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Birth timing generates reproductive trade-offs in a non-seasonal breeding primate

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ABSTRACT

The evolutionary benefits of reproductive seasonality are often measured by a single fitness component, namely offspring survival. Yet different fitness components may be maximised by dissimilar birth timings. This may generate fitness trade-offs that could be critical to understanding variation in reproductive timing across individuals, populations and species. Here, we use long-term demographic and behavioural data from wild chacma baboons (*Papio ursinus*) living in a seasonal environment to test the adaptive significance of seasonal variation in birth frequencies. We identify two distinct optimal birth timings in the annual cycle, located 4-months apart, which maximize offspring survival or minimize maternal interbirth intervals (IBIs), by respectively matching the annual food peak with late or early weaning. Observed births are the most frequent between these optima, supporting an adaptive trade-off between current and future reproduction. Furthermore, infants born closer to the optimal timing favouring maternal IBIs (instead of offspring survival) throw more tantrums, a typical manifestation of mother-offspring conflict. Maternal trade-offs over birth timing, which extend into mother-offspring conflict after birth, may commonly occur in long-lived species where development from birth to independence spans multiple seasons. Our findings therefore open new avenues to understanding the evolution of breeding phenology in long-lived animals, including humans.

MAIN TEXT

Introduction

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

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

Materials and methods

Study population

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

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

Environmental data

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

Daily rainfall in a 0.25 × 0.25 degree grid cell resolution (corresponding to 28 × 28 km at this latitude) was extracted using satellite data sensors from the Giovanni NASA website (product TRMM 3B42) [23]. We computed a rectangular geographic area that encompasses the global ranging area of the Tsaobis baboons, using GPS locations collected by observers every 30 min when following the study groups. We used the minimal and maximal latitude and longitude recorded between 2005 and 2019. Monthly cumulative rainfall (summed across daily values) were computed between 2005 and 2019.

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

Individual data

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

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

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

Fitness data

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

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

Behavioural observations

In order to characterize variation in maternal care and in mother-offspring conflict, we used three behavioural indicators: suckling, infant carrying and tantrum frequencies. We also used these behavioural data, along with life history data, to assign different developmental stages, including the different stages of weaning and the peak of lactation after an infant's birth (see Appendix 3). Field observers collected a total of 1185 hours of focal observation [35] of 20 (in 2017, 2018 and 2019) or 60 (in 2006) minutes long on 69 infants (mean ± SD = 17.1 ± 7.8 hours of observations per infants, range = 6.3–34.6) (see Appendix 4 for more details).

Maternal care during weaning

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

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

Mother-infant conflicts during weaning

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

Statistical analysis

Characterization of the environmental and reproductive seasonality of the Tsaobis baboons

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

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

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

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

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

Birth timing effects on maternal care and tantrum probability

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

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

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

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

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

Statistical methods

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

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

Results

1. Characterization of the environmental and reproductive seasonality of the Tsaobis baboons

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

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

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

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

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

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

3. Birth timing effects on maternal care and tantrum probability

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

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

Discussion

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

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

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

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

Fourth, our results show that the trade-off over birth timing faced by mothers may subsequently translate into mother-offspring conflict after birth. Although mothers adjust maternal care seasonally, they do so regardless of the offspring’s age. Offspring born at suboptimal periods face the dry season in a critical developmental window (i.e., the end of weaning), and maternal care is insufficient to buffer them entirely from the adverse consequences that lead to higher mortality. Consequently, baboon infants respond by throwing more tantrums, which may be an honest signal of need [38,62], just as children do in similar situations [63]. More generally, these results shed light on the potential influence of environmental fluctuations, and specifically seasonality, on mother-offspring conflicts over maternal care. While the literature focusing on optimal birth spacing has mainly examined trade-offs between current and future reproduction for an implicitly stable level of resources [7,64], such a stability may rarely be encountered by mothers in the wild, who typically face extensive, but partly predictable, fluctuations in food availability. Taking into account the intensity and predictability of resource fluctuations may largely re-draw the landscape of strategic decisions available to mothers confronted with trade-offs between current and future reproduction in natural environments [65,66].

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

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TABLES

Table 1: Predictors of female reproductive timing.

Estimates, confidence intervals, X^2 statistics and P-values of the predictors of the two linear mixed models (Models 3 and 4). The response variables are respectively the deviation from the offspring survival optimal birth timing, i.e. from December 15th (Model 3), and the deviation from the maternal IBI optimal birth timing, i.e. from September 1st (Model 4), in days, based on 215 births from 62 females. Female identity and year of infant birth are 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		

FIGURES

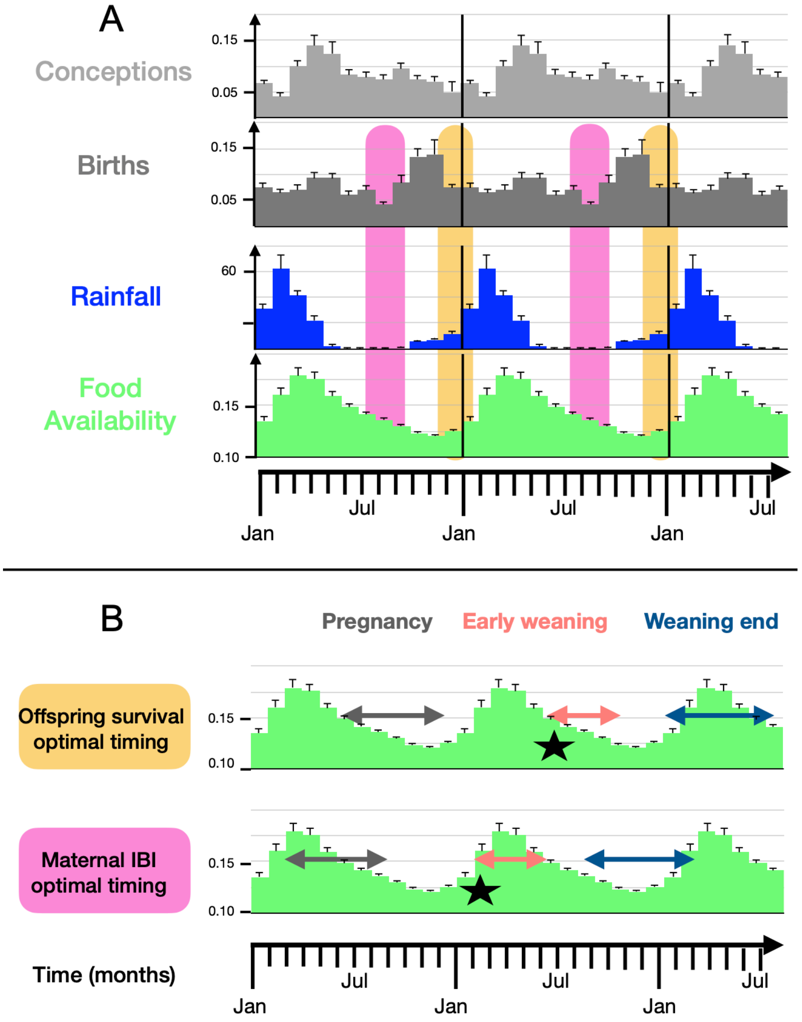

Figure 1: Tsaobis baboons' reproductive timings in relation with environmental seasonality.

In Panel A, we plotted the proportion of conceptions (N=241, in light grey) and births (N=215, in dark grey) recorded in 2005-2019 per month (Jan for January, Jul for July). We plotted the mean monthly cumulative rainfall (in mm) per month in blue and the mean NDVI value per month in green between 2005 and 2019. We represented the standard errors associated with vertical black segments. The pink and orange squares in the background represent respectively the maternal IBI and the offspring survival optimal birth timings. In Panel B, we aimed to represent the different phases of the female reproductive cycle, when the birth date occurs within the offspring survival (December 15th) or maternal IBI (September 1st) optimal timing, according to seasonal variation of NDVI. The green bar plot in the background indicates the mean NDVI per month (see y-axis). Pregnancy, indicated with grey arrows, occurs the 6 months prior a birth. Early-weaning, indicated with salmon-colour arrows, occurs from 6 to 9 months after a birth. Lactation peak, indicated with black stars, occur around 6 months after a birth. Weaning end, indicated with blue arrows, occurs from 12 to 18 months after a birth (see Appendix 3 for the characterization of these different reproductive stages).

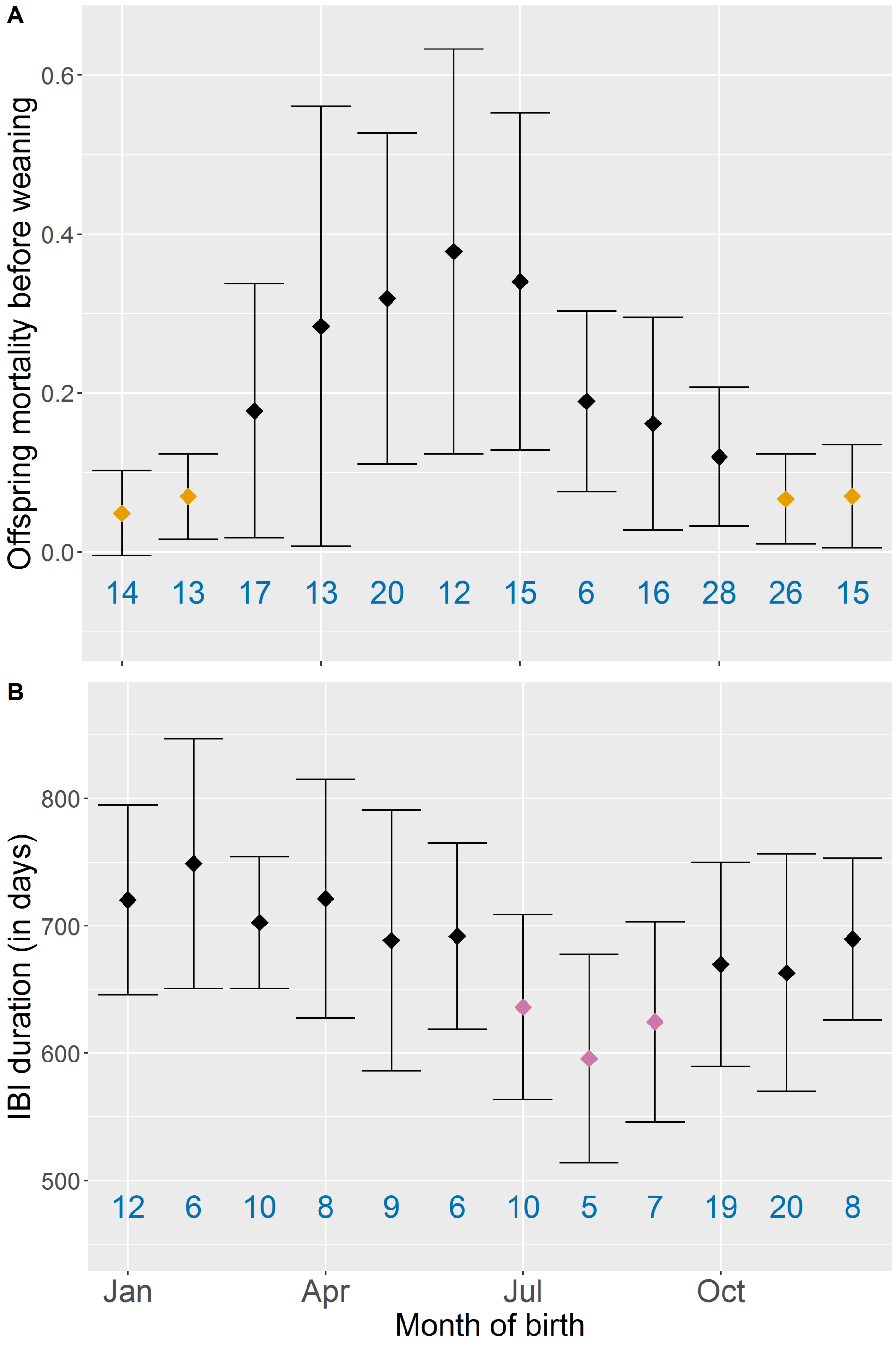

Figure 2: Distinct optimal birth timings for current and future reproduction.

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

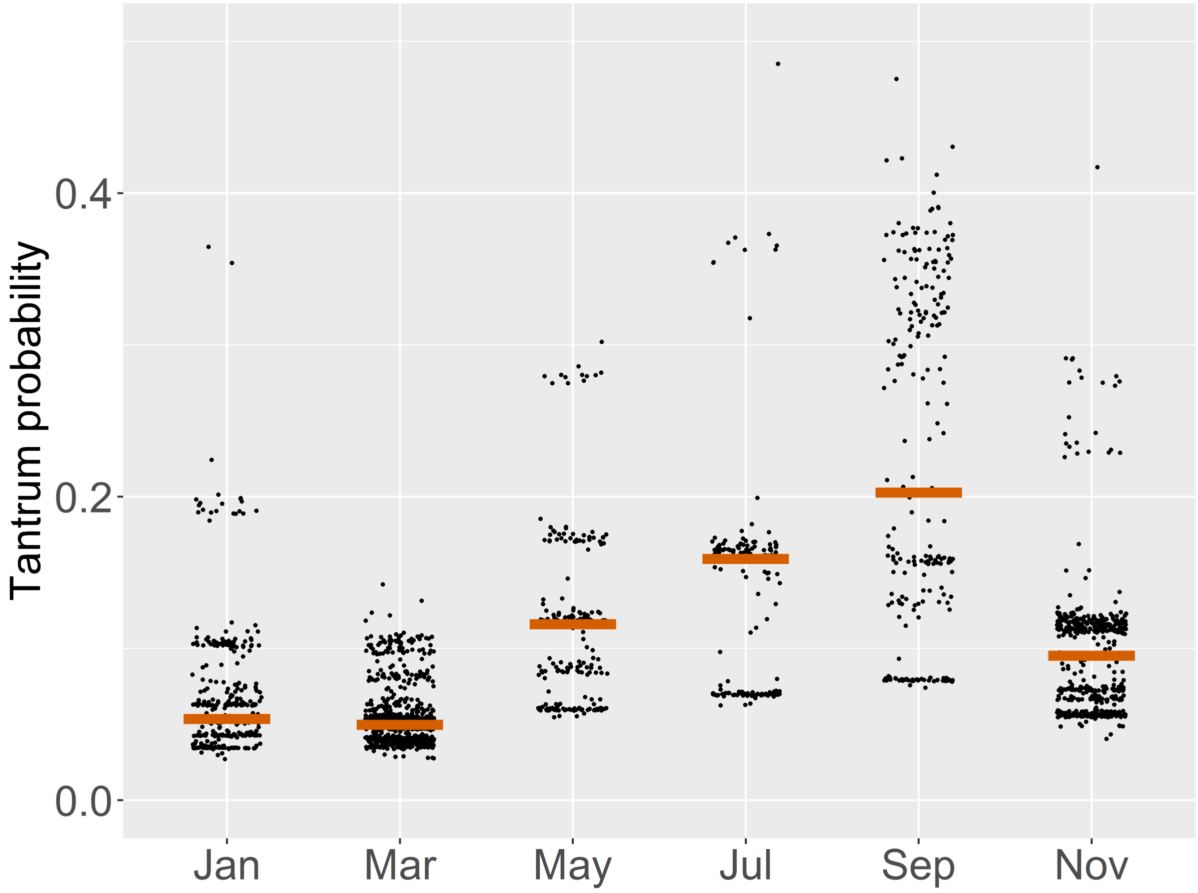

Figure 3: Influence of birth timing on tantrum probability.

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

Supporting Information for:

Birth timing generates reproductive trade-offs in a non-seasonal breeding primate

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CONTENTS

SUPPLEMENTARY TEXT

Appendix 1. Correlations between rainfall and NDVI at Tsaobis

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

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

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

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

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

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

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

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

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

In order to understand which stage of the reproductive cycle might be timed with the seasonal food peak (Figure 1B), we needed to define the sequential behavioural stages of weaning, which is the infant's gradual transition to nutritional independence [3], along with the peak of lactation in our population. First, the onset of weaning can be defined as the period when solid foods start to account for an important part of an infant's energy intake, and is characterized by an increase in maternal refusals to accede to her offspring's suckling demands. The onset of behavioural conflict between a mother and her offspring has therefore often been used as a proximate measure of the early-weaning period [3]. In our population, tantrum probabilities peak between 6 and 9 months of age (Figure S1), and we therefore used this age window to characterize 'early-weaning'. The peak of lactation typically occurs just before the beginning of weaning [3,4], when offspring have grown larger but are still fully dependent. So we can consider that lactation peak occurs around 6 months after birth in our population. Similar ages for early-weaning and lactation peak have been found in other baboon populations [5–7], albeit weaning age and lactation durations can vary substantially between populations [8].

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

All in all, for Figure 1B, in order to better understand the relationship between reproductive phenology and environmental seasonality, we considered the lactation peak to occur around 6 months after birth, early-weaning between 6 and 9 months of age, and the end of weaning between 12 and 18 months of age. As a note of caution, these windows are strictly based on behavioural and life-history data, which show some limitations to evaluate the dynamics of lactation [9,10]. More objective measures, such as isotopic comparisons of mother-offspring hair or faecal samples [11–14], may help to refine these estimates.

Appendix 4. Methodology of infants' focal observations

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

Appendix 5. Controlling for uncertainties in the dates of conceptions, births and cycle resumptions in statistical analyses

Dates of conceptions, births and cycle resumptions were estimated in many cases because the Tsaobis baboons are not followed year round (see Appendix 1). In addition, uncertainty in these estimations varied with the time of year, as we generally follow baboons during the cooler, dryer months. In order to account for these uncertainties in our analyses, we ran a set of randomizations to evaluate the robustness of the fixed effects found to be statistically significant. For each reproductive event (conceptions, births, and cycle resumptions) for which the date was associated to some uncertainty (i.e. exact date unknown), we created an extended dataset including all possible dates of the full range of uncertainty (from the minimum to the maximum date). For example if a baboon birth date was estimated to occur between October 2nd and December 23rd, we included all possible dates between October 2nd and December 23rd in this extended dataset. Using this extended dataset, we generated 1000 simulations; in each iteration, a date was randomly drawn between the minimal and maximal estimate for each reproductive event that was not known with certainty. Events known with certainty did not vary throughout such simulations.

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

In our multivariate mixed models investigating the effect of seasonal birth timing on offspring mortality before weaning (Model 1) and maternal interbirth intervals (Model 2), we controlled for the uncertainties in dates of birth which could affect both our response variables and our main fixed effect of interest (seasonal birth timing). For Model 1, we generated 1000 simulations with random birth dates drawn, for each birth, between minimal and maximal birth date estimations for this particular birth, and subsequently ran 1000 mixed models, one for each simulated value of the offspring's birth date and for each survival outcome (as birth date affects an offspring's age, and therefore its estimated age at death). For Model 2, we similarly generated 1000 simulations with random birth dates drawn between minimum and maximum birth date estimations for the two births defining the IBI. We subsequently ran 1000 models with randomized values for both IBI (the response variable, i.e. number of days between the first and second birth) and the birth date fixed effect. For both models, we then extracted the 1000 p-values of our fixed effect ‘seasonal birth timing’ and computed the confidence intervals of these p-values (see the footnote of Table S6).

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

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

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

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

$$sin(Date\ of\ Birth + \varphi)$$

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

Appendix 7. Seasonal effects on maternal care and tantrum probability

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

$$sin(Date\ of\ observation + \varphi)$$

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

TABLES

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

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

Table S2: Identification of the best birth timing effect for Models 1-2 & 5-7: ΔAIC (Akaike Information Criterion) according to the phase of the sine wave term

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

Phase φ	Date maximised	Date minimised	Δ 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	**0**	1.15
π/12	15th March	15th September	9.42	0.72	1.13	0.17	0.34
2*π/12	1st March	1st September	9.45	**0**	1.62	0.65	**0**
3*π/12	14th February	15th August	8.12	0.33	1.96	1.29	0.39
4*π/12	1st February	1st August	5.66	1.61	1.92	1.85	1.49
5*π/12	15th January	15th July	2.91	3.36	1.46	2.16	2.94
6*π/12	1st January	1st July	0.84	5.02	0.86	2.18	4.20
7*π/12	15th December	15th June	**0**	6.16	0.37	1.93	4.84
8*π/12	1st December	1th June	0.47	6.59	0.09	1.53	4.80
9*π/12	15th November	15th May	1.99	6.29	**0**	1.05	4.20

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

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

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

Fixed Effect		Estimate	IC		X^2	P-value
			Lower	Upper		
Model 5: Suckling						
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
Infant age		**-1.66**	**-1.97**	**-1.35**	**110**	**$<10^{-4}$**
Group	**(L)**	**0.18**	**-0.53**	**0.90**	**7.79**	**0.02**
	(M)	**1.51**	**0.36**	**2.66**		
Observation year	**(2017)**	**0.21**	**-1.22**	**1.63**	**40.45**	**$<10^{-4}$**
	(2018)	**1.73**	**0.84**	**2.62**		
	(2019)	**0.03**	**-0.82**	**0.88**		
Model 6: Infant carrying						
Infant birth date		0.53	-0.18	1.24	2.13	0.14
Infant sex	**(Male)**	**-0.94**	**-1.60**	**-0.28**	**7.78**	**0.005**
Female parity	**(Primiparous)**	**-1.08**	**-2.11**	**-0.05**	**4.21**	**0.040**
Female rank		**-0.51**	**-0.82**	**-0.19**	**10.0**	**0.002**
Infant age		**-1.94**	**-2.69**	**-1.20**	**26.2**	$<10^{-4}$
Group	(L)	0.01	-0.53	0.55	0.67	0.71
	(M)	-0.35	-1.34	0.64		
Observation year	(2017)	-11.5	-262	239	3.69	0.30
	(2018)	1.36	-0.36	3.09		
	(2019)	0.86	-1.19	2.91		
Model 7: Tantrum						
Infant birth date		**-0.32**	**-0.62**	**-0.03**	**4.53**	**0.033^{*}**
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
Infant age	**Age**	**-41.13**	**-54.06**	**-28.21**	**53.28**	**$<10^{-4}$**
	Age^2	**-19.07**	**-28.21**	**-9.92**		
Group	(L)	-0.35	-0.68	-0.01	4.23	0.12
	(M)	-0.21	-0.81	0.40		
Observation year	**(2017)**	**0.12**	**-1.39**	**1.63**	**12.61**	**0.006**
	(2018)	**0.30**	**-0.81**	**1.41**		
	(2019)	**-0.44**	**-1.57**	**0.68**		
Offset		**0.40**	**0.10**	**0.71**	**6.81**	**0.009**

[*] 95% CI: [0.04684 – 0.05234]

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

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

Fixed Effect		Estimate	IC		X^2	P-value
			Lower	Upper		
Model 5bis: Suckling						
Observation date		**-1.66**	**-2.91**	**-0.40**	**6.70**	**0.0096**
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
Infant age		**-1.62**	**-1.94**	**-1.30**	**97.47**	**<10-4**
Group	**(L)**	**0.30**	**-0.46**	**1.06**	**6.71**	**0.035**
	(M)	**1.52**	**0.33**	**2.71**		
Observation year	**(2017)**	**-2.34**	**-4.88**	**0.20**	**29.99**	**<10-4**
	(2018)	**1.74**	**0.82**	**2.66**		
	(2019)	**-2.64**	**-4.95**	**-0.33**		
Model 6bis: Infant carrying						
Observation date		**-1.14**	**-1.98**	**-0.30**	**7.12**	**0.0076**
Infant sex	**(Male)**	**-0.90**	**-1.56**	**-0.24**	**7.20**	**0.0073**
Female parity	(Primiparous)	-0.78	-1.77	0.22	2.33	0.13
Female rank		**-0.45**	**-0.76**	**-0.15**	**8.31**	**0.0039**
Infant age		**-2.40**	**-2.83**	**-1.97**	**120**	**<10-4**
Group	(L)	-0.003	-0.53	0.54	2.04	0.36
	(M)	-0.63	-1.62	0.37		
Observation year	**(2017)**	**-13.10**	**-2410**	**2384**	**12.2**	**0.007**
	(2018)	**0.66**	**-1.19**	**2.52**		
	(2019)	**-0.73**	**-2.77**	**1.31**		
Model 7bis: Tantrum						
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
Infant age	**Age**	**-33.10**	**-43.45**	**-22.75**	**51.09**	**<10-4**
	Age^2	**-20.84**	**-29.87**	**-11.81**		

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

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^2, 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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Table S6: Predictors of offspring mortality before weaning and maternal interbirth interval (IBI) duration.

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

Fixed Effect		Estimate	IC		X^2	P-value
			Lower	Upper		
Model 1: Offspring mortality						
Infant birth date		**-1.12**	**-1.84**	**-0.40**	**9.38**	**0.002**[*]
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		
Model 2: Maternal IBI						
Infant birth date		**36.84**	**7.59**	**66.09**	**6.10**	**0.014** †
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
Female rank		**-25.73**	**-50.68**	**-0.77**	**4.08**	**0.043**
Group	(L)	**-50.41**	-105.19	4.38	3.31	0.191
	(M)	-31.09	-150.57	88.38		

[*] 95% CI: [0.00967 – 0.01087]

† 95% CI: [0.02533 – 0.02821]

FIGURES

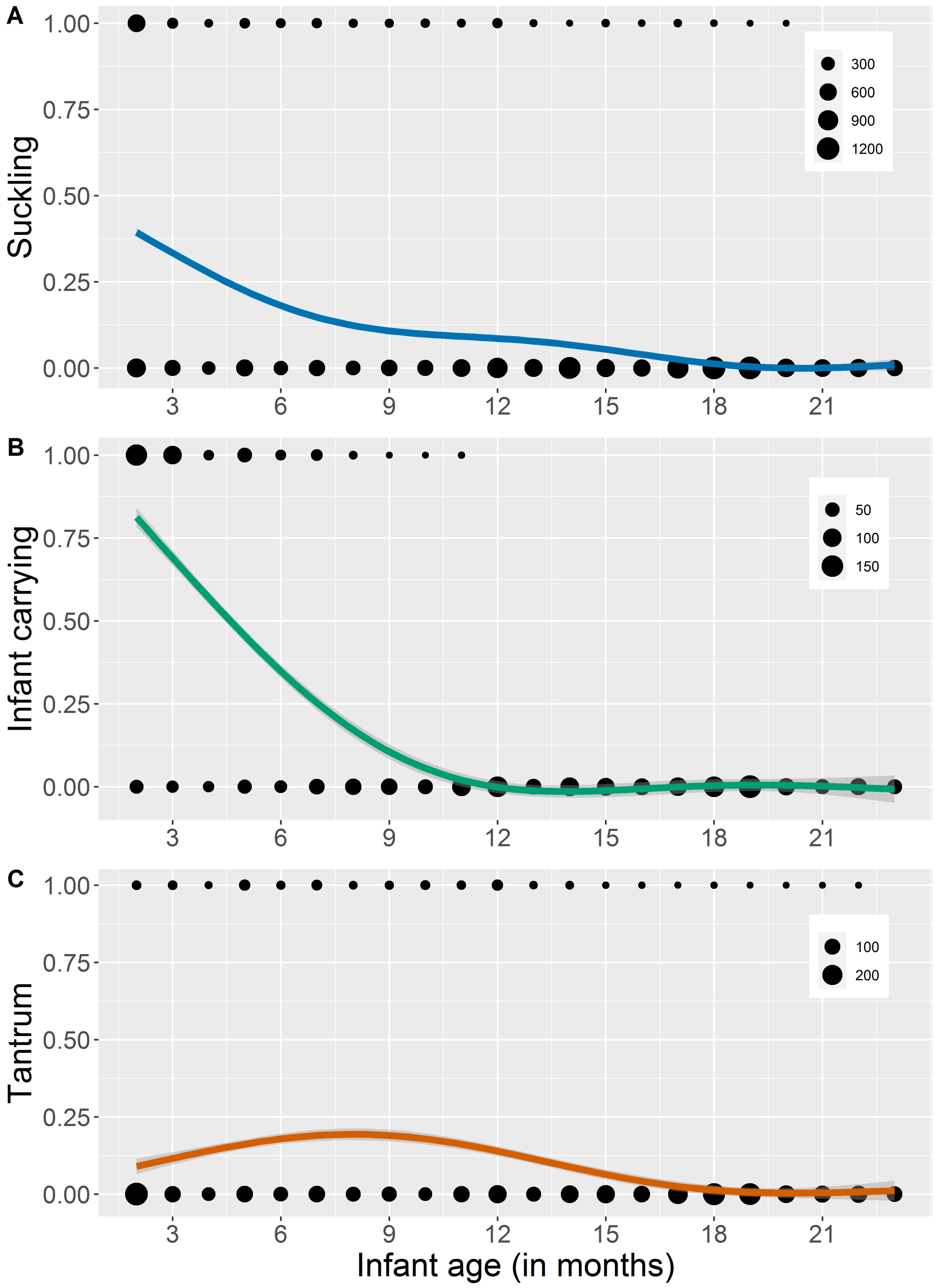

Figure S1: Variation in the probabilities of suckling, infant carrying, and tantrums, according to infant age.

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

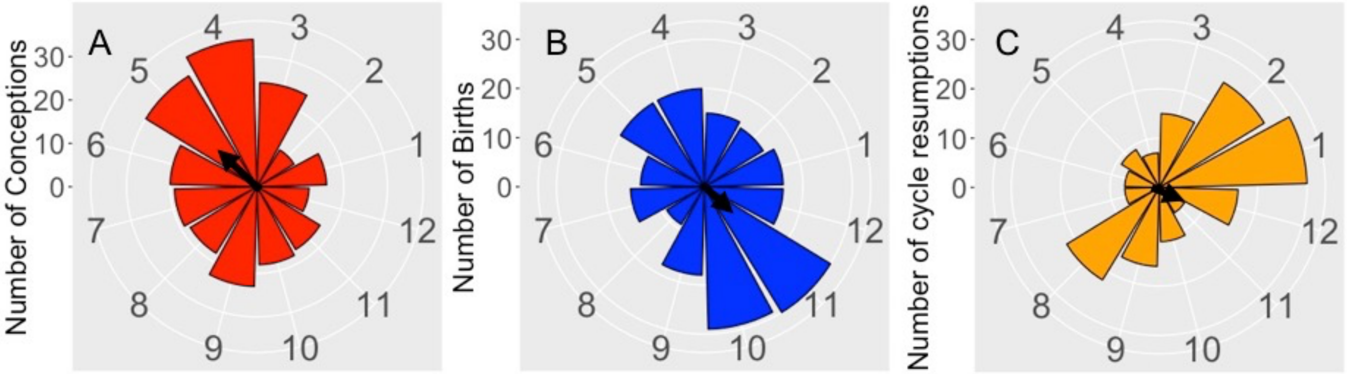

Figure S2: Chacma baboons breed all year round.

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

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