

1 **Breeding seasonality generates reproductive trade-offs in a long-**
2 **lived mammal**

3
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19 **AUTHORS CONTRIBUTIONS**

20 J.D. and E.H. designed the study, and J.D. ran the analysis. J.D., A.B., A.C., G.C. and E.H.
21 collected the data, and all authors contributed to the drafting of the manuscript. E.H. acquired
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23
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26

27 **KEYWORDS**

28 Reproductive seasonality, birth timing, life-history trade-offs, mother-offspring conflict,
29 primates

30

31 **ABSTRACT**

32 The evolutionary benefits of reproductive seasonality are usually measured by a single fitness
33 component, namely offspring survival to nutritional independence (Bronson, 2009). Yet
34 different fitness components may be maximised by dissimilar birth timings. This may generate
35 fitness trade-offs that could be critical to understanding variation in reproductive timing across
36 individuals, populations and species. Here, we use long-term demographic and behavioural data
37 from wild chacma baboons (*Papio ursinus*) living in a seasonal environment to test the adaptive
38 significance of seasonal variation in birth frequencies. Like humans, baboons are eclectic
39 omnivores, give birth every 1-3 years to a single offspring that develops slowly, and typically
40 breed year-round. We identify two distinct optimal birth timings in the annual cycle, located 4-
41 months apart, which maximize offspring survival or minimize maternal interbirth intervals
42 (IBIs), by respectively matching the annual food peak with late or early weaning. Observed
43 births are the most frequent between these optima, supporting an adaptive trade-off between
44 current and future reproduction. Furthermore, infants born closer to the optimal timing
45 favouring maternal IBIs (instead of offspring survival) throw more tantrums, a typical
46 manifestation of mother-offspring conflict (Maestripieri, 2002). Maternal trade-offs over birth
47 timing, which extend into mother-offspring conflict after birth, may commonly occur in long-
48 lived species where development from birth to independence spans multiple seasons. Such
49 trade-offs may substantially weaken the benefits of seasonal reproduction, and our findings

50 therefore open new avenues to understanding the evolution of breeding phenology in long-lived
51 animals, including humans.

52

53 **SIGNIFICANCE STATEMENT**

54 Why some species breed seasonally and others do not remain unclear. The fitness consequences
55 of birth timing have traditionally been measured on offspring survival, ignoring other fitness
56 components. We investigated the effects of birth timing on two fitness components in wild
57 baboons, who breed year-round despite living in a seasonal savannah. Birth timing generates a
58 trade-off between offspring survival and future maternal reproductive pace, meaning that
59 mothers cannot maximize both. When birth timing favours maternal reproductive pace (instead
60 of offspring survival), behavioural manifestations of mother-offspring conflict around weaning
61 are intense. These results open new avenues to understand the evolution of reproductive timings
62 in long-lived animals including humans, where such reproductive trade-offs may commonly
63 weaken the intensity of reproductive seasonality.

64

65 **MAIN TEXT**

66 **Introduction**

67 Empirical studies investigating variation in reproductive timing have mostly focused on fast-
68 lived seasonal breeders, whose development from birth to independence generally occurs
69 within the most productive season (1). In long-lived mammals, the reproductive cycle from
70 birth to weaning cannot similarly be squeezed into one annual food peak, and consequently,
71 females must choose which stage(s) of the reproductive cycle to synchronize with one or more
72 food peak(s). For example, female mammals could match the annual food peak to coincide with
73 either late-weaning or mid-lactation, but usually not both. The reproductive timing strategy is
74 likely to depend on how females trade-off the survival of their offspring (mortality risks tend

75 to peak at the end of weaning) (2–4) with their own reproductive costs (energetic demands tend
76 to peak around mid-lactation) (5, 6). Whether such reproductive timing strategies can vary
77 within populations is largely unknown. In addition, while evolutionary trade-offs between
78 offspring quality and quantity have been described both within and across species, through
79 associations between birth spacing and infant growth and survival (7–11), the existence of
80 maternal trade-offs over birth timing have only been suggested theoretically (3) and never tested
81 empirically in mammals (but see for a bird species, *Fulica atra*: (12)).

82 Here, we investigate variation in maternal reproductive success and mother-offspring
83 relationships associated with variable birth timings in the annual cycle of wild chacma baboons
84 (*Papio ursinus*), living in a seasonal semi-arid savannah (Tsaobis, Namibia). Baboons are
85 African primates distributed across a wide latitudinal range, and a classic model for
86 understanding how early humans adapted to seasonal savannahs (13, 14). In particular, baboons
87 typically breed year-round (15), and are therefore considered non-seasonal breeders, though the
88 distribution of births shows moderate seasonality (i.e. varies along the annual cycle) in some
89 species and populations (16–18). In addition, infant baboons, like many young primates
90 including human toddlers, commonly perform tantrums, a manifestation of mother-offspring
91 conflict (19–22). Using a combination of detailed long-term life-history and behavioural data
92 collected over 15 years (2005–2019), we first characterize the reproductive and environmental
93 seasonality of the Tsaobis baboons. Second, we quantify the consequences of birth timing on
94 two components of female fitness: offspring survival and maternal inter-birth intervals (IBIs),
95 and identify two distinct birth timing optima. We further test whether individual traits predict
96 whether a female is more likely to give birth around one or the other optimum. Third, we
97 investigate if compensatory maternal care mitigates the costs of suboptimal birth timing for
98 offspring, and whether infants born, and subsequently weaned, in suboptimal timings increased
99 their tantrum frequency.

100

101 **Results**

102 **1. Tsaobis baboons breed year-round despite living in a seasonal environment**

103 Conceptions, births and cycle resumptions occurred throughout the year (Figure S1), indicating
104 an absence of a strict breeding season. We used circular statistics to test whether moderate
105 seasonality may still occur, computing respectively the mean annual angle (μ) and Rayleigh
106 tests (R and p-values) for the annual distribution of 241 conceptions, 215 births and 171 cycle
107 resumptions recorded between 2005-2019. The frequency of conceptions and births showed
108 slight seasonal variations, which reached statistical significance for conceptions only
109 (conceptions: μ = May 12, R=0.13, p=0.02; births: μ = November 18, R=0.09, p=0.17; cycle
110 resumptions: μ = December 4, R=0.08, p=0.36, Figure S1).

111 Environmental seasonality was pronounced at Tsaobis (Figure 1A). Mean annual
112 rainfall was low and variable (mean \pm SD = 192 \pm 143mm), falling mostly between January
113 and April (Figure 1A). Following previous baboon studies (23, 24), we quantified food
114 availability for baboons using the Normalized Difference Vegetation Index (NDVI), a satellite-
115 based proxy of primary productivity with higher values corresponding to a higher degree of
116 greenness (25). Seasonal variation in NDVI followed a similar, but slightly lagged pattern, to
117 rainfall (Figure 1A). The highest birth frequency occurred in October-November, preceding the
118 peak in rainfall (February) and NDVI (March-April, Figure 1A).

119

120 **2. Distinct birth timings optimize current versus future reproduction**

121 There was an influence of birth timing on two indicators of maternal fitness. First, birth timing
122 affects offspring survival (Table S1): infants born between November 15th and January 1st were
123 the most likely to survive until weaning (Table S2), indicating an optimal birth timing for

124 offspring survival in the annual cycle (Figure 2A). Second, the duration of maternal IBI is
125 influenced by the timing of the birth opening the IBI (Table S1): females giving birth between
126 August 1st and September 15th had the shortest IBIs (Table S2), indicating another different
127 optimal birth timing for maternal reproductive pace in the annual cycle (Figure 2B). In the first
128 case, the birth timing that maximises offspring survival synchronizes the seasonal food peak
129 with the end of weaning, a highly vulnerable life stage for mammals (26–28), which occurs
130 between 12 and 18 months after birth in this population (Figure 1B). In the second case, the
131 birth timing that maximizes maternal reproductive pace synchronizes the food peak with the
132 peak of lactation (occurring around 6 months after birth) (Figure 1B), which is the most
133 energetically-costly reproductive stage for mothers (3, 26), and may therefore help to alleviate
134 the costs of lactation and enhance maternal condition during the second half of lactation. The
135 two months counting most births are October and November (i.e. 28.4% of annual births, Figure
136 1A) and the mean annual birth date is Nov 18th, indicating a reproductive trade-off over birth
137 timing, that pushes mothers to target the very first days of the offspring survival optimal birth
138 timing, in order to avoid compromising offspring mortality while minimizing the costs on their
139 reproductive pace (Figure 2C).

140 This result raises the possibility that some females might be more likely to time their
141 births to maximise current over future reproduction, or vice versa. In particular, dominance rank
142 and parity can affect various aspects of individual reproductive performance, including
143 offspring survival and IBI (29–31), and may influence birth timing strategies accordingly.
144 Similarly, mothers conceiving close to the optimal timing for maternal IBIs, which alleviates
145 the energetic costs of lactation, may subsequently favour male over female embryos, which are
146 more costly to produce in sexually dimorphic mammals (29, 32, 33). However, we failed to
147 detect any significant variance associated with maternal identity on the deviation between
148 observed birth and the optimal birth timing maximizing offspring survival (LRT=0.66, p=0.42)

149 versus maternal IBI (LRT=0.00, $p=0.98$). This suggests that females did not consistently target
150 one timing over the other across successive births. Moreover, female parity, rank and infant sex
151 did not influence the proximity of birth timing in relation to each optimum (Table 1).

152

153 **3. Birth timings favouring future reproduction intensify mother-offspring conflict**

154 In order to test whether maternal care may compensate for the costs of suboptimal birth timings
155 in offspring, we investigated the effects of birth timing on the frequency of suckling and infant
156 carrying. We did not find any effect of infant birth date on patterns of maternal care (Table S3).
157 Further analyses revealed that mothers increase maternal care in the dryer winter months, but
158 such compensation occurs regardless of an infant's birth date (Appendix 1, Table S4).

159 We also investigated whether infants born in suboptimal timings may beg maternal care
160 more frequently, looking at tantrum frequencies. We found that infants born near the maternal
161 IBI optimal timing, i.e. between August 1st and October 1st (Table S2), were more likely to
162 exhibit tantrums than other infants (Table S3, Figure 3). Observation date did not affect tantrum
163 frequencies, meaning that such an effect was independent of the season of observation (Table
164 S4).

165

166 **Discussion**

167 Our results further our understanding of the evolution of vertebrate reproductive timing in
168 several ways. First, we identify two distinct optimal birth timings in the annual cycle,
169 respectively favouring current reproduction (offspring survival) versus future reproduction
170 (maternal reproductive pace). These are separated by four months, and the highest birth
171 frequency occurs between these optima, indicating that mothers balance current and future
172 reproduction, with a priority for offspring survival. Trade-offs over birth timing may be
173 widespread in long-lived species with slow life histories, for which development from birth to

174 independence spans several months, therefore exceeding the length of the most productive
175 season. In such cases, different stage(s) of the reproductive cycle may be synchronized with
176 one or more seasonal food peaks, with the specific pattern dependent on the trade-offs females
177 make among different fitness components (34). Such variation could account for empirical
178 cases where the observed birth peak fails to coincide with the birth timing expected on the basis
179 of a single fitness measure. For example, in humans from pre-industrial Finland, births did not
180 concentrate in the months with the highest infant survival expectations (35). More generally,
181 such trade-offs may contribute to explain the partial or total lack of breeding seasonality
182 observed in some large mammals (36), such as social primates including apes (18) and humans
183 (37, 38).

184 Second, this study challenges the idea according to which non-seasonal breeding has
185 evolved in response to an absence of optimal birth timing in the annual cycle, especially in
186 species with ecological or physiological traits that buffer seasonal environmental variation (39).
187 For example, chacma baboons and humans share a generalist diet (27), a capacity to extract
188 fall-back foods at times of food scarcity (40), and an ability to store energy (2, 4), which have
189 likely played a critical role in their adaptation to breed year-round in seasonal environments
190 (41, 42). The few studies that have investigated the effects of birth timing on early survival of
191 offspring in non-seasonal breeding primates such as geladas (*Theropithecus gelada*) (43) have
192 indeed failed to detect any effect. In modern humans, fitness variation associated with seasonal
193 birth timing is rare (38, 44), and where detectable, only has mild effects on adult longevity (45,
194 46). The fitness consequences of seasonal birth timing detected here were therefore unexpected,
195 and surprisingly reveal that non-seasonal breeding can be favoured even where reproductive
196 success depends on birth timing. Future work will usefully test the generality of these patterns
197 in other species or populations that breed year-round to shed more light on the conditions
198 favouring evolutionary transitions towards non-seasonal breeding.

199 Third, while different species synchronize different stages of their reproductive cycle
200 with the seasonal food peak (1, 2, 47, 48), this study reveals variations in breeding timing within
201 the same population. However, while mothers experience a trade-off between reproductive pace
202 and offspring survival in their birth timing, it is not clear if particular individuals consistently
203 favour certain strategies, as we did not detect any inter-individual effects of female identity,
204 parity or rank on parturition timing. Instead, intra-individual factors, such as maternal
205 reproductive history, may constrain the evolution of such individually-based specializations, if
206 only because the duration of IBIs - 22 months on average but with extensive variation - prevents
207 females from giving birth every two years at the same season. In addition, the costs of waiting
208 for the next optimal timing may often outweigh the costs of giving birth at suboptimal timings.
209 Overall, the fact that the highest frequency of births occur between the two optima or at the
210 onset of the period maximizing offspring survival suggests that most females attempt to
211 maximize offspring survival while optimizing their own reproductive pace.

212 Fourth, this study underlines the importance of weaning to understand the evolution of
213 mammalian reproductive schedules. Late-weaning is most critical for infants who must learn to
214 ensure their own provisioning. Matching that stage with the most productive season may
215 substantially enhance infant survival (26, 27, 49, 50). Moreover, the peak of lactation typically
216 coincides with the onset of weaning, and matching it with abundant resources can help to
217 accelerate the transition to feeding independence by granting infants access to a wealth of
218 weaning foods (Figure 1B) (26). Earlier weaning, in combination with better maternal
219 nutritional condition, will likely promote the resumption of cycling (51–53), and may contribute
220 to explain the shorter interbirth intervals associated with this birth timing. Such patterns may
221 be very general. In the lemur radiation, for instance, despite a variety of life-histories, ecologies
222 and societies, and the fact that different species mate and give birth at different times of year,
223 all species synchronize weaning with the food peak (49). Our understanding of the ultimate

224 causes of mammalian reproductive seasonality may gain from granting more consideration to
225 the dynamics and consequences of weaning, which may have been underappreciated in
226 comparison to the energetic costs of pregnancy and lactation (1, 2, 4).

227 Fifth, our results show that the trade-off over birth timing faced by mothers may
228 subsequently translate into mother-offspring conflict after birth. Although mothers adjust
229 maternal care seasonally, they do so regardless of the offspring's age. Offspring born at
230 suboptimal periods face the dry season in a critical developmental window (i.e., the end of
231 weaning), and maternal care is insufficient to buffer them entirely from the adverse
232 consequences that lead to higher mortality. Consequently, baboon infants respond by throwing
233 more tantrums, which may be an honest signal of need (21, 54), just as children do in similar
234 situations (22). More generally, these results shed light on the potential influence of
235 environmental fluctuations, and specifically seasonality, on mother-offspring conflicts over
236 maternal care. While the literature focusing on optimal birth spacing has mainly examined
237 trade-offs between current and future reproduction for an implicitly stable level of resources (7,
238 55), such a stability may rarely be encountered by mothers in the wild (56, 57), who typically
239 face extensive, but partly predictable, fluctuations in food availability. Taking into account the
240 intensity and predictability of resource fluctuations may largely re-draw the landscape of
241 strategic decisions available to mothers confronted with trade-offs between current and future
242 reproduction in natural environments (57, 58).

243 Our findings open new perspectives to understand the evolutionary drivers of vertebrate
244 reproductive seasonality, by revealing the occurrence of a maternal trade-off between current
245 and future reproduction over birth timing, extended by mother-offspring conflict during
246 weaning. Such a trade-off may commonly occur in organisms with a slow reproductive pace,
247 and future studies on such taxa should investigate the consequences of reproductive timing on
248 several fitness components. Indeed, multiple optimal birth timings in the annual cycle may

249 generate a bimodal birth peak or an extended birth season. Evolutionary trade-offs over birth
250 timing may therefore account for unexplained variation in the reproductive timing of long-lived
251 vertebrates, including the evolution of non-seasonal breeding in humans and other species.

252

253 **Materials and methods**

254

255 **Study site and population**

256 Three habituated groups of wild chacma baboons were followed between 2005 and 2019: J and
257 L since 2005, and M, a fission group from J, since 2016. They live in a desert-edge population
258 at Tsaobis Nature Park (22°23S, 15°44'50E) in Namibia, in a strongly seasonal environment:
259 the desert vegetation responds quickly to the austral summer rains, which usually fall between
260 December and April, and then dies back during the dry winter months (59). Water is always
261 available through the presence of both natural seeps and artificial water points for wildlife and
262 livestock. A field team was present each year, mainly during winter (between May to October),
263 for a variable number of months (mean = 4.5, range: 1.9-7.9), that collected daily demographic
264 and behavioural data, as well as GPS locations, while following the groups on foot. All
265 individuals, including infants, are individually recognizable thanks to small ear markings
266 performed during capture and/or other distinctive features.

267

268 **Environmental data**

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

272 Daily rainfall in a 0.25 × 0.25 degree grid cell resolution (corresponding to 28 × 28 km
273 at this latitude) was extracted using satellite data sensors from the Giovanni NASA website

274 (product TRMM 3B42) (60), from a rectangular geographic area encompassing the global
275 ranging area of the Tsaobis baboons, computed using GPS locations collected by observers
276 every 30 min when following the study groups. We used the minimal and maximal latitude and
277 longitude recorded between 2005 and 2019. Monthly cumulative rainfall (summed across daily
278 values) were computed between 2005 and 2019.

279 We used the Normalized Difference Vegetation Index (NDVI) as an index of food
280 availability. NDVI is computed using the near-infrared and red light reflected by the surface of
281 an area and measured with satellite sensors; it produces a quantitative index of primary
282 productivity with higher values corresponding to a higher degree of vegetation cover (25). It
283 has previously been used as an indicator of habitat quality for the Tsaobis baboons (24) and
284 other baboon populations (23). We further confirmed that temporal variation in NDVI reflected
285 temporal variation in rainfall: mean cumulative rainfall over the past three months explained
286 between 60-72% of the NDVI variation (Appendix 2). To index food availability using NDVI
287 for each troop, we first computed 100% isopleth home ranges for each group using kernel
288 density estimates with the adehabitatHR package ('kernelUD' function) (61), based on the daily
289 30-min GPS locations from 2005-2019 (from 2016-2019 for M group). We obtained one home
290 range per group for the entire study period. We then extracted the mean NDVI per 16 day-
291 period on a 500 m \times 500 m resolution across these periods using MODIS data (MODIS13A1
292 product) provided by NASA (25) within these home ranges for each group. Daily NDVI was
293 computed by linear interpolation and then averaged to obtain a monthly value. In contrast to
294 rainfall, NDVI was measured with greater resolution and for each group separately because
295 baboons finely adjust their ranging behaviour in relation to food availability (62).

296

297 **Individual data**

298 A female was considered adult when she reached menarche. The reproductive state of each
299 adult female was monitored daily. A female could be: (i) pregnant (assessed by the paracallosal
300 skin turning red and absence of cycles over the following months), with the exact start date of
301 pregnancy being determined *post hoc* following infant birth, and encompassing 190 days (mean
302 gestation length in this population, $n = 13$ pregnancies where both conception and birth were
303 observed, range: 181-200 days, $SD = 5$) between conception and birth; (ii) lactating, as long as
304 the female did not resume cycling after an infant birth; (iii) cycling, including both swollen
305 females in oestrus (i.e., sexually receptive with a perineal swelling) and non-swollen females
306 at other stages of their cycle. Conceptive cycles were established based on the beginning of a
307 pregnancy, and were usually confirmed by a birth. The first post-partum cycle (i.e. cycle
308 resumption) is the first cycle following an infant's birth, when the female resumes cycling after
309 lactation. The exact date of the cycle resumption corresponds to the first day of oestrus of the
310 first post-partum cycle, i.e. the first day when a sexual swelling is recorded. The dates of these
311 reproductive events (conceptions, births and cycling resumptions) were either known with
312 accuracy when recorded by field observers, or estimated in the absence of observers using the
313 methods detailed in Appendix 3 and Table S5.

314 Female parity was known from life history records and defined as primiparous (between
315 the birth of her first and second infant) or multiparous (after the birth of her second infant).

316 Female social rank was established annually for each group using *ad libitum* and focal
317 observations of agonistic interactions between adult females: supplants, displacements, attacks,
318 chases and threats (Huchard and Cowlshaw 2011). We computed a linear hierarchy using
319 Matman 1.1.4 (Noldus Information Technology, 2013), and then converted to a relative rank to
320 control for group size (i.e. the number of adult females in the group). Each female was thus
321 assigned one rank per year, ranging from 0 (lowest ranking) to 1 (highest ranking).

322

323 **Fitness data**

324 We tested the influence of birth timing in the annual cycle on two fitness measures, namely
325 offspring mortality before weaning and the duration of the maternal interbirth interval. For each
326 infant born between 1st January 2005 and 1st August 2018, we investigated whether it died
327 (yes/no) before weaning. The weaning age was identified as 550 days on the basis of the
328 maximum length of post-partum anoestrus (n = 33 cases for which both birth and cycle
329 resumption were known with accuracy, see also Appendix 4), and presumably reflected the
330 upper threshold of weaning age in our population, assuming that females who resumed cycling
331 had weaned their offspring, as lactation has suppressive effects on ovulation among primates
332 (51, 52, 64). Death was recorded when a corpse was observed or when the infant had been
333 missing in the group for five consecutive days. Infants born later than August 2018 were not
334 considered as their survival outcome was unknown. Four infants that disappeared between
335 consecutive field seasons were omitted because we could not establish whether the age of death
336 was before or after 550 days. In our final dataset, a total of 39 infants out of 195 died before
337 reaching 550 days of age, with mortality occurring at a median age of 74 days (range 1-284
338 days, n=17 known dates of death).

339 We defined interbirth intervals (IBI) as the number of days between two consecutive
340 live births of the same female. We only considered IBIs for which the first infant reached
341 weaning (29), i.e. survived until 550 days old. We discarded other IBIs as females resumed
342 cycling rapidly after their infant's death when unweaned (median=21 days, range=9-51, n=9
343 observed death), and their IBIs would have been shortened regardless of environmental
344 seasonality. We computed a total of 120 interbirth intervals from 43 adult females, ranging
345 from 397 to 1132 days with a mean of 678 days (SD=128).

346

347 **Behavioural observations**

348 In order to characterize variation in maternal care and in mother-offspring conflict, we used
349 three behavioural indicators: suckling, infant carrying and tantrum frequencies. We also used
350 these behavioural data, along with life history data, to assign different developmental stages,
351 including the different stages of weaning and the peak of lactation after an infant's birth (see
352 Appendix 4). In addition to life-history data, field observers collected behavioural data on
353 infants aged between 2 and 24 months on a daily basis from dawn until dusk over four periods:
354 from October to December 2006, from July to August 2017, from September to December
355 2018, and from April to July 2019. We collected a total of 1185 hours of focal observation on
356 69 infants across four field seasons (mean \pm SD = 17.1 \pm 7.8 hours of observations per infants,
357 range = 6.3–34.6), with a mean of 40.7 focal observations per individual (SD=29.4). Focal
358 observations were spread equally across the day (divided in four 3-h-long blocks) and focal
359 individuals were chosen randomly, and never sampled more than once within a block. Focal
360 observations durations were 1 h in 2006 and 20 min in 2017-2019, with a minimum of 10 min
361 in all cases. We recorded the following activities on a continuous basis: suckling (when the
362 focal individual had its mouth on its mother's nipple; we could not distinguish comfort from
363 nutritive suckling), travelling alone, infant carrying (carried by the mother, either ventrally or
364 dorsally) and other activities. We also collected events related to mother-offspring conflicts
365 (see below). In addition, we collected scan observations every 5 minutes (n=16702 scans across
366 3081 focal observations), including the activity of the focal individual.

367

368 Maternal care during weaning

369 Maternal care was quantified through two measures: suckling frequency and infant carrying
370 frequency, which represent the two main energetic costs of maternal care before weaning (5,
371 65). First, for each scan observation (taken every 5 min), we considered whether the infant was
372 suckling (1) or not (0) to investigate the effect of birth timing on variation in suckling frequency.

373 In order to determine the best age window to consider, we explored age-related variation in
374 suckling frequency, and found that suckling decreases gradually from 2 to 18 months old,
375 before stabilizing to ca. 2% of the scans from 18 to 24 months old (Figure S2). In addition, the
376 maximum length of post-partum amenorrhea, often used as a proxy for the end of weaning,
377 lasted 550 days (i.e. 18.1 months) in this population (see above). Therefore, we considered only
378 infants aged 2- to 18-months-old for this analysis, using 11687 scans from 55 infants. The birth
379 date uncertainty for these 55 infants ranged from 0 to 130 days (with a median birth date
380 uncertainty of 16 days) and was taken into account in subsequent models (see Appendix 5).

381 Second, for each scan observation during which an infant was travelling, we determined
382 whether the infant was carried by its mother (1) or travelled on its own (0). This variable
383 allowed us to monitor the gradual decrease from full maternal dependence to full independence
384 during travelling. When looking for the best age window to consider, we observed that the
385 proportion of infant carrying gradually decreases during the first year of life in our population
386 (Figure S2), as in other baboon populations (65–67). Therefore, we considered infants aged
387 from 2 to 12 months old for this analysis, using 924 scans from 35 infants.

388

389 Mother-infant conflicts during weaning

390 We considered infant tantrums as a behavioural measure of mother-offspring conflicts,
391 reflecting when an infant's request to access resources from its mother was not initially satisfied
392 (19). Tantrum occurrence started in early-life, peaked when infants were aged around 6-9
393 months, and then gradually decreased during the end of their first and second year of life (Figure
394 S2). Therefore, we considered only infants aged 2 to 18 months old for this analysis, using 2221
395 focal observations from 55 infants. During each focal observation, we determined if a tantrum
396 occurred (1) or not (0), based on a range of distinctive offspring vocalizations (gecks, moans
397 and loud screams) and behaviours (frenzied behaviour when infants hurl themselves to the

398 ground, sometimes accompanied by rapidly rotating their tail) that were recorded on a
399 continuous basis and are characteristic of baboon tantrums (21, 67). A tantrum was considered
400 to occur when at least two of these behaviours or vocalizations were recorded, separated by at
401 least 30s (isolated complaints, and complaints that lasted fewer than 30 seconds, were thus not
402 considered as tantrums here). Tantrums were usually caused by maternal refusal of access to
403 the nipple or to carrying, and more rarely by maternal absence.

404

405 **Statistical analysis**

406 Characterization of the reproductive seasonality of the Tsaobis baboons

407 First, to assess the strength and direction of reproductive seasonality, we used a Rayleigh test,
408 from circular statistics, which characterizes the deviation of circular data from a uniform
409 distribution, via the mean direction μ and length R of the vector summing all observed events
410 across the annual cycle ($R=0$ when the event is evenly distributed, and $R=1$ when all events are
411 synchronized, i.e. occurs the same day) (68). Our sample comprised 241 conceptions, 215 births
412 and 171 cycle resumptions which occurred between 2005 and 2019. Uncertainties in those dates
413 were taken into account using 1000 randomized reproductive events for each variable
414 (Appendix 5).

415

416 Birth timing effects on two fitness traits

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

420 In both models, we used a sine term to describe the timing of an infant's birth in the
421 annual cycle. Sine waves allow the introduction of a circular variable into a multivariate model
422 as a fixed effect: the possible effects of the date of birth are circular with a period of one year,

423 as January 1st is equally close to December 31st than to January 2nd. This sinusoidal term was
424 as follows:

$$425 \quad \sin(\text{Date of Birth} + \varphi)$$

426 The date of birth in the formula above was converted in a radian measure, so that the period,
427 i.e. one year, equalled to $2*\pi$, ranging from $2*\pi/365$ for January 1st to $2*\pi$ for December 31st.
428 We tested 12 different phase values φ ($0, \pi/12, 2*\pi/12, 3*\pi/12, 4*\pi/12, 5*\pi/12, 6*\pi/12, 7*\pi/12,$
429 $8*\pi/12, 9*\pi/12, 10*\pi/12, 11*\pi/12$), to account for different potential optimal periods for the
430 event of interest across the year (24), as offspring mortality and IBI could be minimized for
431 different birth dates (and so tested all potential dates as minimal). For example, a phase of 0
432 could maximize April 1st or October 1st depending on the sign of the estimate (see Table S2).
433 We ran sequentially these 12 multivariate models, containing all other fixed and random effects
434 (see below), and selected the best phase as the one minimizing the Akaike Information Criterion
435 (AIC) in this full model set: the phase of $7*\pi/12$ was retained for offspring mortality probability,
436 and of $2*\pi/12$ for IBI (Table S2). We controlled for birth date uncertainty in both models using
437 a set of 1000 randomized birth dates within the interval of uncertainty (see Appendix 5 for more
438 details).

439 In both models, we included as random effects year of infant birth and identity of the
440 mother to control for repeated observations. In both models, we also included maternal parity,
441 rank (in the birth year of the focal infant) and infant sex as fixed effects, because maternal parity
442 and rank often affect reproductive traits in primates, including baboons (29, 69, 70), while
443 infant sex can affect both the mother's subsequent interbirth interval (71) and the probability
444 of infant survival in sexually dimorphic primates (26, 32). We also control for group identity
445 as a fixed effect in both models, as data were collected from only three groups in this study
446 (72).

447

448 Characterization of optimal birth timings, and individual effects on birth timing

449 We investigated the individual determinants of female reproductive decisions over birth timing,
450 based on 215 births from 62 females. We first used the results of Models 1 and 2 to characterize
451 the optimal birth timings for offspring survival and maternal IBI respectively. Offspring
452 mortality is minimised on December 15th (Table S2), and we thus computed, for each birth date,
453 the deviation in days from December 15th (the maximum value of the deviation being 182 for
454 June 15th). We used this deviation as a response variable of an LMM (Model 3) to investigate
455 the individual determinants of giving birth close to, or away from, the timing that maximizes
456 offspring survival. IBIs are minimised on September 1st (Table S2), and we thus computed, for
457 each birth date, the deviation in days from September 1st (the maximum value of the deviation
458 being 182 for March 1st). We used this deviation as a response variable of an LMM (Model 4),
459 to investigate the individual determinants of giving birth close to, or away from, the timing that
460 minimizes the maternal IBI.

461 For both Models 3 and 4, we tested the influence of infant sex, female parity and rank
462 (as fixed effects) on the proximity of birth to the optimal timing for offspring survival (Model
463 3) or for maternal IBI (Model 4). We also controlled for the identity of the mother and birth
464 year as random effects, and for group identity as fixed effects (as there was only three levels
465 for this factor (72)). We tested the significance of maternal identity using a likelihood-ratio test
466 (LRT), comparing the model with and without this random effect. We controlled for birth date
467 uncertainty in these models using a randomization procedure described in Appendix 5.

468

469 Birth timing effects on maternal care and tantrum probability

470 We ran three GLMMs with a binomial error structure to test the effect of birth timing on the
471 probability of suckling (Model 5), infant carrying (Model 6), and tantrums (Model 7). Models
472 5 and 6 are scan-based data: during a scan observation, the infant is suckling (yes/no, Model

473 5), and during a travelling scan observation, the infant is carried by its mother (yes/no, Model
474 6). Model 7 is based on the entire focal observation as tantrum events are relatively rare: during
475 a focal observation, the infant throws a tantrum (yes/no).

476 In order to investigate the potential effect of birth timing on maternal care and tantrum
477 probability, we used a sine wave term for infant birth date as a fixed effect, following the
478 method explained for Models 1-2. We did so to examine natural minimums or maximums in
479 the frequency of each of these traits along the annual cycle, without making any *a priori*
480 hypothesis on which periods were minimized or maximized, in order to test whether the
481 observed maximums or minimums would match the periods previously identified as the optimal
482 timings favouring current versus future reproduction. We therefore tested 12 different phases
483 in each full model and retained a phase of $9*\pi/12$ for suckling, 0 for infant carrying, and $2*\pi/12$
484 for tantrum probabilities. We controlled for birth dates uncertainty in all three models using the
485 randomization procedure described in Appendix 5.

486 We included, as random effects, the identity of the infant (Models 5-7) to control for
487 repeated observations. We also added the focal observation as a random effect for Models 5-6.
488 We controlled for group identity and year of observation as fixed effects in all models, as there
489 were less than five levels for both factors (72). In all models, we included maternal parity, rank
490 (in the year of birth of the focal infant) and infant sex as fixed effects. Such parameters are
491 likely to affect reproductive performances as well as the probabilities of maternal care and
492 mother-offspring conflict (26, 67). For Model 7, we also controlled for the duration of focal
493 observation as a fixed effect.

494 For Models 5-7, we further controlled for the effects of infant age, which modulates the
495 amount of maternal care and probability of tantrums throughout early development (19, 26).
496 We considered four different possibilities for the form of the relationship between infant age
497 and the response variable, using a regression thin plate spline (general additive model), a simple

498 linear effect, and a polynomial regression (of 2 or 3 degrees), respectively (73). To determine
499 the best fit, we ran these different preliminary models with no other fixed effect but including
500 all random effects (and the duration of focal observation for Model 7), and selected the model
501 minimizing the AIC. The age effect was linear for suckling and infant carrying probabilities
502 (Model 5 and 6), and a second-degree polynomial for tantrum probability (Model 7).

503 Lastly, mothers might be expected to invest more, and similarly infants might be
504 expected to have more requests for maternal care, during the lean season, irrespective of the
505 developmental trajectory of the infant, i.e. regardless of its age and birth timing (whether it was
506 born in the optimal period or not). Therefore, we also investigated the potential effect of
507 seasonality by assessing the influence of the observation date on suckling, infant carrying and
508 tantrum probabilities (see Appendix 1 for more details). We did not include in the same model
509 observation date and birth date, as they give redundant information (observation date is, by
510 definition, the sum of birth date and infant's age, and infant's age is already included as a fixed
511 effect). We present our models of birth date effects in the main text (Models 5-7, see also Table
512 S3), and our models of observation date effects in the Supplementary Information (Models 5bis-
513 7bis, Table S4).

514 The structure of each model, with the different fixed and random effects included,
515 alongside sample size, is summarised in Table S6.

516

517 Statistical methods

518 All statistical analyses were conducted in R version 3.5.0 (74). For the Rayleigh test, we used
519 the function 'r.test' from the R package 'CircStats' (75). To run mixed models, we used 'lmer'
520 (for LMMs) or 'glmer' (for binomial GLMMs) function on the lme4 package (76). To run
521 general additive mixed models (GAMMs) when investigating the best age effects on suckling,
522 infant carrying and tantrum probabilities, we used the 'gam' function of the 'mgcv' package

523 (73). All quantitative fixed effects were z-transformed to facilitate model convergence. When
524 we obtained singular fits, we confirmed the results by running the same models with a Bayesian
525 approach, using the ‘bglmer’ and ‘blmer’ functions of the ‘blme’ package (77). To diagnose the
526 presence of multicollinearity, we calculated the variance inflation factor for each predictor in
527 each full model using the ‘vif’ function of the R ‘car’ package (78). These were lower than 2.5
528 in all cases. To assess the strength of the fixed effects in each model, we used the Wald chi-
529 square tests with associated P-values computed with the ‘Anova’ function of the R package
530 ‘car’ (78), and calculated the 95% Wald level confidence intervals. We further checked the
531 distribution of residuals with ‘qqPlot’ function of the car package for LMMs (78), and with
532 ‘simulateResiduals’ from DHARMA package for binomial GLMMs (79).

533

534 **DATA AND CODE AVAILABILITY**

535 The datasets necessary to run analyses included in this paper and the associated legends have
536 been deposited in the public depository: [https://github.com/JulesDezeure/Maternal-trade-off-](https://github.com/JulesDezeure/Maternal-trade-off-over-birth-timing-in-baboon)
537 [over-birth-timing-in-baboon](https://github.com/JulesDezeure/Maternal-trade-off-over-birth-timing-in-baboon)

538

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553

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- 738
- 739

740 **TABLES**

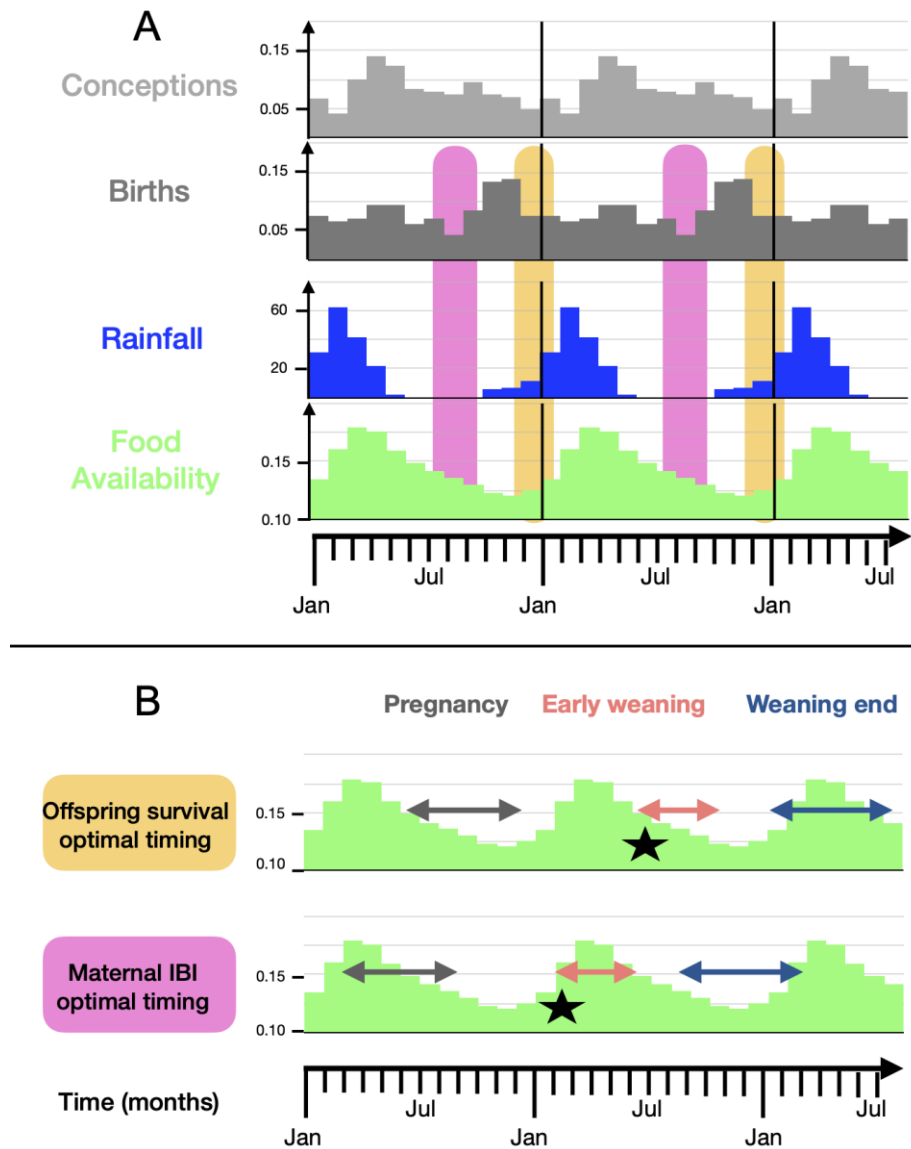
741 **Table 1:** Predictors of female reproductive timing.

742 Estimates, confidence intervals, X^2 statistics and P-values of the predictors of the two linear mixed models (Models
 743 3 and 4). The response variables are respectively the deviation from the offspring survival optimal birth timing,
 744 i.e. from December 15th (Model 3), and the deviation from the maternal IBI optimal birth timing, i.e. from
 745 September 1st (Model 4), in days, based on 215 births from 62 females. Female identity and year of infant birth are
 746 included as random effects. For categorical predictors, the tested category is indicated between parentheses.

Fixed effect		Estimate	IC		X^2	P-value
			Lower	Upper		
Model 3: Deviation from the offspring survival optimal birth timing						
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		
Model 4: Deviation from the maternal IBI optimal birth timing						
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		

747

748 **FIGURES**



749

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

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

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

753 (in mm) per month in blue and the mean NDVI value per month in green between 2005 and 2019. The orange and

754 pink squares in the background represent resp. the offspring survival and the maternal IBI optimal birth timings.

755 In Panel B, we aimed to represent the different phases of the female reproductive cycle, when the birth date occurs

756 within the offspring survival (December 15th) or maternal IBI (September 1st) optimal timing, according to seasonal

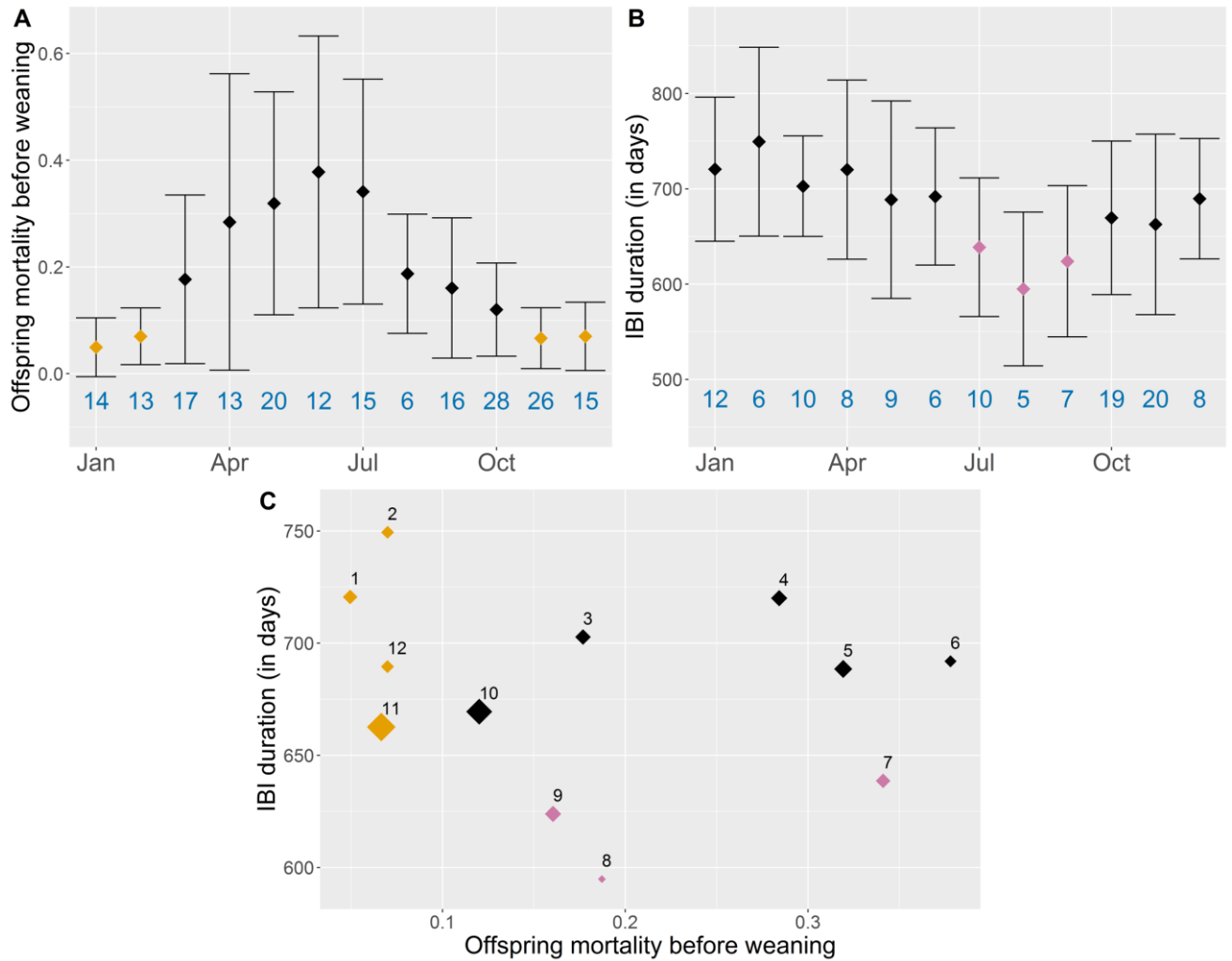
757 variation of NDVI. The green bar plot in the background indicates the mean NDVI per month (see y-axis).

758 Pregnancy, indicated with grey arrows, occurs the 6 months prior a birth. Early-weaning, indicated with salmon-

759 colour arrows, occurs from 6 to 9 months after a birth. Lactation peak, indicated with black stars, occur around 6

760 months after a birth. Weaning end, indicated with blue arrows, occurs from 12 to 18 months after a birth (see

761 Appendix 4 for the characterization of these different reproductive stages).

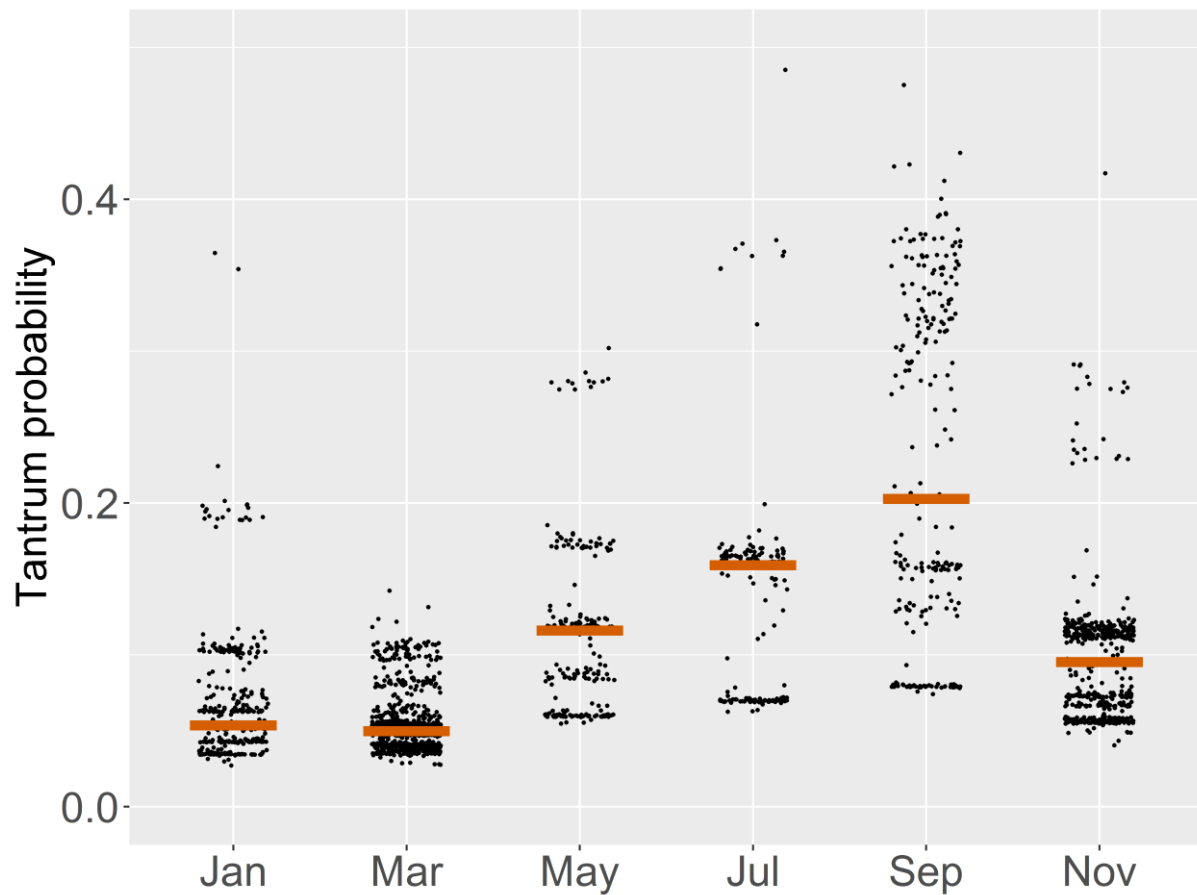


762

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

764 We plotted the predicted values of the full models (Model 1 looking at offspring mortality in panel A, and Model
765 2 looking at IBIs in panel B) according to the month of infant birth (Jan for January, Apr for April, etc.). The
766 number of births observed for each month is indicated in blue below the bar. The dots represent the mean values,
767 while the vertical black bars represent its standard deviations. The offspring survival optimal birth timing is
768 identified as the period minimizing offspring mortality, i.e. from November to February, and indicated with orange
769 dots (Panel A and C). The maternal IBI optimal birth timing is identified as the period minimizing maternal
770 interbirth interval, i.e. from July to September, and indicated with pink dots (Panel B and C). In panel C, we
771 represented the trade-off experienced by mothers over birth timing: each dot represents the predicted value of IBI
772 according to the predicted value of offspring mortality for a given month birth (see label, 1 for January, 2 for
773 February, etc.). The size of the dot is proportional to the number of births observed each month. We can notice an
774 absence of points on the extreme bottom-left corner (i.e. with both low infant mortality - inferior to 0.10 - and
775 short IBI - lower than 650 days), showing the existence of a reproductive trade-off. In addition, the highest number
776 of births occur for the points closer to this bottom-left corner (months 10 & 11), indicating that mothers target a
777 birth timing trading-off these two fitness components.

778



779

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

781 Predicted values of tantrum probability (Model 7) at weaning (age 12 months), according to infants' birth month,
782 based on 2221 focal observations from 55 infants. For graphical reasons, and given the low sample size of infants
783 observed for some birth months, we pooled infants born in 2 consecutive months, so that Jan indicates infants born
784 in both January and February, Mar in both March and April, etc. The brown horizontal bars indicate the median
785 values of fitted values for each birth month category.

786