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1 **Fitness effects of seasonal birth timing in a long-lived social primate**
2 **living in the equatorial forest**

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13

14 Reproductive seasonality is the norm in mammals from temperate regions but less common at
15 lower latitudes, where a broad diversity of reproductive phenology strategies is observed. Our
16 knowledge of the evolutionary determinants shaping this diversity remains fragmentary and
17 may reflect high phenotypic plasticity in individual strategies. Here we investigated the
18 ecological determinants and fitness consequences of variation in birth timing across the annual
19 cycle in a social primate endemic to the Congo basin, the mandrill, *Mandrillus sphinx*, which
20 breeds seasonally. We further examined traits that modulate this variation within and across
21 individuals. We used 9 years of ecological, life history and behavioural data from a natural
22 population to characterize patterns of environmental and reproductive seasonality. We then
23 investigated the consequences of variation in birth timing for pre- and postnatal offspring
24 survival and maternal interbirth intervals. Finally, we studied the influence of within-
25 (reproductive history and age) and between-individual (social rank) traits on variation in birth
26 timing. We found that mandrills' daily foraging time varied seasonally, with greater
27 fluctuations for subordinate than dominant females. Birth timing was plastic, as females gave
28 birth year round without detectable consequences for postnatal offspring survival. Giving birth
29 within the birth peak, however, decreased interbirth intervals and probability of miscarriage.
30 Finally, reproductive history and social rank mediated within- and between-individual variation
31 in birth timing, respectively. Specifically, females that experienced a previous reproductive
32 failure gave birth early in the next birthing season and dominant females bred less seasonally
33 than subordinates, which may reflect their more even access to resources across the year.

34 Overall, the selective pressures shaping mandrill reproductive seasonality differed from a
35 classical scenario of seasonal fluctuations in resources limiting offspring survival. A complex
36 interplay between social and ecological factors may thus determine within- and between-
37 individual variation in phenology strategies of tropical and gregarious mammals.

38

39 **KEYWORDS:** birth timing, fitness, interbirth interval, mandrill, reproductive phenology,
40 reproductive seasonality

41

42 The intensity of reproductive seasonality, which measures the temporal clustering of births
43 during a particular period of the annual cycle (Lindburg, 1987), varies widely across species:
44 from births concentrated over a week in banded mongooses, *Mungos mungo* (Hodge, Bell, &
45 Cant, 2011) to births occurring year round in African elephants, *Loxondata africana* (Moss,
46 2001). Ultimate explanations of this variation in the intensity of reproductive seasonality across
47 species have largely assumed that it mirrors variation in the intensity of environmental
48 seasonality (Conover, 1992; Di Bitetti & Janson, 2000; Rutberg, 1987). Latitude, for example,
49 often accentuates the intensity of seasonality and, as such, tropical species generally exhibit
50 lower reproductive seasonality than temperate or arctic species (Di Bitetti & Janson, 2000;
51 Heldstab et al., 2020; Rutberg, 1987). Nevertheless, reproductive seasonality is common, and
52 sometimes acute, in tropical species such as in Malagasy mammals (Heldstab et al., 2020;
53 Wright, 1999). Yet, much less is known about the evolutionary determinants of reproductive
54 phenology in tropical ecosystems which host most of the biomass (Myers, Mittermeier,
55 Mittermeier, Da Fonseca, & Kent, 2000).

56 Reproduction is energetically costly, and matching the most demanding period of the
57 reproductive cycle with the annual food peak is necessarily adaptive (Baker, 1938; Bronson,
58 2009). Most studies on the fitness consequences of reproductive phenology have concerned
59 fast-lived organisms, such as rodents and passerines, from temperate regions (Bronson, 2009;
60 Bronson & Heideman, 1994; Williams et al., 2017). These studies have usually considered only
61 one fitness component, typically measuring offspring number, survival or growth (Ellison,
62 Valeggia, & Sherry, 2005; Varpe, Jørgensen, Tarling, & Fiksen, 2009) but omitting potential
63 effects on the mother's future reproduction (but see for a bird species, *Fulica atra*: Brinkhof et
64 al., 2002) and miscarriage. This is problematic as the period from conception to weaning often
65 extends over multiple seasons or years in long-lived species. Seasonal food peak(s) can thus be
66 synchronized with some, but not all, reproductive and developmental stages. In such cases, birth
67 timings maximizing offspring survival may be different from those maximizing maternal

68 reproductive pace (Dezeure et al., 2021). When studying long-lived species, it thus appears
69 essential to investigate the consequences of reproductive phenology across multiple fitness
70 components to fully understand the selective pressures shaping reproductive seasonality.

71 In addition, few studies have attempted to identify whether and why reproductive
72 phenology varies across individuals. Some stages of a female reproductive cycle, such as the
73 onset of sexual receptivity or conceptions, are condition dependent (Brockman & van Schaik,
74 2005; Clauss, Zerbe, Bingaman Lackey, Codron, & Müller, 2020). Consequently, factors
75 influencing condition, such as female age, parity and reproductive history, are also likely to
76 affect female reproductive phenology (Garel et al., 2009; Paul & Thommen, 1984; Plard et al.,
77 2014). In gregarious species with social hierarchies, dominant females may also have privileged
78 access to food resources and may subsequently exhibit earlier age at first reproduction, shorter
79 interbirth intervals, higher offspring survival and increased longevity (Clutton-Brock &
80 Huchard 2013; Stockley & Bro-Jørgensen 2011). However, the consequences of rank-related
81 variation in life history traits for reproductive phenology have rarely been examined.

82 In this study, we investigated the causes and consequences of reproductive phenology
83 across multiple measures of female reproductive success in a natural population of a long-lived
84 social Old World primate, the mandrill, *Mandrillus sphinx*, from Gabon. Mandrills form huge
85 multimale–multifemale groups in the wild, up to a few hundreds of individuals, mainly females
86 and their offspring (Abernethy, White, & Wickings, 2002; Hongo, 2014). Female mandrills are
87 philopatric and form a matrilineal social hierarchy. They can live more than 18 years (Setchell
88 et al., 2001) and give birth to a single offspring every 1–3 years (Setchell et al., 2002) which
89 they breastfeed during a variable period (8 months on average: Setchell & Wickings, 2004).
90 Dominant and multiparous females have higher reproductive performances, but neither rank
91 nor parity affects reproductive timings in captivity (Setchell et al., 2002). Most of our
92 knowledge about mandrill reproduction comes from a semifree-ranging population (Setchell,
93 Lee, Jean Wickings, & Dixson, 2001; Setchell, Lee, Wickings, & Dixson, 2002; Setchell &
94 Wickings, 2004) and from a preliminary study on a wild unhabituated population showing that
95 reproduction is seasonal: although inter- and intraindividual variation occur both within and
96 across years, mating happens mainly during the long dry season, while births are concentrated
97 in the rainy season (Hongo, Nakashima, Akomo-Okoue, & Mindonga-Nguelet, 2016). The fact
98 that mandrills breed seasonally despite living in the equatorial forests of central Africa, which
99 exhibit buffered environmental conditions year round compared to most other biomes, remains
100 puzzling. The mandrill is an interesting species to study the determinants of reproductive
101 seasonality because it is an equatorial primate whose births are highly seasonal but there is also

102 a high degree of individual variability in birth timing. Here, we used longitudinal life history
103 and behavioural data collected since 2012 from the only natural population of habituated
104 mandrills to ask three main questions. (1) How is reproductive phenology adjusted to
105 environmental seasonality? We characterized both environmental and reproductive seasonality,
106 predicting that mandrill food availability is affected by environmental seasonality, and further
107 asked which reproductive stage is synchronized with the annual food peak. (2) What are the
108 consequences of variation in birth timing for female reproductive success? We used three
109 measures of reproductive success: pre- and postnatal offspring mortality and the length of the
110 maternal interbirth interval (IBI). We predict that giving birth away from the birth peak affects
111 both offspring mortality and maternal interbirth interval. More precisely, we expected maternal
112 phenology strategies to prioritize offspring survival over reproductive pace in this long-lived
113 species, meaning that birth timing effects may be more detectable on maternal IBI than on pre-
114 and postnatal offspring survival (Dezeure et al., 2021). (3) Do females vary in birth timing and,
115 if so, which individual traits drive this variation? We investigated the effects of female age,
116 recent reproductive history and social rank. We predicted that higher-ranking females would be
117 less seasonal than lower-ranking females, as their privileged access to resources may buffer
118 them from environmental seasonality. We further predicted that a reproductive failure
119 (miscarriage or infant mortality) would disrupt female reproductive phenology and lead females
120 to reproduce early in the birth season or away from the birth peak, depending on the age at
121 infant death.

122

123 <H1>METHODS

124 <H2>Study site and population

125 A natural population of habituated mandrills has been monitored daily since 2012 by the
126 Mandrillus Project, a long-term field research project studying the ecology, life history and
127 behaviour of mandrills. This population originated from 65 captive individuals initially housed
128 at the CIRMF (Centre International de Recherches Médicales de Franceville, Gabon) which
129 were released in the park in two waves, in 2002 and 2006 (Peignot et al., 2008). Study mandrills
130 live in a private park (Lékédi Park) and its vicinity. Their habitat is composed of a mosaic of
131 evergreen forests, grasslands and savannahs. The diet of these mandrills has not been
132 supplemented since April 2012 (Brockmeyer et al., 2015). In early 2021, our study group was
133 composed of approximately 250 individuals. During daily monitoring, we recorded data on
134 individual life history, developmental trajectory, behaviour, group demography and GPS

135 locations. Data used in this study were collected from March 2012 to March 2020 on a total of
136 80 adult females aged 4–24 years.

137 <H2>Individual and reproductive parameters

138 A female was considered adult when she reached menarche (i.e. first menstrual cycle) and her
139 perianal area was turgescient (i.e. swollen) for the first time. Female parity (i.e. number of birth
140 events a female had had), including for those females that were adult in 2012, was determined
141 using data on longitudinal life history and presence of known offspring and defined as
142 nulliparous (before the birth of her first infant), primiparous (between the birth of her first and
143 second infant) and multiparous (at the birth of her second infant).

144 The age of adult females born at CIRMF ($N=15$) and of some of the females born at our
145 field site ($N=26$) after 2012 was exactly known thanks to direct observations. For the remaining
146 females ($N=30$), age was estimated using general condition and patterns of tooth eruption and
147 wear (see also: Dibakou, Basset, Souza, Charpentier, & Huchard, 2019).

148 The reproductive state of each adult female was monitored daily. A female was assigned
149 as (1) pregnant, with pregnancy being determined post hoc following either the birth of a live
150 infant, and encompassing the 175 days before the birth (average gestation length = 175 days in
151 this population, range 163–190 days, $SD=4.7$, $N=103$ pregnancies where both conception and
152 birth were observed with <7 days of uncertainty) or, in cases of births showing ≥ 7 days of
153 uncertainty, using patterns of sexual swellings or the presence of a noticeable small and
154 distinctive pink swelling present about 2 months following fertilization (the main clue
155 confirming pregnancy when a female miscarried), (2) lactating, when a live offspring was less
156 than 6 months old or until the death of the offspring before 6 months of age, or (3) cycling,
157 including both swollen females in oestrus (i.e. sexually active with a perineal tumescent or
158 detumescent swelling) and nonswollen females at other stages of their menstrual cycle.

159 We considered a total of 215 conceptions, 212 births and 150 cycle resummptions,
160 occurring between 2012 and 2020 (see Appendix 1 for more details about their estimations).

161

162 <H2>Fitness estimates

163 For each infant born, we investigated whether it died before 6 months of age. We used this age
164 threshold because older infants are often harder to recognize, generating uncertainty on their
165 survival after this age. Death was recorded when a corpse was observed, often carried by the
166 mother for a few days, or when the mother was seen without her infant for a few days. We
167 discarded records of four infants whose survival outcomes were uncertain. In our data set, 20

168 of 208 infants died before reaching 6 months old, with mortality occurring at a median age of
169 83 days (range 1–163 days).

170 For each conception, we investigated whether a late miscarriage occurred, typically
171 when a female was observed with a pregnancy swelling (as described above) but did not
172 subsequently give birth. We discarded records of a few conceptions for which the pregnancy
173 outcome was unknown and probably resulted in an early miscarriage ($N=4$). Early miscarriages
174 (0–2 months of pregnancy) are difficult, if not impossible, to detect with certainty in the field
175 and were thus not considered in this study. We observed a total of 19 miscarriages from 211
176 conceptions, i.e. 9% of conceptions led to late miscarriages.

177 We defined interbirth intervals (IBI) as the number of days between two consecutive
178 live births for a given female (as in Gesquiere, Altmann, Archie, & Alberts, 2017). We only
179 considered IBIs for which the first infant survived for at least 6 months because females
180 resumed cycling rapidly after their infant's death (median number of days between an infant's
181 death and a mother's cycle resumption was 15, range 7–111 days, $N=15$ cases where the
182 infant's date of death was known with less than 30 days of uncertainty, and for which the mother
183 resumed cycling afterwards). We computed a total of 122 IBIs from 47 adult females
184 (median=566, range 323–1024 days).

185

186 <H2>Environmental data

187 We extracted rainfall using satellite data from a point close to the centre of the Lékédi Park
188 where mandrills were ranging ($1^{\circ}47'51.85''S$, $13^{\circ}01'12.92''E$). More precisely, daily rainfall
189 in a 0.25×0.25 degree resolution (corresponding to 28×28 km at this equatorial latitude) was
190 extracted from this geographical point using satellite data sensors from the Giovanni NASA
191 website (product TRMM 3B42; Huffman, Bolvin, Nelkin, & Adler, 2016). Monthly cumulated
192 rainfalls (summed across daily values) were computed between January 2012 and December
193 2019.

194

195 <H2>Behavioural data

196 Five-minute focal observations (Altmann, 1974) were performed daily on all individuals chosen
197 randomly. During focal observations, we recorded all activities, including foraging bouts, on a
198 continuous basis, as well as other point events, such as dyadic approach–avoidance interactions.
199 We used these data to compute seasonal variation in the time adult females spent foraging and
200 adult females' social rank.

201

202 <H3>*Seasonal variation in time budgets*

203 We used the proportion of time adult females (≥ 4 years; corresponding to the youngest age at
204 which females may conceive; here we excluded females aged 3–4 years from above because
205 these females may have cycled but not conceived yet) spent foraging to characterize the
206 environmental seasonality of food availability (as per Dunbar & Dunbar 1988; Muruthi et al.
207 1991; Byrne et al. 1993; Doran 1997; Overdorff et al. 1997; Alberts et al. 2005; Swedell 2011).
208 Mandrills are omnivorous with a frugivorous tendency and eat a wide range of items from more
209 than 150 plant species (Nsi Akoue et al., 2017), making it difficult to assess food availability
210 based on phenological records. We excluded focal observations shorter than 1 min as they may
211 not be representative. We made 29 774 focal observations (2116 h) obtained from 80 females.
212 For each focal observation, we computed the time the female spent foraging and the total
213 observation time.

214

215 <H3>*Female rank*

216 Social rank was established yearly using ad libitum and focal observations of approach–
217 avoidance interactions (Charpentier et al., 2018). We computed a linear hierarchy using
218 corrected David scores (David, 1987). Individual social ranks were highly correlated across
219 years (example between the two extreme years of the study, i.e. 2012–2013 and 2019: $r=0.81$,
220 $t=5.92$, $P<10^{-4}$). Therefore, each adult female was assigned one relative rank from 2012 to
221 2020, ranging from 0 (lowest ranking) to 1 (highest ranking).

222

223 <H2>**Statistical methods**

224 All statistical analyses were conducted in R version 3.5.0 (R Core Team, 2019).

225

226 <H3>*Characterization of reproductive and environmental seasonality*

227 To characterize the direction and strength of reproductive seasonality, we used circular
228 statistics, converting dates of reproductive events into radian angles. More precisely, for the
229 three studied reproductive parameters (conceptions, births and cycle resumptions), we first
230 estimated their mean direction (μ) using the function ‘circ.summary’ from the ‘CircStats’
231 package (Agostinelli & Lund, 2018). Second, we assessed the strength of their seasonality with
232 the mean resultant length, R ($R=0$ when the event is evenly distributed, and $R=1$ when all events
233 are synchronized to the same day), and ran a Rayleigh test (Batschelet, 1981) to investigate its
234 significance using the ‘r.test’ function from ‘CircStats’ package (Agostinelli & Lund, 2018).

235 In addition to the graphical representation of monthly rainfall variation, we assessed
236 environmental variation in food availability using the time spent foraging by females aged at
237 least 4 years. More precisely, we used a generalized linear mixed model (GLMM) with a
238 negative binomial error structure investigating seasonal variation in the time spent foraging per
239 focal observation (Model 1), using the ‘glmmTMB’ function from the glmmTMB package
240 (Brooks et al., 2017). We used the time (s) spent foraging per focal observation as a response
241 variable and the log-transformed time (s) of observation as an offset term. We included the
242 female’s identity and the year of observation as random effects to control for the
243 nonindependence of multiple observations from the same female and from the same year,
244 respectively. In addition, the random effect ‘year of observation’ controlled for temporal
245 variation such as between-year changes in group size and composition or observational effort.

246 To test for the effect of seasonality, we used a sine term as a fixed effect (see Appendix
247 2 for more details on this procedure). Briefly, this sinusoidal term allows the introduction of
248 circular variables into a multivariate model (Dezeure et al., 2021; English, Bateman, & Clutton-
249 Brock, 2012; Rickard et al., 2012) to account for the circularity of seasonality (i.e. January is
250 as close to December as it is to February). This term ($\sin(\text{date of observation} + \phi)$) assumed
251 only one maximum (food peak season) and one minimum (lean season) per year, 6 months
252 apart. We further controlled for female rank, age and reproductive state, as these fixed-effect
253 parameters could affect the proportion of time females allocate to foraging (Byrne et al., 1993;
254 Muruthi et al., 1991). Female reproductive state was a categorical variable with six classes: (1)
255 ‘pregnant’, (2) ‘L1’, the first third of lactation when infants are 0–2 months old, (3) ‘L2’, the
256 second third of lactation when infants are 2–4 months old, (4) ‘L3’, the last third of lactation
257 when infants are 4–6 months old, (5) ‘cycling’ (with tumescent or detumescent sexual
258 swellings) and (6) ‘noncycling’ (i.e. females neither pregnant nor cycling nor with an infant
259 aged < 6 months). Although lactation probably lasts longer than 6 months in mandrills, it
260 decreases significantly after this date (M.J.E. Charpentier, personal observation).

261

262 <H3>Consequences of reproductive phenology for female reproductive success

263 We investigated the effect of reproductive timing on three indicators of female reproductive
264 success: offspring mortality probability before 6 months of age (Model 2), miscarriage
265 probability (Model 3) and the duration of subsequent maternal IBIs (Model 4). To quantify the
266 effects of birth and conception timings on offspring mortality and on the probability of
267 miscarriage, respectively, we ran GLMMs with a binomial error structure (Models 2 and 3),
268 using the function ‘glmer’ from the package lme4 (and for all subsequent binomial GLMMs;

269 Bates, Mächler, Bolker, & Walker, 2015). To quantify the effects of birth timing on IBI duration
270 (Model 4), we ran a linear mixed model (LMM) using the function ‘lmer’ from the package
271 lme4 (and for all subsequent LMMs; Bates et al., 2015).

272 For each birth, we assessed whether it occurred within (yes) or outside (no) the annual
273 birth peak, defined as follows. We first assigned a birth ‘cohort’ for each birth ($N=212$). We
274 considered 1 July as the transition date from one cohort to the next (as the mean population
275 birth dates, $\mu_{\text{birth}}=1$ January, occur 6 months apart). As a result, two births occurring in
276 November 2014 and February 2015 belonged to the same cohort (2014–2015). We first
277 computed the mean annual birth date for each birth cohort (see Appendix 3 for details). For
278 Models 2 and 4 ($N=212$ births), we considered that a female gave birth within the annual birth
279 peak (yes) if her parturition occurred in the 30 days preceding or following the mean annual
280 birth date and outside the birth peak (no) otherwise. The threshold of 30 days was chosen given
281 that the birth peak (i.e. 53% of births) spanned 2 months (December–January, see Fig. A1). For
282 Model 3 focusing on miscarriages, we first computed the mean annual conception date for each
283 ‘conceptive cohort’ (Appendix 3). For each conception ($N=215$), we considered that it occurred
284 within (yes) the annual conception peak if occurring in the 30 days preceding or following the
285 mean annual conception date and outside (no) otherwise.

286 In addition, for each birth ($N=212$), we calculated the deviation from the mean annual
287 birth date in days, capturing whether an infant was born early or late within the cohort, with
288 negative values for births occurring before the mean birth date of a cohort and positive values
289 afterwards. For Model 3 on miscarriages, we used the deviation (number of days) between the
290 focal conception and the mean annual conception date of this ‘conceptive cohort’.

291 These two factors (within/outside the birth season and early/late in the birth season)
292 were used as fixed effects in our mixed models but were not included together in the same
293 model as they addressed different questions and were not statistically independent (although
294 not collinear). Models with the fixed effect ‘within or outside’ the annual peak were labelled
295 ‘A’ (Models 2–4A), while models with the fixed effect deviation from the mean date were
296 labelled ‘B’ (Models 2–4B).

297 In these models (Models 2–4), we included the female’s (mother) identity and the
298 birth/conception cohort as random effects. We also added, as fixed effects, female parity, rank
299 and infant sex (except for Model 3 as infant sex is unknown during pregnancy) because all these
300 parameters affect the reproductive performances of female mandrills in captivity (Setchell et
301 al., 2002; Setchell & Wickings, 2004). Primiparous and lower-ranking mothers and mothers
302 with sons are expected to have longer interbirth intervals and higher pre- and postnatal offspring

303 mortality than multiparous, higher-ranking mothers and mothers with daughters (Brown, 2001;
304 Gesquiere, Altmann, Archie, & Alberts, 2017; Setchell et al., 2002).

305

306 <H3>*Female determinants of variation in birth timing*

307 Finally, we investigated different determinants of variation in female strategies of reproductive
308 seasonality, that is, which female trait was associated with a birth occurring inside versus
309 outside the annual birth season (Model 5) and with a birth occurring early versus late in the
310 birth season (Model 6). We used as a response variable whether the birth occurred within (yes)
311 or outside (no) the annual birth season, as defined previously for the binomial GLMM (Model
312 5), and the deviation from the mean annual birth date (in days) for the LMM (Model 6).

313 Both models included as fixed effects female rank, age (years) and previous
314 reproductive outcome because these effects are likely to affect birth timings (Holand et al.,
315 2004; Paul & Thommen, 1984). We expected dominant and older females to be more likely to
316 give birth away from the birth season than subordinate and younger females. Previous
317 reproductive outcome was a categorical variable with the following classes: (1) previous infant
318 survived to 6 months ($N=130$), (2) previous conception was a miscarriage ($N=16$), (3) previous
319 infant died before 6 months ($N=16$) or (4) primiparous female (no previous conception; $N=41$).
320 We predicted that following an infant death or miscarriage, females would be more likely to
321 give birth away from the birth season. In both models, we included the female's identity and
322 the year of birth as random effects. We further tested whether there was within-individual
323 consistency in birth timing and tested the significance of the female's identity in both models
324 by using a likelihood ratio test (LRT) comparing models with and without this random effect.

325

326 <H3>*Models' validity diagnostic*

327 Information about the structure (type of models, fixed and random effects) and sample sizes of
328 each model performed in this study are summarized in Table A1. For all six models, all
329 quantitative fixed effects were z-transformed (so that the mean equalled 0 and the standard
330 deviation equalled 1) to facilitate model convergence. When we obtained singular fits, we
331 confirmed the results by running the same models with a Bayesian approach, using the 'bglmer'
332 or 'blmer' functions of the 'blme' package (Dorie, 2015). To diagnose the presence of
333 multicollinearities, we calculated the variance inflation factor for each predictor in each full
334 model using the 'vif' function of the R 'car' package (Fox et al., 2019). We checked that
335 variance inflation factors were <2 for each fixed effect in all models. For each model, in addition
336 to the Wald chi-square tests with associated P values computed with the 'Anova' function of

337 the R package ‘car’ (Fox et al., 2019), we calculated the 95% Wald confidence intervals for the
338 estimate of each fixed effect. We also checked the distribution of residuals using the ‘qqPlot’
339 function of the ‘car’ package for LMMs (Fox et al., 2019) and using ‘simulateResiduals’ from
340 the DHARMA package for binomial GLMMs (Hartig, 2020). We used the ‘visreg’ package
341 (Breheny & Burchett, 2017) to plot the partial residuals effects shown in the figures. We set up
342 different levels as reference before running Models 5 and 6 to compare the different levels of
343 the fixed effect ‘previous reproductive outcome’.

344

345 <H2>Ethical note

346 This study was approved by the CENAREST institute (permit number:
347 AR0060/18/MESRS/CENAREST/CG/CST/CSAR). Only noninvasive procedures based on
348 daily behavioural monitoring were used for this study.

349

350 <H1>RESULTS

351 <H2>Reproductive phenology and environmental seasonality

352 Conceptions, births and cycle resumptions all showed one pronounced seasonal peak (Figs 1,
353 A1): 64% of conceptions, 66% of births and 54% of postlactation cycle resumptions occurred
354 during a 3-month time window. Rayleigh tests, based on circular statistics, confirmed that all
355 three reproductive events were significantly different from a uniform distribution along the
356 annual cycle (conceptions: $N=215$, $\mu=14$ July, $R=0.63$, $P<10^{-4}$; births: $N=212$, $\mu=1$ January,
357 $R=0.68$, $P<10^{-4}$; cycle resumptions: $N=150$, $\mu=19$ June, $R=0.52$, $P<10^{-4}$), although births
358 appeared more seasonal than both conceptions and cycle resumptions (Fig. A1).

359 Mean annual cumulative rainfall was high, with moderate interannual variability ($N=8$
360 years, mean \pm SD=1871 \pm 175 mm). Rainfall was highly seasonal, with a long rainy season
361 (October–May) characterized by two peaks, in October–November and April, followed by a
362 long dry season (June–September; Fig. 1). The proportion of observation time that females
363 spent foraging also varied seasonally (Table 1, Fig. 1) with females spending more time
364 foraging around mid-August (long dry season) than mid-February (long rainy season; see
365 Appendix 2). The birth peak happened midway through the long rainy season, just before the
366 peak of food availability (Fig. 1).

367 Finally, lactating, older and higher-ranking females spent significantly less time
368 foraging than cycling and noncycling, younger and lower-ranking females, respectively (Table
369 1).

370

371 **<H2>Fitness consequences of variation in reproductive phenology**

372 First, birth timing did not affect offspring survival probability to 6 months (Table 2). However,
373 conceptions that occurred outside the annual conceptive peak (Fig. 2a), especially later in the
374 mating season (Fig. 2b), were more likely to lead to miscarriages than other conceptions (Table
375 3).

376 Second, females that gave birth outside the annual birth peak had longer IBIs (Table 4,
377 Fig. 2c), with an effect size of approximately 29 days, especially those that gave birth late in
378 the birth season (Table 4, Fig. 2d).

379 Finally, subordinate females were more likely to abort (Table 3) and had longer IBIs
380 than dominant females (Table 4; high-ranking females: median IBI=15.0 months; mid-ranking
381 females: 20.5 months; low-ranking females: 22.0 months; see also Fig. A2).

382

383 **<H2>Variation in female reproductive phenology**

384 We did not detect any effect of female identity on her birth timing (Model 5: LRT=1.15,
385 $P=0.28$; Model 6: LRT=0.00, $P=1.00$), meaning that there was no within-individual consistency
386 in birth timing. However, dominant females were more likely to give birth outside the birth
387 season, although neither earlier nor later, than subordinate females (Table 5, Figs 3a, c, A3). In
388 addition, females that lost an infant or miscarried were more likely to subsequently give birth
389 early in the birth season (Table 5, Fig. 3b, d). Finally, female age did not affect birth timing
390 (Table 5).

391

392 **<H1>DISCUSSION**

393 Here, we showed that wild equatorial mandrills live in a seasonal habitat and are seasonal
394 breeders, despite their ability to breed year round. Conceiving during the conception peak
395 decreased the risk of miscarriage and giving birth during the birth peak decreased the time to
396 the mother's next reproduction. However, birth timing did not affect offspring survival. We
397 further showed rank-related variation in reproductive success and phenology, with dominant
398 females being less seasonal, having shorter IBIs and miscarrying less than subordinates.

399 **<H2>Environmental seasonality in equatorial forests**

400 Several reasons may explain why equatorial organisms may breed seasonally despite living in
401 environmental conditions where food may remain available year round compared to most other
402 biomes. First, most equatorial environments show important seasonal variation in rainfall
403 (Feng, Porporato, & Rodriguez-Iturbe, 2013; Van Schaik, Terborgh, & Wright, 1993), reflected
404 in food availability that mirrors variation in plant phenology (Takenoshita, Ando, Iwata, &

405 Yamagiwa, 2008). Accordingly, mandrills spent more time feeding during the long dry season
406 (this study) and also show qualitative seasonal shifts in diet (Nsi Akoue et al., 2017). Such
407 within-year variation in food resources may thus affect reproductive timing and performance,
408 even in long-lived omnivorous species. In addition, these habitats could be characterized by
409 low interannual variation (i.e. high predictability) promoting breeding seasonality (English,
410 Chauvenet, Safi, & Pettoirelli, 2012; Jönsson, 1997), although this relationship needs to be
411 confirmed in a comparative context.

412

413 <H2>Female reproductive pace

414 Births preceded the seasonal food peak by around 2 months, whereas cycle resumptions and
415 conceptions mainly occurred during the long dry season when food was scarce. We hypothesize
416 that the mandrill's birth peak has evolved to match the food peak with early lactation. In line
417 with this, females that gave birth within the birth peak accelerated their future reproduction
418 (shorter IBIs) suggesting that this phenology strategy brings reproductive benefits for female
419 mandrills. It is possible that the first half of lactation is the most costly energetic stage of
420 reproduction in female mandrills because mothers cover the full nutritional needs of their
421 infants, in contrast with the second half where infants start feeding independently (Langer,
422 2008; Lee, 1996). Those females that give birth early in the birth peak probably time their peak
423 in energy demands more closely with the food peak than females giving birth later in the birth
424 peak. Such adjustments are the norm among fast-lived and temperate or arctic species (Bronson,
425 2009; Bronson & Heideman, 1994), and similar patterns of phenology have also been observed
426 in some tropical species including primates (Brockman & van Schaik, 2005; Carnegie, Fedigan,
427 & Melin, 2011; Heesen, Rogahn, Ostner, & Schülke, 2013; Janson & Verdolin, 2005) and
428 ungulates (Sinclair, Mduma, & Arcese, 2000). Our study therefore emphasizes that
429 reproductive seasonality in equatorial species can, at least partly, emerge in response to seasonal
430 variation in food availability to enhance maternal reproductive pace.

431

432

433 <H2>Postnatal offspring survival

434 Despite seasonal variation in food availability, female mandrills could give birth year round
435 without any significant cost to postnatal offspring survival. This result may reflect, however,
436 analytical limitations due to the low numbers of infants born outside the birth season (only six
437 births, i.e. 3%, between May and August). Alternatively, female mandrills may mitigate the
438 costs of giving birth outside the birth peak by extending lactation, as reflected by longer IBIs

439 following such births. Indeed, gestation length is nearly fixed in cercopithecoid primates
440 (Gesquiere, Altmann, Archie, & Alberts, 2017), while the length of the cycling period does not
441 vary much relative to IBI in semicaptive mandrills (Setchell & Wickings, 2004) suggesting that
442 lactation period is the most variable part of the IBI. Finally, the moderate rate of infant mortality
443 observed (9%) and the fact that females can be lactating and pregnant simultaneously (Fig, A3)
444 may, in combination, indicate that seasonal food shortage is rarely a cause of poor condition
445 and death for mothers or their offspring. Similarly, in white-faced capuchins, *Cebus capucinus*,
446 a seasonal-breeding monkey living in a rich tropical habitat, deviance from the birth season
447 does not translate into increased offspring mortality (Carnegie et al., 2011). Taken together, our
448 results indicate that female mandrills may prioritize current (offspring survival) over future
449 (shorter IBI) reproduction when giving birth outside the birth peak. Buffering the costs of a
450 suboptimal birth timing on current reproduction by delaying future reproduction may only be
451 possible in productive environments where the selective pressures favouring a strict breeding
452 season are weakened, although other factors may also play a role, such as the ability to store
453 energy or access to alloparental care (Heldstab, van Schaik, & Isler, 2017). In contrast, when
454 food availability is more limiting, the costs of giving birth away from the optimal season on
455 offspring survival may be too high, resulting in a strict breeding seasonality, as generally
456 observed in long-lived temperate and arctic species (Bronson, 2009; Rutberg, 1987).

457

458 <H2>Miscarriage probability

459 Here, we also showed that miscarriages increased when females conceived too late in the
460 mating season. Such pregnancy failures are probably unrelated to food scarcity during
461 pregnancy, as they are in yellow baboons, *Papio cynocephalus*, for example (Beehner,
462 Onderdonk, Alberts, & Altmann, 2006), because in mandrills most conceptions and
463 pregnancies occurred during the long dry season when food was scarce. Alternatively, we
464 speculate that infants born late in the birth season could be targeted by infanticidal males.
465 Indeed, males generally immigrate at the onset of the mating season, around April (Abernethy,
466 White, & Wickings, 2002; Hongo et al., 2016; M.J.E. Charpentier, personal observation).
467 Giving birth late would result in highly vulnerable offspring aged only a few weeks/months
468 when most males immigrate (Palombit, 2015). In support of this hypothesis, 55% (11 of 20) of
469 infant deaths occurred in March–May, which is significantly more often than at any other time
470 of the year ($\chi^2=17.2$, $P<10^{-3}$). For four of these deaths, male infanticide was the most plausible
471 scenario (M.J.E. Charpentier, personal observation), although infanticide by males has not been
472 formally documented in mandrills. In contrast, when females gave birth within the birth peak,

473 and especially when they gave birth early in the peak, they usually resumed cycling early in the
474 next mating season, meaning that males do not need to kill their infants to mate with them.
475 Spontaneous abortions may thus represent an adaptive female counterstrategy, as shown in
476 geladas, *Theropithecus gelada*, where females preferentially abort rather than invest in a fetus
477 which would be a likely target of infanticide following a male take-over (Roberts, Lu, Bergman,
478 & Beehner, 2012). Interestingly, in geladas, the seasonality of male take-overs leads to a
479 decrease in the intensity of reproductive seasonality because the suboptimal ‘social birth peak’
480 resulting from male take-overs and subsequent miscarriages occurs a few months from the
481 optimal ‘ecological birth peak’ (Roberts, Lu, Bergman, & Beehner, 2017). By contrast, in
482 mandrills, it appears that the timing of male immigrations strengthens the intensity of
483 reproductive seasonality by selecting against births occurring late in or after the birth peak,
484 explaining at least partially why births are more seasonal than conceptions. This ‘Bruce effect’
485 (spontaneous abortion due to maternal exposure to an unrelated adult male) is relatively well
486 documented in several small mammals and horses, in addition to geladas (Inzani et al., 2019;
487 Schwagmeyer, 1979; Zippel, 2020; Zippel, Roberts, Alberts, & Beehner, 2021). Additional
488 years of observations will be necessary to confirm (or not) the seasonality of infanticide risk in
489 mandrills and investigate the nature of potential female counterstrategies.

490

491 <H2>The evolution of plastic birth timing

492 If births outside the peak are partly selected against for the reasons highlighted above, it is
493 unclear why they may still occur. Several results indicate that birth timing is a highly plastic
494 phenotype in mandrills. First, births occurred year round, although at variable frequencies.
495 Second, there was no within-female consistency in birth timing across successful births. Third,
496 previous reproductive history, a source of within-individual variation, impacted birth timing.
497 Specifically, female mandrills often rapidly resumed cycling and conceived regardless of the
498 season following infant or fetal death, which may disrupt reproductive seasonality. Plasticity in
499 birth timing is common across primates, with within-species variation in seasonality across
500 different latitudes (Heldstab et al., 2020), and can represent a direct target of selection in
501 response to ecological or social changes in the environment (Charmantier et al., 2008; de
502 Villemereuil et al., 2020). In species where infanticide occurs, females’ ability to conceive
503 outside the mating season may have evolved to mitigate the costs of infanticide to decrease the
504 gaps introduced in females’ reproductive careers. Such a capacity is, however, probably
505 contingent on environmental conditions, and may only evolve in climates that are not too cold
506 or arid for females to raise offspring outside the best season. We further expect females’ ability

507 to conceive outside the mating season in species that are sufficiently generalist to exploit a
508 diversity of resources including fallback foods during the lean season, as well as able to store
509 energy from one season to the next. In such species and environmental conditions, the costs of
510 reproducing outside the birth season may be of roughly similar magnitude as the costs of
511 waiting until the next breeding season, meaning that females can switch from one strategy to
512 the next depending on their reproductive history, physical condition and context-dependent
513 changes in the social or ecological environment.

514

515 <H2>Dominant females breed less seasonally than subordinates

516 Finally, we documented between-female variation in birth timing. Dominant females were more
517 likely to give birth outside the birth peak than subordinate females, an effect that, to our
518 knowledge, was not previously reported in primates. Rank-related variation in reproductive
519 phenology directly echoes our result showing that dominant female mandrills spent less time
520 foraging than subordinates, probably because they have better access to food resources year
521 round, as observed in baboons (Barton, 1993; Barton & Whiten, 1993). This scenario is further
522 supported by the important rank-related variation in IBIs: dominant females gave birth nearly
523 every year while subordinates gave birth every 2 years on average (Fig. A3). In addition, this
524 rank-related effect does not occur in captive mandrills, probably because food provisioning
525 offsets rank-related effects (Setchell et al., 2002). For dominant females, the costs of giving
526 birth outside the optimal season may thus be lower than the costs of waiting for the next optimal
527 season. Rank-related effects on reproductive phenology have been described in a handful of
528 other species. In the Kalahari meerkat, *Suricata suricatta*, the dominant female breeds almost
529 year round while subordinate breeding is only tolerated during the rainy season, around the
530 annual food peak, at a time when the birth of subordinate offspring does not compromise the
531 growth and development of dominant pups (Clutton-Brock, Hodge, Flower, Spong, & Young,
532 2010). In addition, in reindeer, *Rangifer tarandus*, social rank also affects birth timing:
533 dominant females, in better condition, give birth earlier in the birth season than subordinates
534 (Holand et al., 2004). Given that dominant females probably have priority of access over food
535 compared to subordinate females, we may expect this influence of rank on reproductive
536 phenology to be widespread across taxa. Overall, these results highlight the importance of social
537 competition in shaping the intensity of reproductive seasonality at the population level.

538

539 <H2>Conclusions

540 Mandrills face seasonal variation in food availability despite living in an equatorial, food-rich
541 environment. Our results indicate that their reproductive phenology is highly plastic and not
542 drastically limited by food availability as females can give birth and successfully raise offspring
543 year round. Nevertheless, seasonal variation in food availability has partly shaped seasonal
544 schedules in this population, where matching early lactation with the most productive season
545 enhances maternal reproductive pace. Lastly, our results indicate that sociality can have
546 profound effects on patterns of reproductive phenology, where infanticide may shorten the birth
547 season by selecting against late births, and dominant females breed less seasonally than
548 subordinates. This study therefore illustrates how ecological and social factors can interact to
549 shape population and individual level patterns of reproductive phenology, opening new
550 perspectives to understand the diverse strategies of reproductive seasonality observed in long-
551 lived social mammals living in the intertropical belt.

552

553

554 **Author Contributions**

555 J.D., M.J.E.C. and E.H. conceived the ideas and designed the methodology; M.J.E.C. collected
556 and formatted the data; J.D. analysed the data and led the writing of the manuscript. All authors
557 contributed critically to the drafts and gave final approval for publication.

558

559 **Data Availability**

560 Data sets and scripts used in this study are available on the following Github repository:
561 <https://github.com/JulesDezeure/Mandrill-Reproductive-Seasonality.git>

562

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810 **Appendix 1: Dates of Conceptions, Births and Cycle Resumptions**

811 We considered a total of 215 conceptive cycles (median uncertainty of 2 days; range=0-30 days)
812 that either result in the birth of a live offspring (N=192), a confirmed miscarriage (N=19) or an
813 unknown outcome (N=4), as described above. The day of conception is defined as the first day
814 of deturgescence (D-day) of the swelling during a conceptive cycle. In 60 cases, observers were
815 present on the D-day while in 114 other cases, conceptions occurred during a gap in the
816 reproductive recordings, generating uncertainty in the conceptive dates (median=4 days,
817 range=1-22). Finally, in 41 cases, a birth was observed but not the D-day. The latter was
818 estimated to occur 175 days prior to the birth, as described above. We discarded from our
819 dataset all conceptions (and associated births) with more than a month of uncertainty
820 (conceptions: N=1, births: N=18).

821 In addition, we observed a total of 212 births (median uncertainty of 2 days; range=0-30 days).
822 For 80 births, observers were in the field the day of birth. For 132 births, we observed a newborn
823 infant a few days after birth (uncertainty in the actual date: median=4 days, range=1-30).

824 Finally, the first post-partum cycle (i.e. cycle resumption) is the first menstrual cycle following
825 a birth, when the female resumes cycling following lactation. The exact date of cycle
826 resumption corresponds to the first day of estrus of the first post-partum cycle, i.e. the first day
827 when a sexual swelling is recorded following a period of lactation. In total, our sample

828 comprised 150 cycle resumptions, either following an infant that survived (N=133) or died
829 (N=17) during its first 6 months of life. We chose to include cycle resumptions following the
830 death of an unweaned infant, as such events contribute to shape the timing and intensity of
831 reproductive seasonality at the population level.

832

833 **Appendix 2: Quantifying Seasonal Effects on Time Females Spent Foraging.**

834 To quantify the effects of the season of the year on the time females spent foraging, a proxy of
835 food availability, we included as a fixed effect a sinusoidal term: $\text{sine}(\text{date of observation} + \varphi)$.
836 This unimodal pattern is supported by the raw distribution of rainfall as well as of seasonal
837 variation in the mean proportion of time spent foraging per month (Fig. 1). The date of
838 observation in this formula was converted to a radian measure, so that the period of 1 year
839 equalled to 2π , ranging from $2\pi/365$ for 1 January to 2π for 31 December. We tested 12 different
840 phase values of φ ($0, \pi/12, 2\pi/12, 3\pi/12, 4\pi/12, 5\pi/12, 6\pi/12, 7\pi/12, 8\pi/12, 9\pi/12, 10\pi/12,$
841 $11\pi/12$), to account for potential phase shifts across the year. For example, a phase of 0
842 maximizes 1 March and minimizes 1 October if the estimate is positive, and the reverse if the
843 estimate is negative (see also Dezeure et al. 2021 for more details on this procedure). We
844 sequentially ran 12 multivariate models, which contained the sinusoidal term as fixed effect,
845 our two random effects (observation year and female identity) and the offset term, and all were
846 strictly similar, except for the value of the phase φ . We selected the best phase to be the one
847 minimizing the Akaike information criterion in this model set, which retained a value of $3\pi/12$
848 for the phase φ . We present the results of this model containing the best phase in the main text.

849

850 **Appendix 3: Computing Mean Annual Birth (and Conception) Dates**

851 We discarded all birth records occurring outside the birth season, i.e. between April and
852 September (N=20), to compute the mean annual birth date. Indeed, these births were clear
853 outliers that may disproportionately influence the mean annual birth date. We recorded on
854 average 24 births per cohort (SD=8, range 15–39 over eight cohorts). We computed the mean
855 annual birth date for each cohort, using the function ‘circ.summary’ from the ‘CircStats’
856 package (Agostinelli & Lund 2018). The mean annual birth date varied from 6 December (for
857 the 2017–2018 cohort) to 31 January (for the 2012–2013 cohort), and the birth distributions
858 between these 2 extreme years were significantly different (Watson–Williams test for
859 homogeneity of means: $F=56.2, P < 10^{-4}$). This indicates substantial between-year variation in
860 the timing of the annual birth peak, which may reflect either between-year variation in
861 environmental seasonality or stochastic variation due to low sample sizes.

862 For Model 3 focusing on miscarriages, we similarly assessed a ‘conceptive cohort’ for each
863 conception, considering 14 January as the transition date from one cohort to the next (as the
864 mean population conception date, i.e. 14 July, occurred 6 months later). We then used the same
865 method as described above to compute the mean annual conception date for each ‘conceptive
866 cohort’, discarding all conception records that occurred between 14 October and 14 April ($N=24$
867 conceptions).

868

869

870 **Table 1:** Determinants of the proportion of time mandrill females spent foraging

871

Fixed effect	Estimate	CI		χ^2	<i>P</i>
		Lower	Upper		
Model 1: Time spent foraging					
Day of observation–sine term	-0.14	-0.15	-0.12	282.12	<10⁻⁴
	(Pregnant)	-0.02	-0.05	0.00	
	(L1)	-0.50	-0.55	-0.46	
Female reproductive state	(L2)	-0.23	-0.27	-0.19	622.59
	(L3)	-0.09	-0.13	-0.05	<10⁻⁴
	(Cycling)	-0.03	-0.08	0.02	
Female age	-0.10	-0.14	-0.06	27.17	<10⁻⁴
Female rank	-0.17	-0.23	-0.11	29.33	<10⁻⁴

872 The table displays the estimates, 95% confidence intervals (CI), chi-square statistics and *P* values for the
 873 predictors of the negative binomial GLMM (Model 1), based on 29 774 observations from 80 adult females,
 874 including female identity and year as random effects and focal duration (s) as offset term. Significant effects are
 875 shown in bold. For categorical predictors, the tested category is indicated within parentheses. The reference
 876 category of the fixed effect ‘female reproductive state’ is noncycling females. L1 refers to the first third of
 877 lactation (infants aged 0–2 months), L2 to the second third of lactation (infants aged 2–4 months) and L3 to the
 878 last third of lactation (infants aged 4–6 months).

879 **Table 2:** Determinants of offspring mortality

880

Fixed effect	Estimate	CI		χ^2	<i>P</i>
		Lower	Upper		
Model 2A: offspring mortality					
Reproductive phenology (Within peak)	0.17	-1.28	1.62	0.05	0.819
Female rank	-0.02	-0.78	0.75	0.00	0.969
Female parity (Primiparous)	0.56	-1.06	2.18	0.46	0.496
Infant sex (Male)	-1.10	-2.59	0.39	2.09	0.149
Model 2B: offspring mortality					
Reproductive phenology–Deviation	-0.01	-4.72	-1.59	0.00	0.979
Female rank	-0.03	-0.78	0.72	0.01	0.932
Female parity (Primiparous)	0.59	-1.03	2.20	0.51	0.475
Infant sex (Male)	-1.11	-2.60	0.38	2.12	0.146

881 The table displays the estimates, 95% confidence intervals (CI), chi-square statistics and *P* values for the
882 predictors of the two binomial GLMMs (Models 2A and 2B), based on 208 offspring from 71 females, including
883 female identity and birth cohort as random effects. For Model 2A, the fixed effect ‘Reproductive phenology’
884 distinguishes births occurring within (1) versus outside (0) the annual birth season, while for Model 2B, the fixed
885 effect ‘Reproductive phenology’ represents the deviation (number of days) from the mean annual birth date. For
886 categorical predictors, the tested category is indicated within parentheses.

887 **Table 3:** Determinants of female miscarriage probability.

888

Fixed effect	Estimate	CI		χ^2	<i>P</i>
		Lower	Upper		
Model 3A: miscarriage					
Reproductive phenology (Within peak)	-4.39	-7.00	-1.77	10.82	0.001
Female rank	-1.07	-1.97	-0.18	5.52	0.019
Female parity (Nulliparous)	-1.51	-4.31	1.28	3.40	0.182
(Primiparous)	1.48	-0.53	3.49		
Model 3B: miscarriage					
Reproductive phenology–Deviation	2.02	0.78	3.25	10.22	0.001
Female rank	-0.83	-1.66	-0.01	3.96	0.047
Female parity (Nulliparous)	-0.45	-3.03	2.13	2.51	0.286
(Primiparous)	1.38	-0.46	3.21		

889 The table displays the estimates, 95% confidence intervals (CI), chi-square statistics and *P* values for the
890 predictors of the two binomial GLMMs (Models 3A and 3B), based on 211 conceptions from 64 females,
891 including female identity and conception cohort as random effects. For Model 3A, the fixed effect ‘Reproductive
892 phenology’ distinguishes conceptions occurring within (1) versus outside (0) the annual conception season,
893 while for Model 3B, the fixed effect ‘Reproductive phenology’ represents the deviation (number of days) from
894 the mean annual conception date. Significant effects are shown in bold. For categorical predictors, the tested
895 category is indicated within parentheses.

896 **Table 4:** Determinants of maternal interbirth intervals

897

Fixed effect	Estimate	CI		χ^2	<i>P</i>
		Lower	Upper		
Model 4A: interbirth intervals					
Reproductive phenology (Within peak)	-51.01	-101.66	-0.36	3.90	0.048
Female rank	-72.91	-102.79	-43.02	22.86	<10⁻⁴
Female parity (Primiparous)	56.73	-5.64	119.11	3.18	0.075
Infant sex (Male)	-2.85	-47.21	41.52	0.02	0.900
Model 4B: interbirth intervals					
Reproductive phenology–Deviation	21.00	-2.76	44.76	3.00	0.083
Female rank	-68.22	-97.87	-38.57	20.33	<10⁻⁴
Female parity (Primiparous)	36.99	-25.54	99.53	1.34	0.246
Infant sex (Male)	-4.17	-48.84	40.50	0.03	0.855

898 The table shows the estimates, 95% confidence intervals (CI), chi-square statistics and *P* values of the predictors
899 of the two LMMs (Models 4A and 4B) based on 122 interbirth intervals from 47 females, including female
900 identity and birth cohort as random effects. For Model 4A, the fixed effect ‘Reproductive phenology’
901 distinguishes births occurring within (1) versus outside (0) the annual birth season, while for Model 4B, the fixed
902 effect ‘Reproductive phenology’ represents the deviation (number of days) from the mean annual birth date.
903 Significant effects are shown in bold. For categorical predictors, the tested category is indicated within
904 parentheses.

905 **Table 5:** Determinants of birth timings

906

Fixed effect	Estimate	CI		χ^2	<i>P</i>	
		Lower	Upper			
Model 5: probability of giving birth within the annual birth season						
Female rank	-0.62	-1.05	-0.18	7.74	0.005	
Female age	-0.23	-0.68	0.23	0.97	0.325	
	(Infant died)	-0.69	-2.10	0.72		
Previous reproductive outcome	(Miscarriage)	-0.42	-1.72	0.87	2.55	0.467
	(Primiparous)	0.50	-0.62	1.63		
Model 6: Deviation from the mean annual birth date						
Female rank	0.29	-6.06	8.18	0.08	0.771	
Female age	0.52	-10.36	6.04	0.27	0.606	
	(Infant died)	-3.84	-76.68	-24.89		
Previous reproductive outcome	(Miscarriage)	-2.23	-54.6	-3.57	19.65	2.01×10⁻⁴
	(Primiparous)	0.48	-15.86	26.11		

907 The table shows the estimates, 95% confidence intervals (CI), chi-square statistics and *P* values of the predictors
 908 of the binomial GLMM (Model 5) and LMM (Model 6) including female identity and birth cohort as random
 909 effects, based on 212 births from 72 females. Significant effects are shown in bold. For categorical predictors,
 910 the tested category is indicated within parentheses. The reference category for the previous reproductive
 911 outcome fixed effect is 'infant survived'.

912 **Table A1:** Summary of our statistical models.

Indicators	Food availability seasonality	Maternal reproductive success			Determinants of birth timing	
Model ID	1	2	3	4	5	6
Response variables	Time spent foraging	Offspring survival	Female miscarriage	Female interbirth interval	Birth within the annual birth peak	Deviation from the mean annual birth date
Model types	Negative binomial GLMM	Binomial GLMM	Binomial GLMM	LMM	Binomial GLMM	LMM
Sample sizes	29774	208	211	122	212	212
Number of individuals (juveniles / mothers)	80	71	64	47	72	72
Fixed effects	Observation date, focal observation duration (log offset term)	Birth date, female rank, female parity, infant sex	Conception date, female rank, female parity	Birth date, female rank, female parity, infant sex	Female rank, female age, previous reproductive outcome	Female rank, female age, previous reproductive outcome
Random effects	Female identity, observation year	Female identity, birth cohort	Female identity, conception cohort	Female identity, birth cohort	Female identity, birth cohort	Female identity, birth cohort

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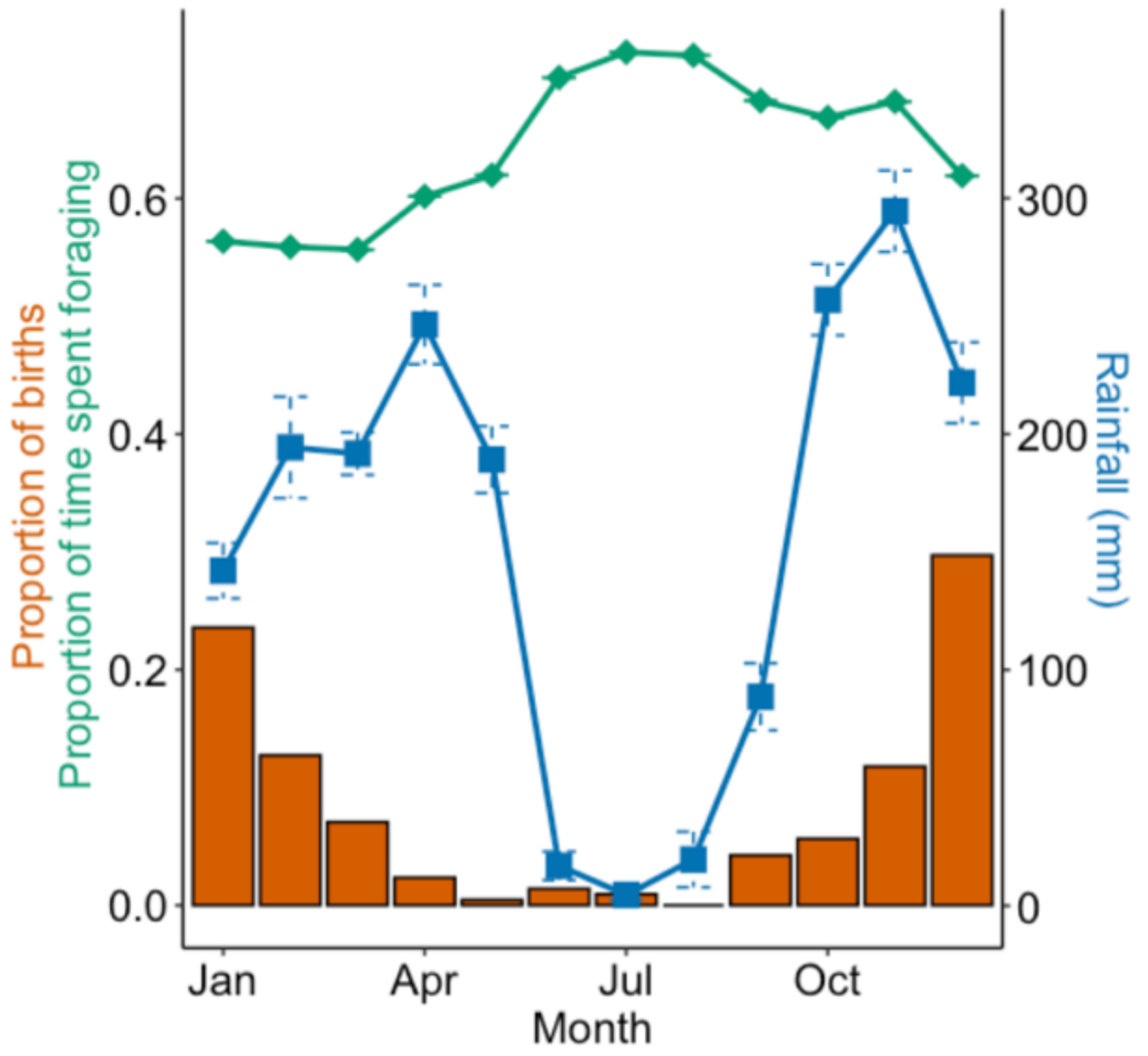
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916 **FIGURES**

917

918 **Figure 1.**

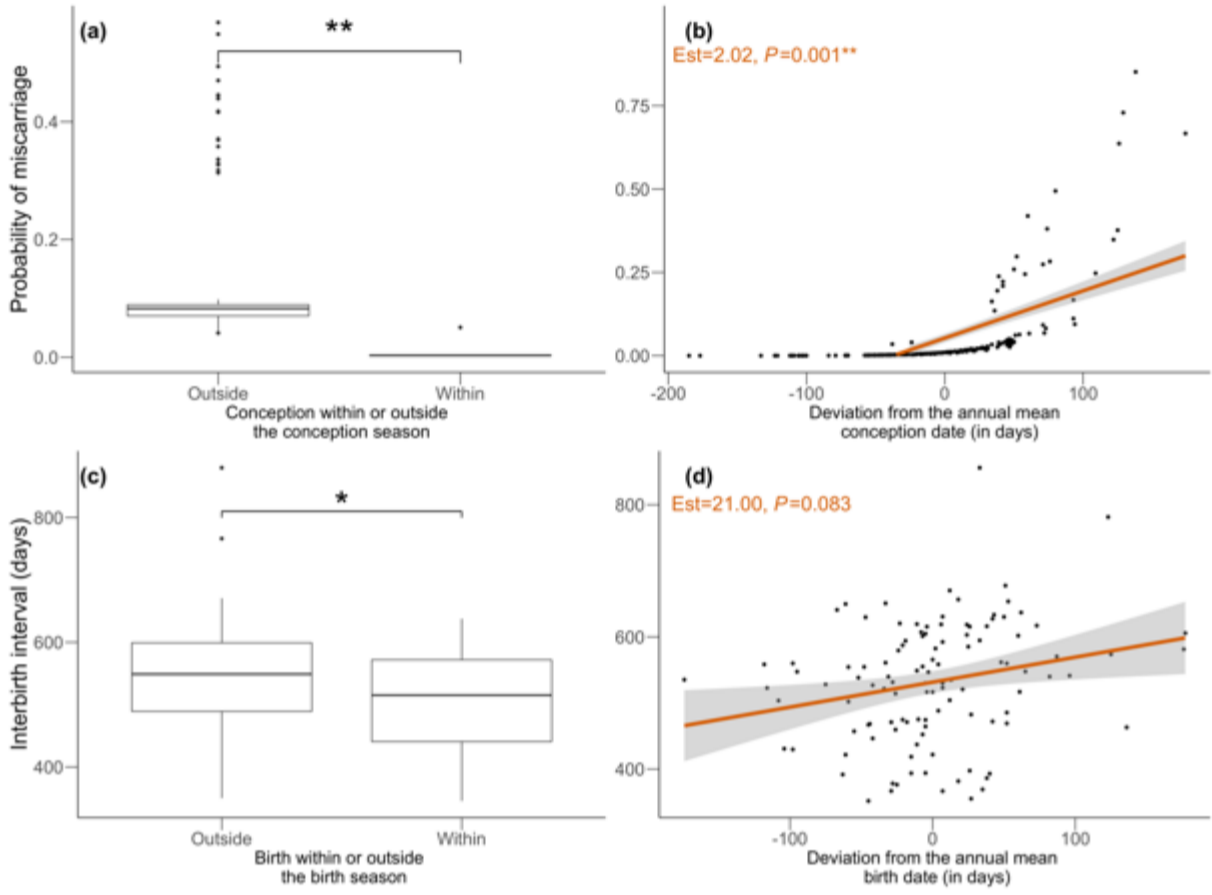
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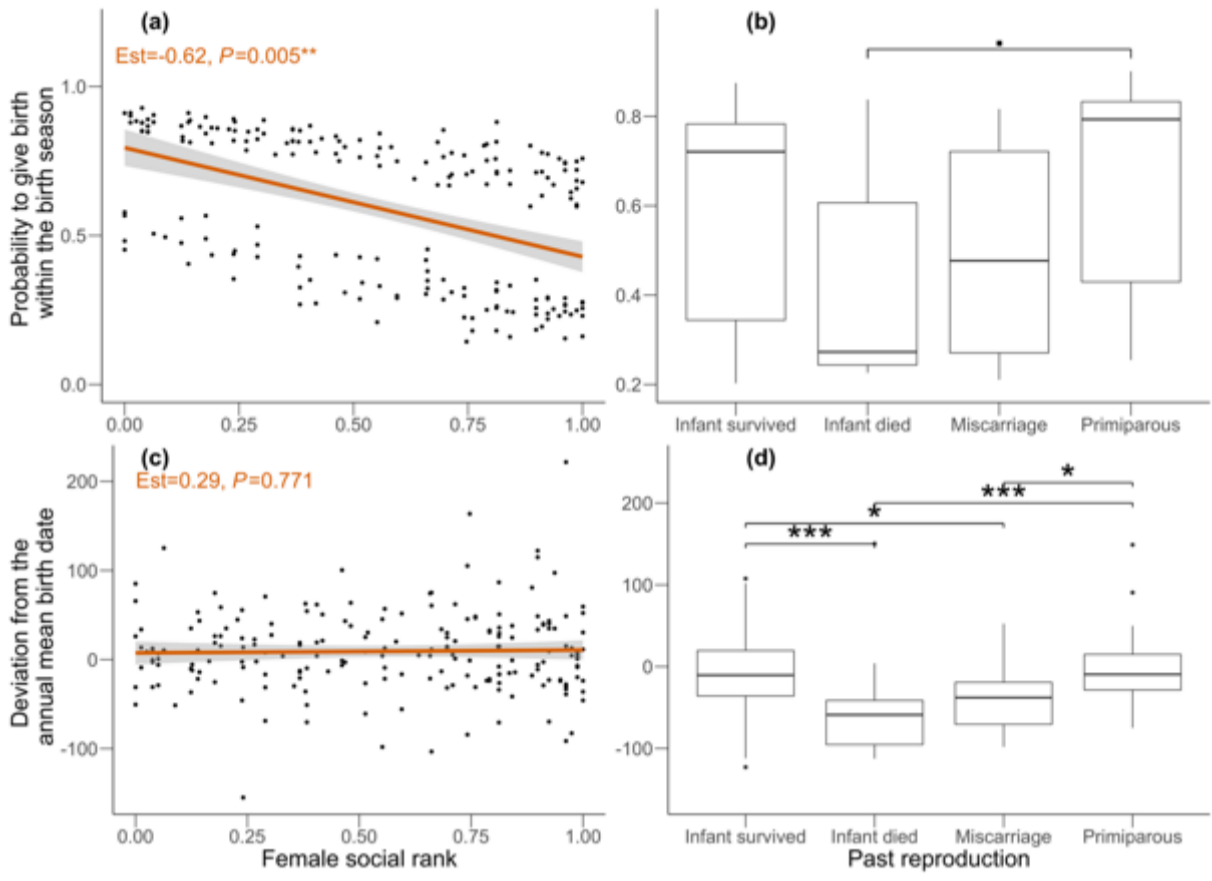
Figure 2.



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926

927 **Figure 3.**

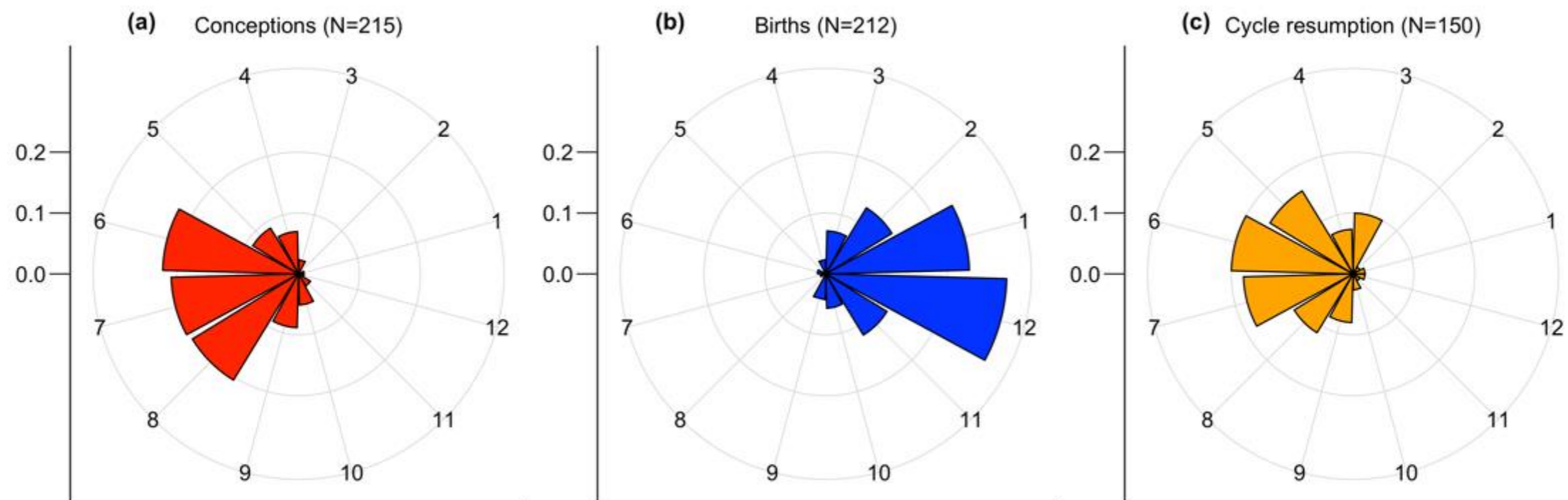


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930 **Figure A1.**

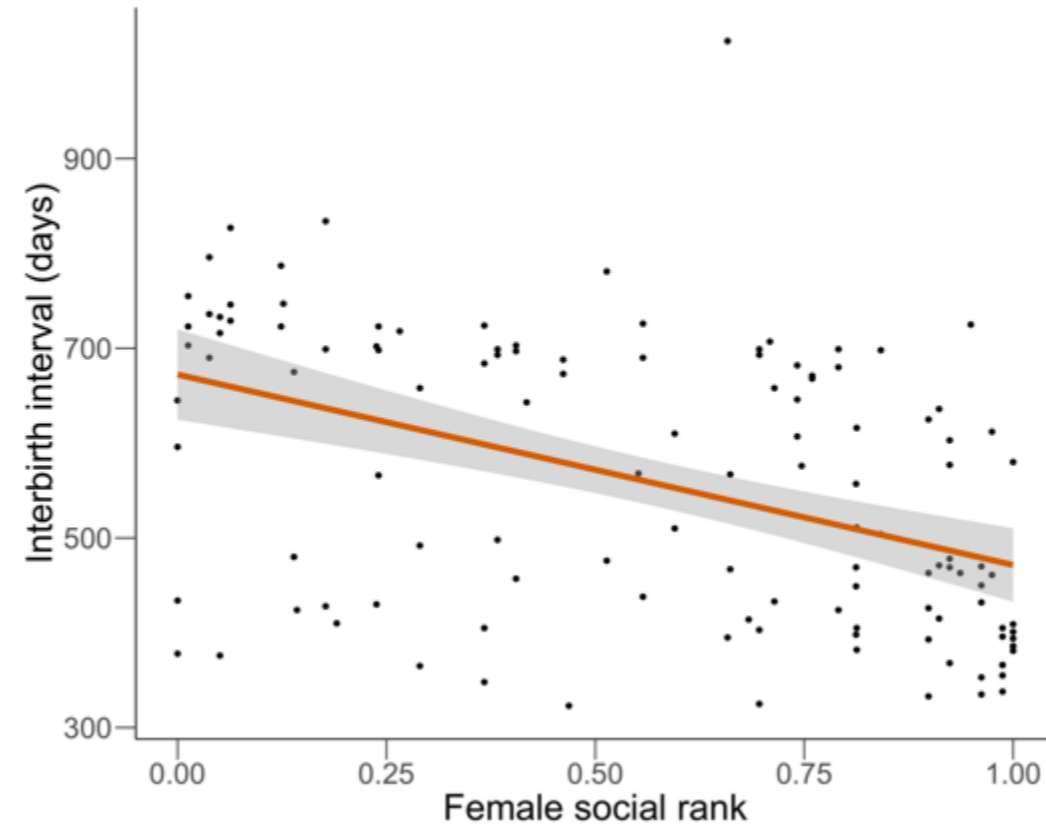
931



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933 **Figure A2.**

934

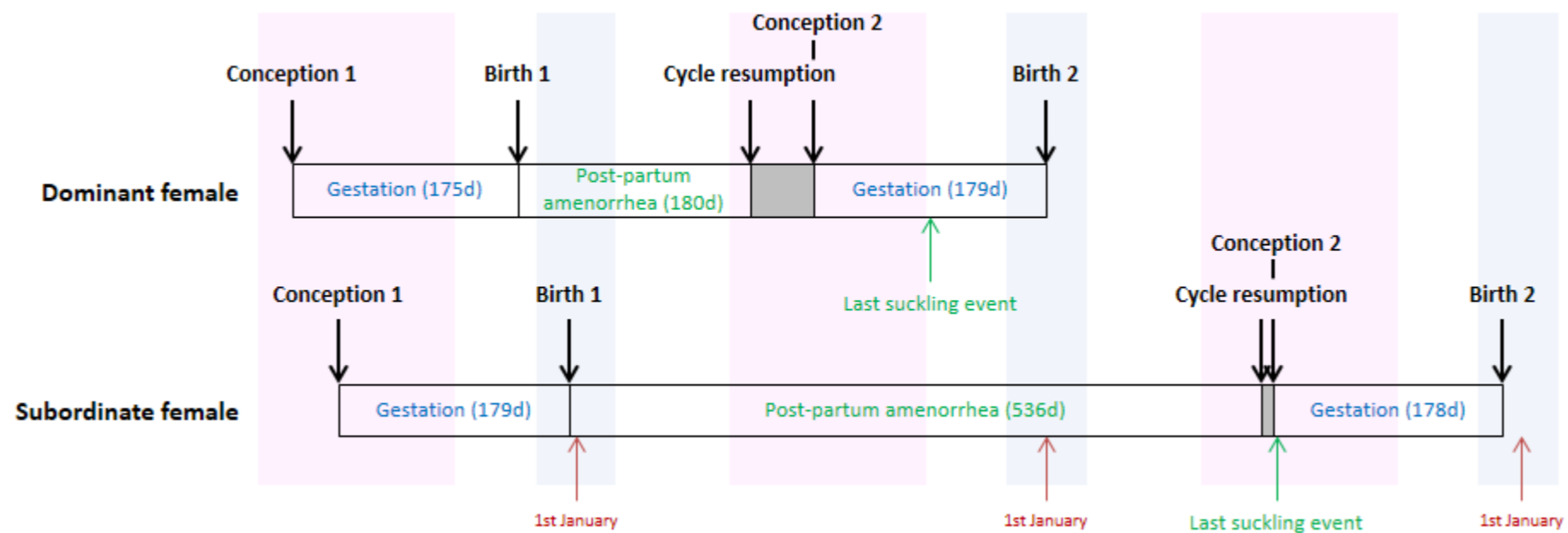


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936

937 **Figure A3.**

938



939

940

941 **FIGURE LEGENDS**

942

943 **Figure 1:** Environmental and reproductive seasonality of the study mandrills (2012–2020).

944 Brown bars represent the monthly proportion of births ($N=212$). Green diamonds represent the monthly mean
945 proportion of time adult females spent foraging (an indicator of food availability). Blue squares display the
946 monthly mean cumulated rainfall (mm). Standard errors of the mean are shown as vertical dashed bars.

947

948 **Figure 2:** Influence of reproductive phenology on miscarriage probability and interbirth

949 interval lengths. Miscarriage probabilities (211 observations on 64 females) in relation to (a) conceiving within

950 or outside the conception season (partial residuals of Model 3A) and (b) the deviation from the mean annual

951 conception date (partial residuals of Model 3B). Similarly, interbirth interval lengths (122 observations on 47

952 females) in days are plotted in relation to (c) giving birth within or outside the birth season (partial residuals of

953 Model 4A) and (d) the deviation from the mean annual birth date (partial residuals of Model 4B). For graphical

954 purposes, the regression lines in brown are simple linear fits, and the shaded areas display 95% confidence

955 intervals; estimates and P values are also shown. In (a) and (c), the internal line represents the median, the lower

956 and upper hinges correspond to the first and the third quantiles (the 25th and 75th percentiles), the lower and upper

957 whisker extends to, respectively, the smallest and largest value no further than 1.5 times the interquartile range

958 from the hinge and black dots represent outlier points (i.e. beyond the end of the whiskers). Asterisks indicate

959 significant differences between the levels ‘within’ and ‘outside’ the categorical fixed effect of reproductive

960 phenology: $*P<0.05$; $**P<0.01$.

961

962 **Figure 3:** Influence of female social rank and previous reproductive outcome on birth timing.

963 The probability of a female giving birth within/outside the birth season (partial residuals of Model 5, based on 212

964 births from 72 females) as a function of (a) her rank (0: the lowest-ranking female in the group; 1: the highest-

965 ranking female in the group) and (b) her previous reproductive outcome and the deviation between a given birth

966 date and the mean annual birth date (in days; partial residuals of Model 6, based on 212 births from 72 females)

967 as a function of (c) rank and (d) previous reproductive outcome. For graphical purposes, the regression lines in

968 brown are simple linear fits, and the shaded areas display 95% confidence intervals; estimates and P values are

969 also shown. In (b) and (d), the internal line represents the median, the lower and upper hinges correspond to the

970 first and the third quantiles (the 25th and 75th percentiles), the lower and upper whisker extends to, respectively,

971 the smallest and largest value no further than 1.5 times the interquartile range from the hinge and black dots

972 represent outlier points (i.e. beyond the end of the whiskers). Asterisks indicate significant differences between

973 the levels ‘within’ and ‘outside’ the categorical fixed effect of previous reproductive outcome: $*P<0.05$;

974 $***P<0.001$.

975

976

977 **Figure A1:** Reproductive phenology. Proportions of (a) conceptions ($N=215$), (b) births ($N=212$) and (c)

978 cycle resumptions ($N=150$), per month (1 for January, 2 for February, etc.) for the reproductive events that

979 occurred between 2012 and 2020 in the study mandrill group.

980

981 **Figure A2:** Interbirth intervals in relation to rank. Interbirth interval lengths in days (raw data) as a
982 function of female social rank (0: the lowest-ranking female in the group; 1: the highest-ranking female in the
983 group). The brown curve shows the linear fit and the shaded area displays its 95% confidence intervals.

984

985 **Figure A3:** Graphical representation of real, randomly chosen, cycles of a dominant and a
986 subordinate female from the conception of the first offspring to the birth of the second offspring.

987 Pink indicates mating seasons (considered here from 1 May to 30 September) and blue indicates birth peaks (from
988 1 December to 31 January). The last suckling event recorded from each first offspring is also indicated in green.

989 Both cycles have been scaled to the day and aligned between the two females although they did not occur in the
990 same year.

991