.67	0.71
(M)	-0.35	-1.34	0.64		
(2017)	-11.5	-262	239		
Observation year (2018)	1.36	-0.36	3.09	3.69	0.30
(2019)	0.86	-1.19	2.91		
<b>Model 7: Tantrum</b>					
<b>Infant birth date</b>	<b>-0.32</b>	<b>-0.62</b>	<b>-0.03</b>	<b>4.53</b>	<b>0.033*</b>
Infant sex (Male)	-0.10	-0.45	0.25	0.33	0.57

Female parity	(Primiparous)	0.35	-0.32	1.02	1.02	0.31
Female rank		0.03	-0.14	0.19	0.11	0.74
<b>Infant age</b>	<b>Age</b>	<b>-41.13</b>	<b>-54.06</b>	<b>-28.21</b>	<b>53.28</b>	<b>&lt;10<sup>-4</sup></b>
	<b>Age<sup>2</sup></b>	<b>-19.07</b>	<b>-28.21</b>	<b>-9.92</b>		
Group	(L)	-0.35	-0.68	-0.01	4.23	0.12
	(M)	-0.21	-0.81	0.40		
<b>Observation year</b>	<b>(2017)</b>	<b>0.12</b>	<b>-1.39</b>	<b>1.63</b>		
	<b>(2018)</b>	<b>0.30</b>	<b>-0.81</b>	<b>1.41</b>	<b>12.61</b>	<b>0.006</b>
	<b>(2019)</b>	<b>-0.44</b>	<b>-1.57</b>	<b>0.68</b>		
<b>Offset</b>		<b>0.40</b>	<b>0.10</b>	<b>0.71</b>	<b>6.81</b>	<b>0.009</b>

968 \* 95% CI: [0.04684 – 0.05234]

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972 **Table S4:** Seasonality and other predictors of the probability of suckling, infant carrying and  
 973 tantrums

974 Estimates, confidence intervals,  $X^2$  statistics and P-values of the predictors of the binomial GLMMs of the  
 975 probability of suckling (Model 5bis), infant carrying (Model 6bis), and tantrums (Model 7bis). Each model  
 976 includes infant's identity and year of infant's birth as random effects. Models 5bis and 6bis also included focal  
 977 observation as random effects, whereas Model 7bis included focal observation duration as an offset fixed effect.  
 978 Observation date is fitted as a sine term with a phase of  $7*\pi/12$  for suckling probability,  $3*\pi/12$  for infant carrying  
 979 probability, and  $10*\pi/12$  for tantrum probability. Significant effects are indicated in bold. For categorical  
 980 predictors, the tested category is indicated between parentheses.

Fixed Effect	Estimate	IC		$X^2$	P-value
		Lower	Upper		
<b>Model 5bis: Suckling</b>					
<b>Observation date</b>	<b>-1.66</b>	<b>-2.91</b>	<b>-0.40</b>	<b>6.70</b>	<b>0.0096</b>
Infant sex (Male)	-0.03	-0.79	0.74	0.00	0.95
Female parity (Primiparous)	-0.89	-2.25	0.47	1.63	0.20
Female rank	-0.11	-0.46	0.23	0.40	0.53
<b>Infant age</b>	<b>-1.62</b>	<b>-1.94</b>	<b>-1.30</b>	<b>97.47</b>	<b>&lt;10-4</b>
<b>Group (L)</b>	<b>0.30</b>	<b>-0.46</b>	<b>1.06</b>	<b>6.71</b>	<b>0.035</b>
<b>(M)</b>	<b>1.52</b>	<b>0.33</b>	<b>2.71</b>		
<b>(2017)</b>	<b>-2.34</b>	<b>-4.88</b>	<b>0.20</b>		
<b>Observation year (2018)</b>	<b>1.74</b>	<b>0.82</b>	<b>2.66</b>	<b>29.99</b>	<b>&lt;10-4</b>
<b>(2019)</b>	<b>-2.64</b>	<b>-4.95</b>	<b>-0.33</b>		
<b>Model 6bis: Infant carrying</b>					
<b>Observation date</b>	<b>-1.14</b>	<b>-1.98</b>	<b>-0.30</b>	<b>7.12</b>	<b>0.0076</b>
<b>Infant sex (Male)</b>	<b>-0.90</b>	<b>-1.56</b>	<b>-0.24</b>	<b>7.20</b>	<b>0.0073</b>
Female parity (Primiparous)	-0.78	-1.77	0.22	2.33	0.13
<b>Female rank</b>	<b>-0.45</b>	<b>-0.76</b>	<b>-0.15</b>	<b>8.31</b>	<b>0.0039</b>
<b>Infant age</b>	<b>-2.40</b>	<b>-2.83</b>	<b>-1.97</b>	<b>120</b>	<b>&lt;10-4</b>
Group (L)	-0.003	-0.53	0.54	2.04	0.36
(M)	-0.63	-1.62	0.37		
<b>(2017)</b>	<b>-13.10</b>	<b>-2410</b>	<b>2384</b>		
<b>Observation year (2018)</b>	<b>0.66</b>	<b>-1.19</b>	<b>2.52</b>	<b>12.2</b>	<b>0.007</b>
<b>(2019)</b>	<b>-0.73</b>	<b>-2.77</b>	<b>1.31</b>		
<b>Model 7bis: Tantrum</b>					
Observation date	0.63	-0.16	1.42	2.44	0.12
Infant sex (Male)	-0.09	-0.45	0.26	0.27	0.60
Female parity (Primiparous)	0.07	-0.57	0.72	0.05	0.83
Female rank	0.04	-0.13	0.21	0.23	0.63
<b>Infant age Age</b>	<b>-33.10</b>	<b>-43.45</b>	<b>-22.75</b>	<b>51.09</b>	<b>&lt;10-4</b>
<b>Age<sup>2</sup></b>	<b>-20.84</b>	<b>-29.87</b>	<b>-11.81</b>		



Group	(L)	-0.32	-0.66	0.02	3.86	0.15
	(M)	-0.05	-0.64	0.53		
	(2017)	0.57	-1.12	2.27		
Observation year	(2018)	0.20	-0.91	1.30	0.45	0.93
	(2019)	0.45	-1.18	2.09		
<b>Offset</b>		<b>0.40</b>	<b>0.10</b>	<b>0.71</b>	<b>6.73</b>	<b>0.0095</b>

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983 **Table S5:** Summary of the structure of all models included in the study.

Indicators	Fitness traits		Birth timing		Maternal care		
Model number	1	2	3	4	5	6	7
Response variable	Offspring survival before weaning	Interbirth intervals (days)	Deviation from the offspring survival optimal birth timing	Deviation from the maternal IBI optimal birth timing	Suckling	Infant carrying	Tantrum
Model type	Binomial GLMM	LMM	LMM	LMM	Binomial GLMM	Binomial GLMM	Binomial GLMM
Number of observations	195	120	215	215	5089	924	2221
Number of individuals (juveniles / mothers)	57	43	62	62	55	35	55
Fixed effects	Infant birth date, infant sex, female parity, female rank, group	Infant birth date, infant sex, female parity, female rank, group	Infant sex, female parity, female rank, group	Infant sex, female parity, female rank, group	Infant birth date (or observation date, see Table S4), infant sex, female parity, female rank, infant age, group, observation year	Infant birth date (or observation date, see Table S4), infant sex, female parity, female rank, infant age, group, observation year	Infant birth date, (or observation date, see Table S4), infant sex, female parity, female rank, Infant age <sup>2</sup> , group, observation year, focal duration
Random effects	Birth year, female identity	Birth year, female identity	Birth year, female identity	Birth year, female identity	Infant identity, focal number	Infant identity, focal number	Infant identity

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987 **Table S6:** Predictors of offspring mortality before weaning and maternal interbirth interval  
 988 (IBI) duration.

989 Estimates, confidence intervals,  $X^2$  statistics and P-values of the predictors of a binomial generalized mixed model  
 990 of the probability of offspring mortality before weaning (0/1: survived/died, Model 1) and a linear mixed model  
 991 of the duration of the maternal birth interval (IBI) (in days, Model 2), based on 195 observations from 57 females  
 992 for Model 1 and 120 observations from 43 females for Model 2. Female identity and year of infant's birth are  
 993 included as random effects in both models. Significant effects are indicated in bold. For the fixed effect 'birth  
 994 date', we also indicate in the footnote the 95% confidence interval of the average p-value of the simulated models  
 995 taking into account birth date uncertainty. Infant birth date is fitted using a sine term with a phase of  $7*\pi/12$  for  
 996 infant mortality and of  $2*\pi/12$  for IBI, and. For categorical predictors, the tested category is indicated between  
 997 parentheses.

Fixed Effect	Estimate	IC		$X^2$	P-value
		Lower	Upper		
<b>Model 1: Offspring mortality</b>					
<b>Infant birth date</b>	<b>-1.12</b>	<b>-1.84</b>	<b>-0.40</b>	<b>9.38</b>	<b>0.002*</b>
Infant sex (Male)	0.20	-0.76	1.15	0.16	0.685
Female parity (Primiparous)	-0.83	-2.32	0.67	1.17	0.279
Female rank	-0.44	-0.95	0.07	2.87	0.090
Group (L)	-1.29	-2.39	-0.18	5.25	0.072
(M)	-0.10	-4.08	3.88		
<b>Model 2: Maternal IBI</b>					
<b>Infant birth date</b>	<b>36.84</b>	<b>7.59</b>	<b>66.09</b>	<b>6.10</b>	<b>0.014 †</b>
Infant sex (Male)	37.04	-0.36	74.45	3.77	0.052
Female parity (Primiparous)	44.53	-3.24	92.29	3.34	0.068
<b>Female rank</b>	<b>-25.73</b>	<b>-50.68</b>	<b>-0.77</b>	<b>4.08</b>	<b>0.043</b>
Group (L)	<b>-50.41</b>	-105.19	4.38	3.31	0.191
(M)	-31.09	-150.57	88.38		

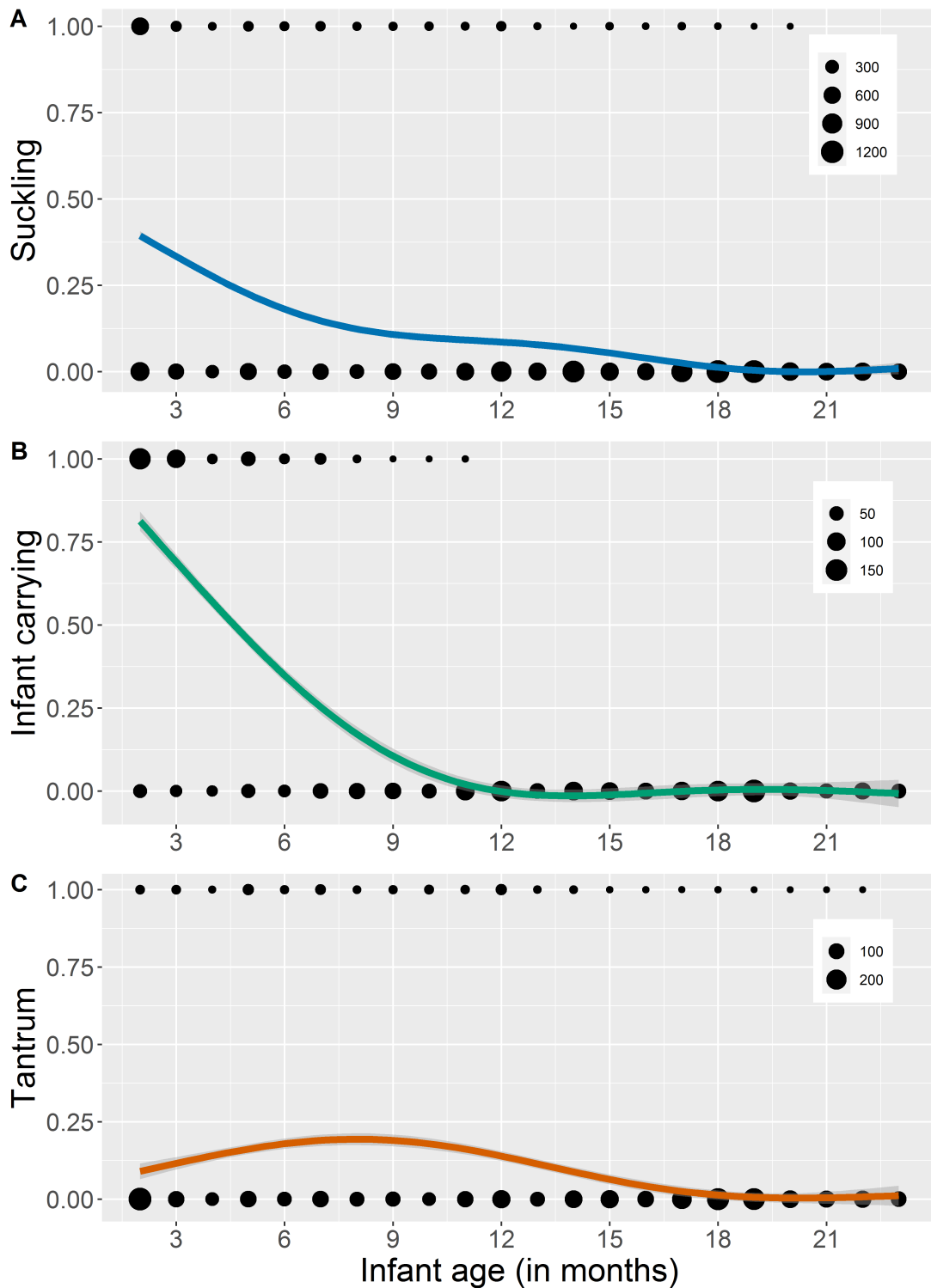
998 \* 95% CI: [0.00967 – 0.01087]

999 † 95% CI: [0.02533 – 0.02821]

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1002 FIGURES



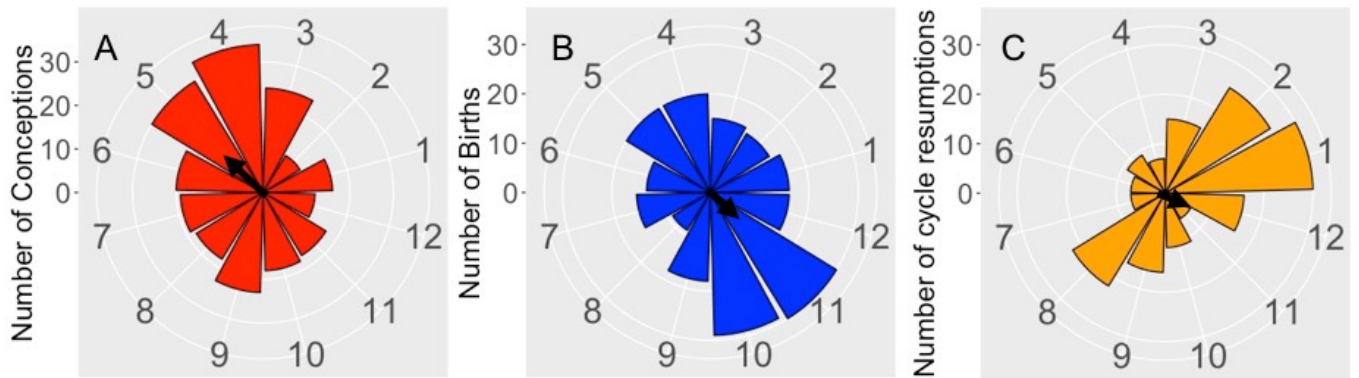
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1004 **Figure S1:** Variation in the probabilities of suckling, infant carrying, and tantrums, according  
 1005 to infant age.

1006 We plotted (A) the probability of suckling during a scan, (B) the probability of infant carrying during a travelling  
 1007 scan, and (C) the probability of tantrum during a focal observation according to infant age (in months). For all

1008 panels, the size of black dots is proportional to the number of observations (see plot legends). The coloured curves  
1009 show the predicted fit using a general additive function (method 'gam' of geom\_smooth function in 'ggplot2' R  
1010 package). The darker area around each curve represents the confidence interval of the fitted curve. In order to  
1011 determine the best infants' age window for each models (Models 5-7), we explored age-related variation in  
1012 suckling (Panel A, Model 5), infant carrying (Panel B, Model 6) and tantrum (Panel C, Model 7) probabilities. We  
1013 found that (A) suckling decreases gradually from 2 to 18 months old, before stabilizing to ca. 2% of the scans from  
1014 18 to 24 months old, (B) the proportion of infant carrying gradually decreases during the first year of life in our  
1015 population as in other baboon populations [6,15,16], and (C) tantrum occurrence started in early-life, peaked when  
1016 infants were aged around 6-9 months, and then gradually decreased during the end of their first and second year  
1017 of life.

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1020 **Figure S2:** Chacma baboons breed all year round.

1021 Number of conceptions (Panel A, N=241), births (Panel B, N=215) and cycle resumptions (Panel C, N=171) per  
1022 month (from 1=January to 12=December) between 2005 and 2019. Births and cycle resumptions do not show  
1023 significant seasonality, while conceptions significantly deviate from non-seasonality, with an average conception  
1024 date in May. The black arrow length is the value of the Rayleigh statistic R, and its direction is  $\mu$ . The numbers on  
1025 the y-axis of each plot indicate the scale for the number of events on that plot.

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1029 REFERENCES

- 1030 1. Dezeure J, Dagherrette J, Baniel A, Carter AJ, Cowlishaw G, Marshall HH, Martina C,  
1031 Raby CL, Huchard E. 2021 Developmental transitions in body color in chacma baboon  
1032 infants: Implications to estimate age and developmental pace. *Am. J. Phys. Anthropol.*  
1033 **174**, 89–102. (doi:10.1002/ajpa.24118)
- 1034 2. Higham JP, Heistermann M, Ross C, Semple S, MacLarnon A. 2008 The timing of  
1035 ovulation with respect to sexual swelling detumescence in wild olive baboons.  
1036 *Primates* **49**, 295–299. (doi:10.1007/s10329-008-0099-9)
- 1037 3. Lee PC. 1996 The meanings of weaning: growth, lactation, and life history. *Evol.*  
1038 *Anthropol.* **5**, 87–98. (doi:https://doi.org/10.1002/(SICI)1520-6505(1996)5:3<87::AID-  
1039 EVAN4>3.0.CO;2-T)
- 1040 4. Langer P. 2008 The phases of maternal investment in eutherian mammals. *Zoology*  
1041 **111**, 148–162. (doi:10.1016/j.zool.2007.06.007)
- 1042 5. Altmann J. 1980 *Baboon Mothers and Infants*. The University of Chicago Press.
- 1043 6. Nicolson N. 1982 *Weaning and the Development of Independence in Olive Baboons*.  
1044 Harvard University, Cambridge, Massachusetts. (doi:10.13140/RG.2.1.4000.9761)
- 1045 7. Rhine RJ, Norton GW, Wynn GM, Wynn RD. 1989 Plant feeding of yellow baboons  
1046 (*Papio cynocephalus*) in Mikumi national park, Tanzania, and the relationship between  
1047 seasonal feeding and immature survival. *Int. J. Primatol.* **10**, 319–342.  
1048 (doi:10.1007/BF02737420)
- 1049 8. Barrett L, Henzi SP, Lycett JE. 2006 Whose Life Is It Anyway? Maternal Investment,  
1050 Developmental Trajectories, and Life History Strategies in Baboons. In *Reproduction*  
1051 *and Fitness in Baboons: Behavioral, Ecological, and Life History Perspectives*, pp.  
1052 199–224.
- 1053 9. Bădescu I. 2018 The attainment of independence from the mother in primate infants

- 1054 and its implications for the evolution of cooperative breeding in hominins. In *The*  
1055 *talking species : perspectives on the evolutionary, neuronal and cultural foundations of*  
1056 *language* (eds EM Luef, MM Marin), pp. 169–194. Uni-Press Graz.
- 1057 10. Borries C, Lu A, Ossi-Lupo K, Larney E, Koenig A. 2014 The meaning of weaning in  
1058 wild Phayre’s leaf monkeys: Last nipple contact, survival, and independence. *Am. J.*  
1059 *Phys. Anthropol.* **154**, 291–301. (doi:10.1002/ajpa.22511)
- 1060 11. Reitsema LJ. 2012 Introducing Fecal Stable Isotope Analysis in Primate Weaning  
1061 Studies. *Am. J. Primatol.* **74**, 926–939. (doi:10.1002/ajp.22045)
- 1062 12. Bădescu I, Watts DP, Katzenberg MA, Sellen DW. 2016 Alloparenting is associated  
1063 with reduced maternal lactation effort and faster weaning in wild chimpanzees. *R. Soc.*  
1064 *Open Sci.* **3**. (doi:10.1098/rsos.160577)
- 1065 13. Crowley BE, Reitsema LJ, Oelze VM, Sponheimer M. 2015 Advances in Primate  
1066 Stable Isotope Ecology — Achievements and Future Prospects. *Am. J. Primatol.* **78**,  
1067 995–1003. (doi:10.1002/ajp.22510)
- 1068 14. Reitsema LJ, Partrick KA, Muir AB. 2016 Inter-individual variation in weaning among  
1069 rhesus macaques (*Macaca mulatta*): Serum stable isotope indicators of suckling  
1070 duration and lactation. *Am. J. Primatol.* **78**, 1113–1134. (doi:10.1002/ajp.22456)
- 1071 15. Altmann J, Samuels A. 1992 Costs of maternal care: infant-carrying in baboons. *Behav.*  
1072 *Ecol. Sociobiol.* **29**, 391–398. (doi:10.1007/BF00170168)
- 1073 16. Rhine RJ, Norton GW, Westlund BJ. 1984 The Waning of Dependence in Infant Free-  
1074 Ranging Yellow Baboons (*Papio cynocephalus*) of Mikumi National Park. *Am. J.*  
1075 *Primatol.* **7**, 213–228.
- 1076
- 1077