



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

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

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The intensity of reproductive seasonality, which measures the temporal clustering of births during a particular period of the annual cycle (Lindburg, 1987), varies widely across species: from births concentrated over a week in banded mongooses, *Mungos mungo* (Hodge, Bell, & Cant, 2011) to births occurring year round in African elephants, *Loxondata africana* (Moss, 2001). Ultimate explanations of this variation in the intensity of reproductive seasonality across species have largely assumed that it mirrors variation in the intensity of environmental seasonality (Conover, 1992; Di Bitetti & Janson, 2000; Rutberg, 1987). Latitude, for example, often accentuates the intensity of seasonality and, as such, tropical species generally exhibit lower reproductive seasonality

than temperate or arctic species (Di Bitetti & Janson, 2000; Heldstab et al., 2020; Rutberg, 1987). Nevertheless, reproductive seasonality is common, and sometimes acute, in tropical species such as in Malagasy mammals (Heldstab et al., 2020; Wright, 1999). Yet, much less is known about the evolutionary determinants of reproductive phenology in tropical ecosystems which host most of the biomass (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000).

Reproduction is energetically costly, and matching the most demanding period of the reproductive cycle with the annual food peak is necessarily adaptive (Baker, 1938; Bronson, 2009). Most studies on the fitness consequences of reproductive phenology have concerned fast-lived organisms, such as rodents and passerines, from temperate regions (Bronson, 2009; Bronson & Heideman, 1994; Williams et al., 2017). These studies have usually considered only one fitness component, typically measuring offspring number, survival or

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growth (Ellison, Valeggia, & Sherry, 2005; Varpe, Jørgensen, Tarling, & Fiksen, 2009) but omitting potential effects on the mother's future reproduction (but see for a bird species, *Fulica atra*: Brinkhof et al., 2002) and miscarriage. This is problematic as the period from conception to weaning often extends over multiple seasons or years in long-lived species. Seasonal food peak(s) can thus be synchronized with some, but not all, reproductive and developmental stages. In such cases, birth timings maximizing offspring survival may be different from those maximizing maternal reproductive pace (Dezeure, Baniel, et al., 2021). When studying long-lived species, it thus appears essential to investigate the consequences of reproductive phenology across multiple fitness components to fully understand the selective pressures shaping reproductive seasonality.

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

In this study, we investigated the causes and consequences of reproductive phenology across multiple measures of female reproductive success in a natural population of a long-lived social Old World primate, the mandrill, *Mandrillus sphinx*, from Gabon. Mandrills form huge multimale–multifemale groups in the wild, up to a few hundreds of individuals, mainly females and their offspring (Abernethy, White, & Wickings, 2002; Hongo, 2014). Female mandrills are philopatric and form a matrilineal social hierarchy. They can live more than 18 years (Setchell et al., 2001) and give birth to a single offspring every 1–3 years (Setchell et al., 2002) which they breastfeed during a variable period (8 months on average: Setchell & Wickings, 2004). Dominant and multiparous females have higher reproductive performances, but neither rank nor parity affects reproductive timings in captivity (Setchell et al., 2002). Most of our knowledge about mandrill reproduction comes from a semifree-ranging population (Setchell, Lee, Jean Wickings, & Dixson, 2001; Setchell, Lee, Wickings, & Dixson, 2002; Setchell & Wickings, 2004) and from a preliminary study on a wild unhabituated population showing that reproduction is seasonal: although inter- and intraindividual variation occur both within and across years, mating happens mainly during the long dry season, while births are concentrated in the rainy season (Hongo, Nakashima, Akomo-Okoue, & Mindonga-Nguelet, 2016). The fact that mandrills breed seasonally despite living in the equatorial forests of central Africa, which exhibit buffered environmental conditions year round compared to most other biomes, remains puzzling. The mandrill is an interesting species to study the determinants of reproductive seasonality because it is an equatorial primate whose births are highly seasonal but there is also a high degree of individual variability in birth timing. Here, we used longitudinal life history and behavioural data collected since 2012 from the only natural population of habituated mandrills to ask three main questions. (1) How is reproductive phenology adjusted to environmental seasonality? We characterized both environmental and reproductive seasonality, predicting that mandrill food availability is affected by environmental seasonality,

and further asked which reproductive stage is synchronized with the annual food peak. (2) What are the consequences of variation in birth timing for female reproductive success? We used three measures of reproductive success: pre- and postnatal offspring mortality and the length of the maternal interbirth interval (IBI). We predict that giving birth away from the birth peak affects both offspring mortality and maternal interbirth interval. More precisely, we expected maternal phenology strategies to prioritize offspring survival over reproductive pace in this long-lived species, meaning that birth timing effects may be more detectable on maternal IBI than on pre- and postnatal offspring survival (Dezeure, Baniel, et al., 2021). (3) Do females vary in birth timing and, if so, which individual traits drive this variation? We investigated the effects of female age, recent reproductive history and social rank. We predicted that higher-ranking females would be less seasonal than lower-ranking females, as their privileged access to resources may buffer them from environmental seasonality. We further predicted that a reproductive failure (miscarriage or infant mortality) would disrupt female reproductive phenology and lead females to reproduce early in the birth season or away from the birth peak, depending on the age at infant death.

METHODS

Study Site and Population

A natural population of habituated mandrills has been monitored daily since 2012 by the Mandrillus Project, a long-term field research project studying the ecology, life history and behaviour of mandrills. This population originated from 65 captive individuals initially housed at the CIRMF (Centre International de Recherches Médicales de Franceville, Gabon) which were released in the park in two waves, in 2002 and 2006 (Peignot et al., 2008). Study mandrills live in a private park (Lékédi Park) and its vicinity. Their habitat is composed of a mosaic of evergreen forests, grasslands and savannahs. The diet of these mandrills has not been supplemented since April 2012 (Brockmeyer et al., 2015). In early 2021, our study group was composed of approximately 250 individuals. During daily monitoring, we recorded data on individual life history, developmental trajectory, behaviour, group demography and GPS locations. Data used in this study were collected from March 2012 to March 2020 on a total of 80 adult females aged 4–24 years.

Individual and Reproductive Parameters

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

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

The reproductive state of each adult female was monitored daily. A female was assigned as (1) pregnant, with pregnancy being determined post hoc following either the birth of a live infant, and encompassing the 175 days before the birth (average gestation length = 175 days in this population, range 163–190 days, $SD = 4.7$,

$N = 103$ pregnancies where both conception and birth were observed with <7 days of uncertainty) or, in cases of births showing ≥ 7 days of uncertainty, using patterns of sexual swellings or the presence of a noticeable small and distinctive pink swelling present about 2 months following fertilization (the main clue confirming pregnancy when a female miscarried), (2) lactating, when a live offspring was less than 6 months old or until the death of the offspring before 6 months of age, or (3) cycling, including both swollen females in oestrus (i.e. sexually active with a perineal tumescent or detumescent swelling) and nonswollen females at other stages of their menstrual cycle.

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

Fitness Estimates

For each infant born, we investigated whether it died before 6 months of age. We used this age threshold because older infants are often harder to recognize, generating uncertainty on their survival after this age. Death was recorded when a corpse was observed, often carried by the mother for a few days, or when the mother was seen without her infant for a few days. We discarded records of four infants whose survival outcomes were uncertain. In our data set, 20 of 208 infants died before reaching 6 months old, with mortality occurring at a median age of 83 days (range 1–163 days).

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

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

Environmental Data

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

Behavioural Data

Five-minute focal observations ([Altmann, 1974](#)) were performed daily on all individuals chosen randomly. During focal observations, we recorded all activities, including foraging bouts, on a continuous

basis, as well as other point events, such as dyadic approach–avoidance interactions. We used these data to compute seasonal variation in the time adult females spent foraging and adult females' social rank.

Seasonal variation in time budgets

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

Female rank

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

Statistical Methods

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

Characterization of reproductive and environmental seasonality

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

In addition to the graphical representation of monthly rainfall variation, we assessed environmental variation in food availability using the time spent foraging by females aged at least 4 years. More precisely, we used a generalized linear mixed model (GLMM) with a negative binomial error structure investigating seasonal variation in the time spent foraging per focal observation (Model 1), using the 'glmmTMB' function from the glmmTMB package ([Brooks et al., 2017](#)). We used the time (s) spent foraging per focal observation as a response variable and the log-transformed time (s) of observation as an offset term. We included the female's identity and the year of observation as random effects to control for the nonindependence of multiple observations from the same female and from the same year, respectively. In addition, the random effect 'year of

observation' controlled for temporal variation such as between-year changes in group size and composition or observational effort.

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

Consequences of reproductive phenology for female reproductive success

We investigated the effect of reproductive timing on three indicators of female reproductive success: offspring mortality probability before 6 months of age (Model 2), miscarriage probability (Model 3) and the duration of subsequent maternal IBIs (Model 4). To quantify the effects of birth and conception timings on offspring mortality and on the probability of miscarriage, respectively, we ran GLMMs with a binomial error structure (Models 2 and 3), using the function 'glmer' from the package lme4 (and for all subsequent binomial GLMMs; [Bates, Mächler, Bolker, & Walker, 2015](#)). To quantify the effects of birth timing on IBI duration (Model 4), we ran a linear mixed model (LMM) using the function 'lmer' from the package lme4 (and for all subsequent LMMs; [Bates et al., 2015](#)).

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

In addition, for each birth ($N = 212$), we calculated the deviation from the mean annual birth date in days, capturing whether an infant was born early or late within the cohort, with negative values for births occurring before the mean birth date of a cohort and positive values afterwards. For Model 3 on miscarriages, we used

the deviation (number of days) between the focal conception and the mean annual conception date of this 'conceptive cohort'.

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

In these models (Models 2–4), we included the female's (mother) identity and the birth/conception cohort as random effects. We also added, as fixed effects, female parity, rank and infant sex (except for Model 3 as infant sex is unknown during pregnancy) because all these parameters affect the reproductive performances of female mandrills in captivity ([Setchell et al., 2002](#); [Setchell & Wickings, 2004](#)). Primiparous and lower-ranking mothers and mothers with sons are expected to have longer interbirth intervals and higher pre- and postnatal offspring mortality than multiparous, higher-ranking mothers and mothers with daughters ([Brown, 2001](#); [Gesquiere, Altmann, Archie, & Alberts, 2017](#); [Setchell et al., 2002](#)).

Female determinants of variation in birth timing

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

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

Models' validity diagnostic

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

square tests with associated P values computed with the 'Anova' function of the R package 'car' (Fox et al., 2019), we calculated the 95% Wald confidence intervals for the estimate of each fixed effect. We also checked the distribution of residuals using the 'qqPlot' function of the 'car' package for LMMs (Fox et al., 2019) and using 'simulateResiduals' from the DHARMA package for binomial GLMMs (Hartig, 2020). We used the 'visreg' package (Breheny & Burchett, 2017) to plot the partial residuals effects shown in the figures. We set up different levels as reference before running Models 5 and 6 to compare the different levels of the fixed effect 'previous reproductive outcome'.

Ethical Note

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

RESULTS

Reproductive Phenology and Environmental Seasonality

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

Mean annual cumulative rainfall was high, with moderate interannual variability ($N = 8$ years, mean \pm SD = 1871 \pm 175 mm). Rainfall was highly seasonal, with a long rainy season

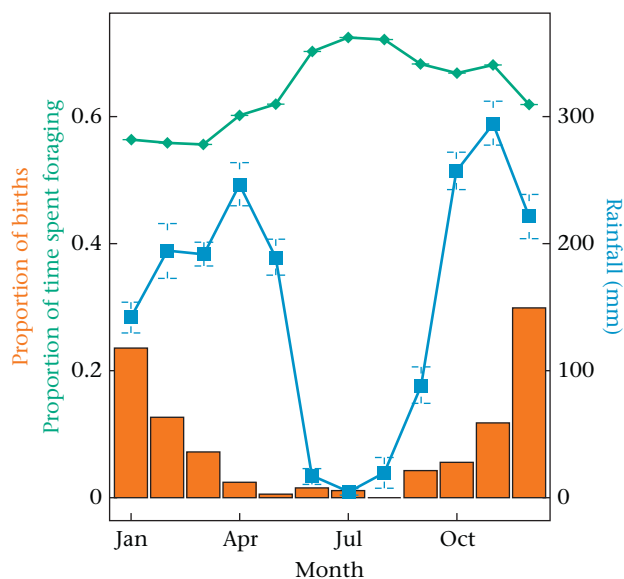


Figure 1. Environmental and reproductive seasonality of the study mandrills (2012–2020). Orange bars represent the monthly proportion of births ($N = 212$). Green diamonds represent the monthly mean proportion of time adult females spent foraging (an indicator of food availability). Blue squares display the monthly mean cumulated rainfall (mm). Standard errors of the mean are shown as vertical dashed bars.

(October–May) characterized by two peaks, in October–November and April, followed by a long dry season (June–September; Fig. 1). The proportion of observation time that females spent foraging also varied seasonally (Table 1, Fig. 1) with females spending more time foraging around mid-August (long dry season) than mid-February (long rainy season; see Appendix 2). The birth peak happened midway through the long rainy season, just before the peak of food availability (Fig. 1).

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

Fitness Consequences of Variation in Reproductive Phenology

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

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

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

Variation in Female Reproductive Phenology

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

DISCUSSION

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

Environmental Seasonality in Equatorial Forests

Several reasons may explain why equatorial organisms may breed seasonally despite living in environmental conditions where food may remain available year round compared to most other biomes. First, most equatorial environments show important seasonal variation in rainfall (Feng, Porporato, & Rodriguez-Iturbe, 2013; Van Schaik, Terborgh, & Wright, 1993), reflected in food availability that mirrors variation in plant phenology (Takenoshita, Ando, Iwata, & Yamagiwa, 2008). Accordingly, mandrills spent more time feeding during the long dry season (this study) and also show qualitative seasonal shifts in diet (Nsi Akoue et al., 2017). Such within-year variation in food resources may thus affect

Table 1
Determinants of the proportion of time mandrill females spent foraging

Fixed effect	Estimate	CI		χ^2	P
		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	622.59	<10⁻⁴
Female reproductive state	(L1)	-0.50	-0.55		
	(L2)	-0.23	-0.27		
	(L3)	-0.09	-0.13		
	(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

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

reproductive timing and performance, even in long-lived omnivorous species. In addition, these habitats could be characterized by low interannual variation (i.e. high predictability) promoting breeding seasonality (English, Chauvenet, Safi, & Pettorelli, 2012; Jönsson, 1997), although this relationship needs to be confirmed in a comparative context.

Female Reproductive Pace

Births preceded the seasonal food peak by around 2 months, whereas cycle resumptions and conceptions mainly occurred during the long dry season when food was scarce. We hypothesize that the mandrill's birth peak has evolved to match the food peak with early lactation. In line with this, females that gave birth within the birth peak accelerated their future reproduction (shorter IBIs) suggesting that this phenology strategy brings reproductive benefits for female mandrills. It is possible that the first half of lactation is the most costly energetic stage of reproduction in female mandrills because mothers cover the full nutritional needs of their infants, in contrast with the second half where infants start feeding independently (Langer, 2008; Lee, 1996). Those females that give birth early in the birth peak probably time their peak in energy demands more closely with the food peak than females giving birth later in the birth peak. Such adjustments are the norm among fast-lived and temperate or arctic species (Bronson, 2009; Bronson & Heideman, 1994), and similar patterns of phenology have also been observed in some tropical species including primates (Brockman & van Schaik, 2005; Carnegie, Fedigan, & Melin, 2011;

Heesen, Rogahn, Ostner, & Schülke, 2013; Janson & Verdolin, 2005) and ungulates (Sinclair, Mduma, & Arcese, 2000). Our study therefore emphasizes that reproductive seasonality in equatorial species can, at least partly, emerge in response to seasonal variation in food availability to enhance maternal reproductive pace.

Postnatal Offspring Survival

Despite seasonal variation in food availability, female mandrills could give birth year round without any significant cost to postnatal offspring survival. This result may reflect, however, analytical limitations due to the low numbers of infants born outside the birth season (only six births, i.e. 3%, between May and August). Alternatively, female mandrills may mitigate the costs of giving birth outside the birth peak by extending lactation, as reflected by longer IBIs following such births. Indeed, gestation length is nearly fixed in cercopithecoid primates (Gesquiere, Altmann, Archie, & Albers, 2017), while the length of the cycling period does not vary much relative to IBI in semicaptive mandrills (Setchell & Wickings, 2004) suggesting that lactation period is the most variable part of the IBI. Finally, the moderate rate of infant mortality observed (9%) and the fact that females can be lactating and pregnant simultaneously (Fig. A3) may, in combination, indicate that seasonal food shortage is rarely a cause of poor condition and death for mothers or their offspring. Similarly, in white-faced capuchins, *Cebus capucinus*, a seasonal-breeding monkey living in a rich tropical habitat, deviance from the birth season does not translate into increased offspring mortality (Carnegie et al., 2011). Taken together, our results indicate

Table 2
Determinants of offspring mortality

Fixed effect	Estimate	CI		χ^2	P	
		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

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

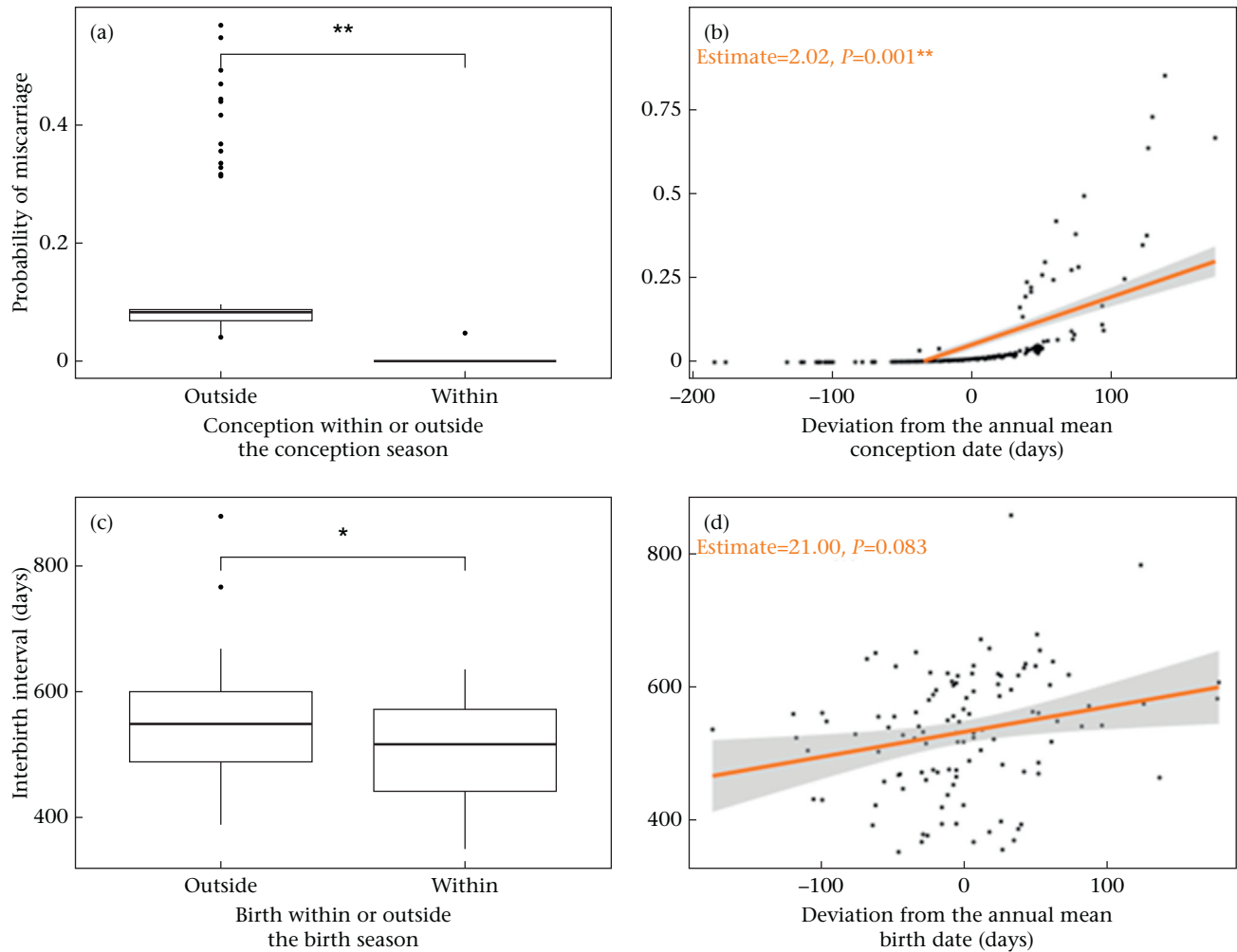


Figure 2. Influence of reproductive phenology on miscarriage probability and interbirth interval lengths. Miscarriage probabilities (211 observations on 64 females) in relation to (a) conceiving within or outside the conception season (partial residuals of Model 3A) and (b) the deviation from the mean annual conception date (partial residuals of Model 3B). Similarly, interbirth interval lengths (122 observations on 47 females) in days are plotted in relation to (c) giving birth within or outside the birth season (partial residuals of Model 4A) and (d) the deviation from the mean annual birth date (partial residuals of Model 4B). For graphical purposes, the regression lines in orange are simple linear fits, and the shaded areas display 95% confidence intervals; estimates and *P* values are also shown. In (a) and (c), the internal line represents the median, the lower and upper hinges correspond to the first and the third quantiles (the 25th and 75th percentiles), the lower and upper whisker extends to, respectively, the smallest and largest value no further than 1.5 times the interquartile range from the hinge and black dots represent outlier points (i.e. beyond the end of the whiskers). Asterisks indicate significant differences between the levels 'within' and 'outside' the categorical fixed effect of reproductive phenology: **P* < 0.05; ***P* < 0.01.

that female mandrills may prioritize current (offspring survival) over future (shorter IBI) reproduction when giving birth outside the birth peak. Buffering the costs of a suboptimal birth timing on current reproduction by delaying future reproduction may only be possible in productive environments where the selective pressures favouring a strict breeding season are weakened, although other factors may also play a role, such as the ability to store energy or access to alloparental care (Heldstab, van Schaik, & Isler, 2017). In contrast, when food availability is more limiting, the costs of giving birth away from the optimal season on offspring survival may be too high, resulting in a strict breeding seasonality, as generally observed in long-lived temperate and arctic species (Bronson, 2009; Rutberg, 1987).

Miscarriage Probability

Here, we also showed that miscarriages increased when females conceived too late in the mating season. Such pregnancy failures are probably unrelated to food scarcity during pregnancy, as they

are in yellow baboons, *Papio cynocephalus*, for example (Beehner, Onderdonk, Alberts, & Altmann, 2006), because in mandrills most conceptions and pregnancies occurred during the long dry season when food was scarce. Alternatively, we speculate that infants born late in the birth season could be targeted by infanticidal males. Indeed, males generally immigrate at the onset of the mating season, around April (Abernethy, White, & Wickings, 2002; Hongo et al., 2016; M.J.E. Charpentier, personal observation). Giving birth late would result in highly vulnerable offspring aged only a few weeks/months when most males immigrate (Palombit, 2015). In support of this hypothesis, 55% (11 of 20) of infant deaths occurred in March–May, which is significantly more often than at any other time of the year ($\chi^2 = 17.2$, $P < 10^{-3}$). For four of these deaths, male infanticide was the most plausible scenario (M.J.E. Charpentier, personal observation), although infanticide by males has not been formally documented in mandrills. In contrast, when females gave birth early in the peak, they usually resumed cycling early in the next mating season, meaning that males do not need to kill their infants

Table 3
Determinants of female miscarriage probability

Fixed effect	Estimate	CI		χ^2	P
		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		

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

to mate with them. Spontaneous abortions may thus represent an adaptive female counterstrategy, as shown in geladas, *Theropithecus gelada*, where females preferentially abort rather than invest in a fetus which would be a likely target of infanticide following a male take-over (Roberts, Lu, Bergman, & Beehner, 2012). Interestingly, in geladas, the seasonality of male take-overs leads to a decrease in the intensity of reproductive seasonality because the suboptimal 'social birth peak' resulting from male take-overs and subsequent miscarriages occurs a few months from the optimal 'ecological birth peak' (Roberts, Lu, Bergman, & Beehner, 2017). By contrast, in mandrills, it appears that the timing of male immigrations strengthens the intensity of reproductive seasonality by selecting against births occurring late in or after the birth peak, explaining at least partially why births are more seasonal than conceptions. This 'Bruce effect' (spontaneous abortion due to maternal exposure to an unrelated adult male) is relatively well documented in several small mammals and horses, in addition to geladas (Inzani et al., 2019; Schwagmeyer, 1979; Zipple, 2020; Zipple, Roberts, Alberts, & Beehner, 2021). Additional years of observations will be necessary to confirm (or not) the seasonality of infanticide risk in mandrills and investigate the nature of potential female counterstrategies.

The Evolution of Plastic Birth Timing

If births outside the peak are partly selected against for the reasons highlighted above, it is unclear why they may still occur. Several results indicate that birth timing is a highly plastic phenotype in mandrills. First, births occurred year round, although at variable frequencies. Second, there was no within-female consistency in birth timing across successful births. Third, previous reproductive history, a source of within-individual variation, impacted birth timing. Specifically, female mandrills often rapidly resumed cycling and conceived regardless of the season following infant or fetal death, which may disrupt reproductive seasonality. Plasticity in birth timing is common across primates, with within-species variation in seasonality across different latitudes (Heldstab et al., 2020), and can represent a direct target of selection in response to ecological or social changes in the environment (Charmantier et al., 2008; de

Villemereuil et al., 2020). In species where infanticide occurs, females' ability to conceive outside the mating season may have evolved to mitigate the costs of infanticide to decrease the gaps introduced in females' reproductive careers. Such a capacity is, however, probably contingent on environmental conditions, and may only evolve in climates that are not too cold or arid for females to raise offspring outside the best season. We further expect females' ability to conceive outside the mating season in species that are sufficiently generalist to exploit a diversity of resources including fallback foods during the lean season, as well as able to store energy from one season to the next. In such species and environmental conditions, the costs of reproducing outside the birth season may be of roughly similar magnitude as the costs of waiting until the next breeding season, meaning that females can switch from one strategy to the next depending on their reproductive history, physical condition and context-dependent changes in the social or ecological environment.

Dominant Females Breed less Seasonally than Subordinates

Finally, we documented between-female variation in birth timing. Dominant females were more likely to give birth outside the birth peak than subordinate females, an effect that, to our knowledge, was not previously reported in primates. Rank-related variation in reproductive phenology directly echoes our result showing that dominant female mandrills spent less time foraging than subordinates, probably because they have better access to food resources year round, as observed in baboons (Barton, 1993; Barton & Whiten, 1993). This scenario is further supported by the important rank-related variation in IBIs: dominant females gave birth nearly every year while subordinates gave birth every 2 years on average (Fig. A3). In addition, this rank-related effect does not occur in captive mandrills, probably because food provisioning offsets rank-related effects (Setchell et al., 2002). For dominant females, the costs of giving birth outside the optimal season may thus be lower than the costs of waiting for the next optimal season. Rank-related effects on reproductive phenology have been described in a handful of other species. In the Kalahari meerkat, *Suricata suricatta*, the dominant female breeds almost year round while subordinate breeding is only tolerated during the rainy

Table 4
Determinants of maternal interbirth intervals

Fixed effect	Estimate	CI		χ^2	P
		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

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

Table 5
Determinants of birth timings

Fixed effect	Estimate	CI		χ^2	P	
		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	
Previous reproductive outcome	(Infant died)	-0.69	-2.10	0.72	2.55	0.467
	(Miscarriage)	-0.42	-1.72	0.87		
	(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	
Previous reproductive outcome	(Infant died)	-3.84	-76.68	-24.89	19.65	2.01 × 10⁻⁴
	(Miscarriage)	-2.23	-54.6	-3.57		
	(Primiparous)	0.48	-15.86	26.11		

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

season, around the annual food peak, at a time when the birth of subordinate offspring does not compromise the growth and development of dominant pups (Clutton-Brock, Hodge, Flower,

Spong, & Young, 2010). In addition, in reindeer, *Rangifer tarandus*, social rank also affects birth timing: dominant females, in better condition, give birth earlier in the birth season than subordinates

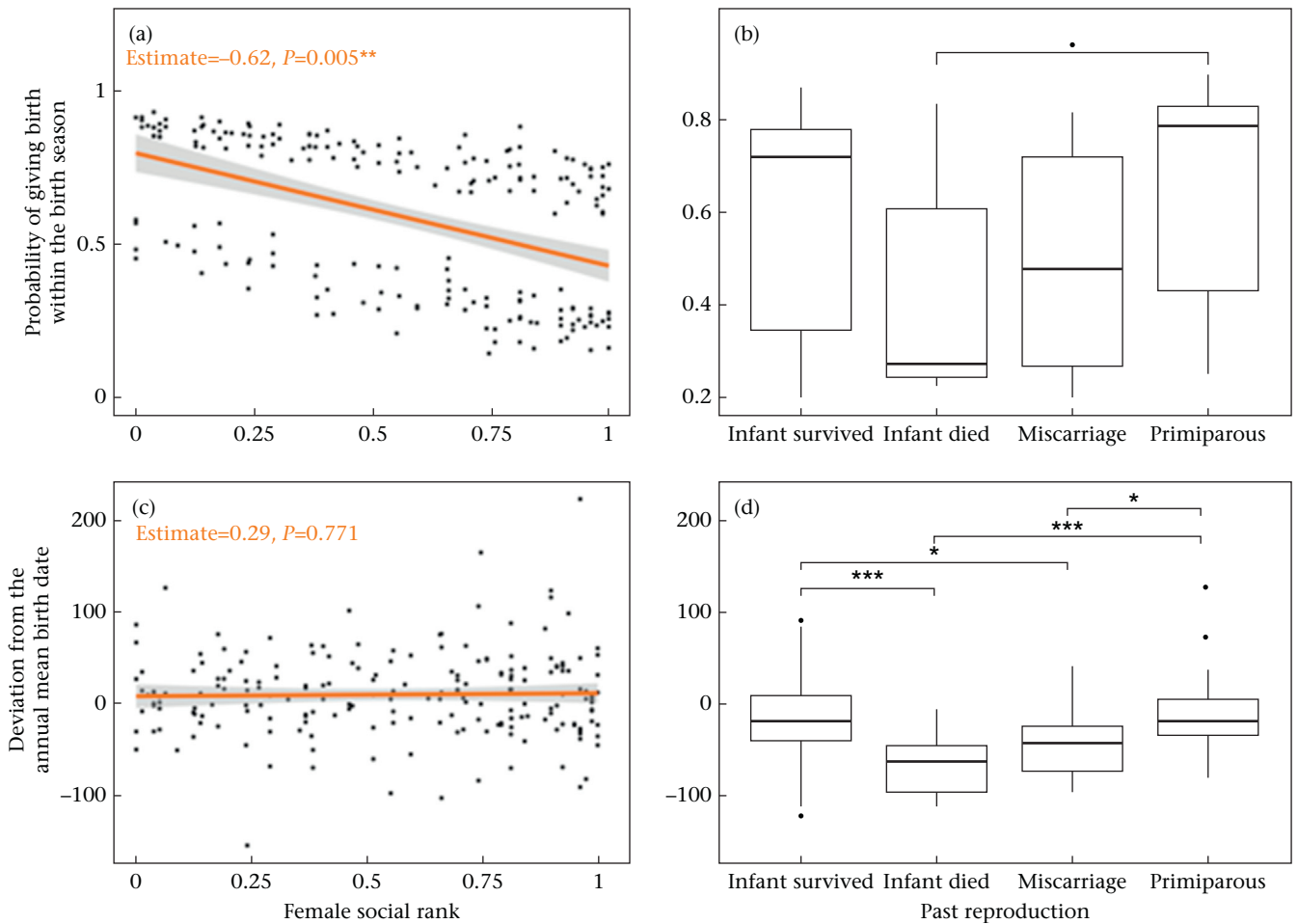


Figure 3. Influence of female social rank and previous reproductive outcome on birth timing. The probability of a female giving birth within/outside the birth season (partial residuals of Model 5, based on 212 births from 72 females) as a function of (a) her rank (0: the lowest-ranking female in the group; 1: the highest-ranking female in the group) and (b) her previous reproductive outcome and the deviation between a given birth date and the mean annual birth date (in days; partial residuals of Model 6, based on 212 births from 72 females) as a function of (c) rank and (d) previous reproductive outcome. For graphical purposes, the regression lines in orange are simple linear fits, and the shaded areas display 95% confidence intervals; estimates and P values are also shown. In (b) and (d), the internal line represents the median, the lower and upper hinges correspond to the first and the third quartiles (the 25th and 75th percentiles), the lower and upper whisker extends to, respectively, the smallest and largest value no further than 1.5 times the interquartile range from the hinge and black dots represent outlier points (i.e. beyond the end of the whiskers). Asterisks indicate significant differences between the levels 'within' and 'outside' the categorical fixed effect of previous reproductive outcome: *P < 0.05; ***P < 0.001. The dot in (b) represents P < 0.10.

(Holand et al., 2004). Given that dominant females probably have priority of access over food compared to subordinate females, we may expect this influence of rank on reproductive phenology to be widespread across taxa. Overall, these results highlight the importance of social competition in shaping the intensity of reproductive seasonality at the population level.

Conclusions

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

Author Contributions

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

Data Availability

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

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APPENDIX 1: DATES OF CONCEPTIONS, BIRTHS AND CYCLE RESUMPTIONS

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

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

Finally, the first postpartum cycle (i.e. cycle resumption) is the first menstrual cycle following a birth, when the female resumes cycling following lactation. The exact date of cycle resumption corresponds to the first day of oestrus of the first postpartum cycle, i.e. the first day when a sexual swelling is recorded following a period of lactation. In total, our sample comprised 150 cycle resumptions, following an infant that either survived ($N = 133$) or died ($N = 17$) during its first 6 months of life. We chose to include cycle resumptions following the death of an unweaned infant, as such events contribute to shaping the timing and intensity of reproductive seasonality at the population level.

APPENDIX 2: QUANTIFYING SEASONAL EFFECTS ON TIME FEMALES SPENT FORAGING

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

APPENDIX 3: COMPUTING MEAN ANNUAL BIRTH (AND CONCEPTION) DATES

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

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

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

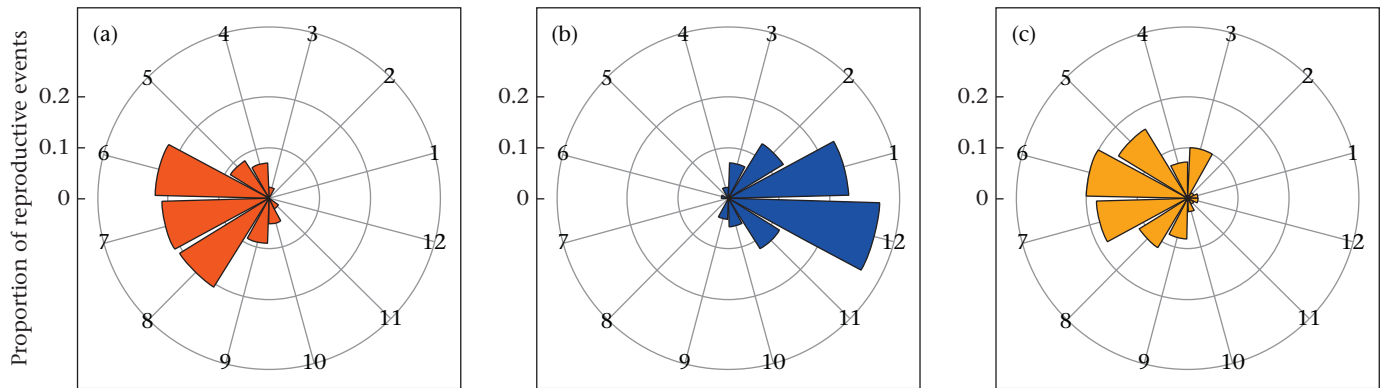


Figure A1. Reproductive phenology. Proportions of (a) conceptions ($N = 215$), (b) births ($N = 212$) and (c) cycle resumptions ($N = 150$), per month (1 for January, 2 for February, etc.) for the reproductive events that occurred between 2012 and 2020 in the study mandrill group.

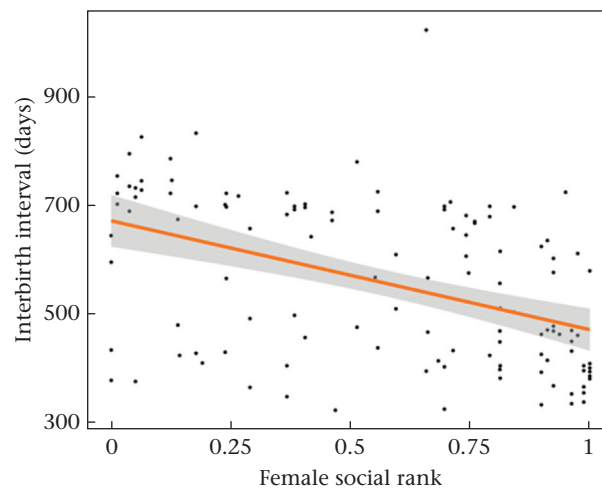


Figure A2. Interbirth intervals in relation to rank. Interbirth interval lengths in days (raw data) as a function of female social rank (0: the lowest-ranking female in the group; 1: the highest-ranking female in the group). The orange line shows the linear fit and the shaded area displays its 95% confidence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

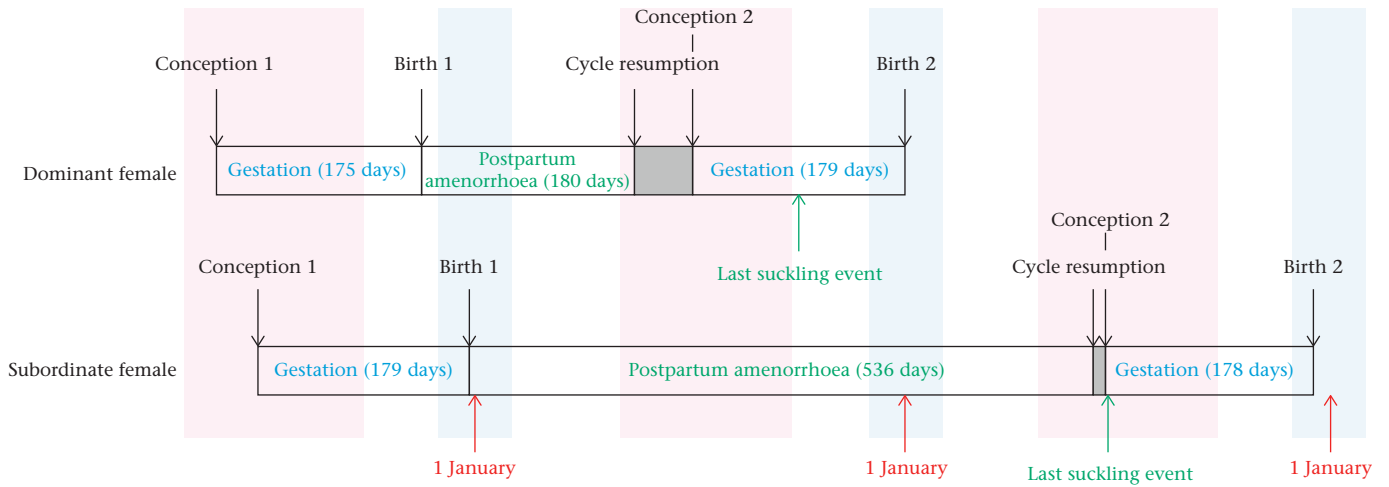


Figure A3. Graphical representation of real, randomly chosen, cycles of a dominant and a subordinate female from the conception of the first offspring to the birth of the second offspring. Pink indicates mating seasons (considered here from 1 May to 30 September) and blue indicates birth peaks (from 1 December to 31 January). The last suckling event recorded from each first offspring is also indicated in green. Both cycles have been scaled to the day and aligned between the two females although they did not occur in the same year.