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The evolution of reproductive seasonality in large tropical terrestrial monkeys

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The evolution of reproductive seasonality in large tropical terrestrial monkeys

Reproductive seasonality refers to the periodic temporal clustering of reproductive events in the annual cycle. It is often adaptive, because synchronizing the costliest stage of the female reproductive cycle with the most productive season can enhance maternal and offspring conditions and survival. Most studies investigating the evolutionary determinants of reproductive seasonality were done on fast-lived species from temperate habitats, while little is known for long-lived tropical species. In this thesis, we investigated the evolutionary determinants and fitness consequences of reproductive seasonality in two wild primate populations: non-seasonal breeding chacma baboons (*Papio ursinus*) from the seasonal and arid Namibian savannah and seasonal breeding mandrills (*Mandrillus sphinx*) from the Gabonese equatorial forest. Using a combination of long-term life history, morphological, behavioural and climatic data, we first reveal that despite their omnivorous diet and tropical habitats, mandrills and baboons are both subject to important seasonal variation in food availability, mainly caused by rainfall fluctuations. Consequently, we find that matching the peak of lactation with the seasonal food peak enhances female future reproduction (i.e. maternal reproductive pace) in both populations. We further show that two distinct optimal birth timing in chacma baboons maximise either maternal reproductive pace or offspring survival, by matching early versus late weaning with the seasonal food peak, respectively. The occurrence of multiple optimal birth timings weakens the strength of reproductive seasonality. In contrast, mandrill females do not face a similar trade-off between current and future reproduction over birth timing, and maximise their fitness by giving birth seasonally. In these two social species, we further find social effects on reproductive synchrony and seasonality. In chacma baboons, rank-related reproductive suppression leads to birth asynchrony and contributes to explain the absence of seasonal reproduction. In mandrills, dominant females are less seasonal than subordinates. Lastly, a comparative analysis on 16 populations from 7 species of wild baboons and relatives show unusually flexible patterns of reproductive phenology – with seasonal and non-seasonal breeding populations in a same species – and climatic unpredictability acts as a major driver of the loss of reproductive seasonality. Altogether, this work extends our understanding of the diverse patterns of reproductive seasonality observed in long-lived tropical species, by shedding light on previously overlooked determinants of reproductive phenology, such as climatic predictability, life history traits and trade-offs, and various social factors likely to affect other long-lived and social species.

Keywords: Reproductive phenology, seasonal breeding, life history, sociality, primate

L'évolution de la saisonnalité reproductive chez des grands singes terrestres tropicaux

La saisonnalité reproductive réfère au regroupement temporel périodique d'événements reproductifs dans le cycle annuel. Elle est souvent adaptative, car synchroniser l'étape la plus coûteuse du cycle reproducteur des femelles avec la meilleure saison peut améliorer la condition et survie des mères et de leurs progénitures. La plupart des études portant sur les déterminants évolutifs de la saisonnalité reproductive ont été menées sur des espèces à rythme de vie rapide des habitats tempérés, et l'on sait relativement peu de choses sur les espèces tropicales longévives. Dans cette thèse, nous avons étudié les déterminants évolutifs et les conséquences en termes de valeur sélective de la saisonnalité reproductive de deux populations de primates sauvages: les babouins chacma à reproduction non-saisonnière (*Papio ursinus*) de la savane aride et saisonnière namibienne et les mandrills à reproduction saisonnière (*Mandrillus sphinx*) de la forêt équatoriale gabonaise. En utilisant une combinaison de données de long-terme d'histoire de vie, morphologiques, comportementales et climatiques, nous révélons tout d'abord que malgré leurs régimes omnivores et leurs habitats tropicaux, mandrills et babouins sont tous deux soumis à d'importantes variations saisonnières de la disponibilité alimentaire, principalement causées par des fluctuations de précipitations. Par conséquent, nous constatons que faire correspondre le pic de lactation avec le pic alimentaire saisonnier améliore la reproduction future des femelles (accélère le rythme de reproduction maternel) chez les deux populations. En outre, nous montrons que deux périodes de naissance optimales distinctes chez les babouins chacma maximisent soit le rythme de reproduction maternel, soit la survie de la progéniture, en faisant correspondre le début ou la fin du sevrage avec le pic alimentaire saisonnier, respectivement. L'existence de multiples périodes optimales de naissance affaiblit l'intensité de leur saisonnalité reproductive. En revanche, les mandrills ne font pas face à ce même compromis entre reproduction actuelle et future sur le moment de la naissance, et maximisent leurs valeurs sélectives en donnant naissance dans le pic saisonnier de naissance. Chez ces deux espèces sociales, nous trouvons de plus des effets sociaux sur la saisonnalité reproductive: la suppression de la reproduction, liée au rang et conduisant à l'asynchronie des naissances dans un groupe, contribue à expliquer l'absence de reproduction saisonnière chez les babouins chacma, et les femelles dominantes sont moins saisonnières que les subordonnées chez les mandrills. Enfin, une analyse comparative sur 16 populations de 7 espèces de babouins sauvages et proches apparentés révèle une rare flexibilité de leur phénologie reproductive - avec des populations à reproduction saisonnière et non-saisonnière au sein d'une même espèce - et l'imprévisibilité climatique agit comme un facteur majeur de la perte de saisonnalité reproductive. Dans l'ensemble, ce travail élargit notre compréhension des divers patrons de saisonnalité reproductive observés chez les espèces tropicales à longue durée de vie, en mettant en lumière des déterminants précédemment négligés de la phénologie de la reproduction, tels que la prévisibilité climatique, les traits et compromis d'histoire de vie, et divers facteurs sociaux susceptibles d'affecter d'autres espèces sociales et à rythme de vie lent.

Mots-clés : phénologie reproductive, reproduction saisonnière, histoire de vie, socialité, primate

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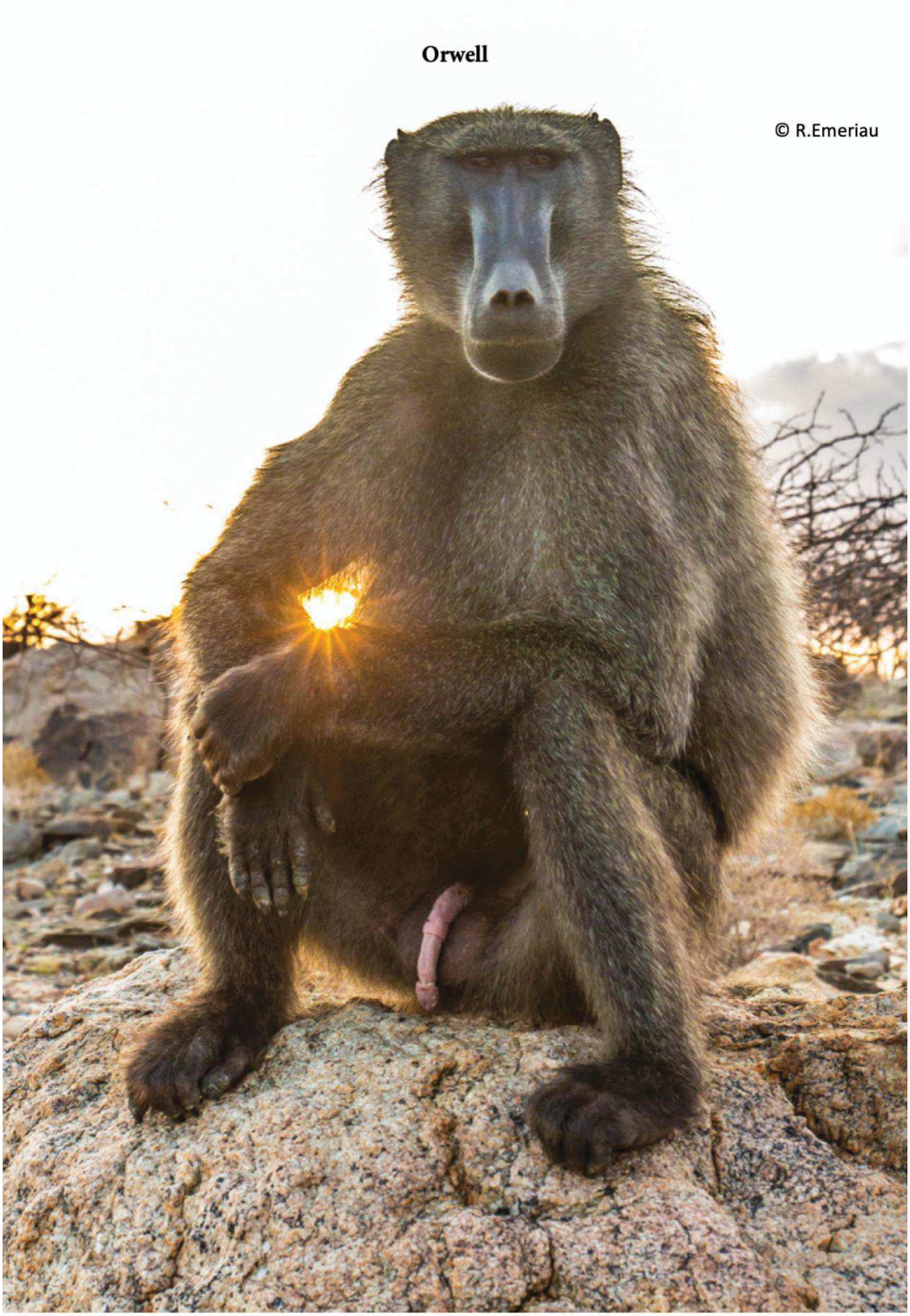
Orwell



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GENERAL INTRODUCTION



Climate change is having a major and increasing impact on various environments and habitats. In particular, both the levels of within-year (i.e. environmental seasonality) and between-year (i.e. environmental predictability) environmental variation often increase. Reproductive seasonality, which characterizes the timing of reproduction in the annual cycle, is a critical aspect of reproduction as it can affect individual fitness. Climate change, via modulating environmental fluctuations, can modify the fitness costs and benefits associated with reproductive seasonality, and consequently affects a species demography and evolution.

However, our understanding of the evolution of reproductive seasonality is limited, as the literature is biased towards short-lived species, mainly rodents and passerines, living in high-latitude and showing strong reproductive seasonality. Little is known about the evolutionary determinants of reproductive seasonality among long-lived species in tropical environment. Such limitations contrast with our detailed knowledge of its physiological regulation (that will not be discussed in this manuscript).

This thesis is an attempt to better understand the evolutionary determinants of reproductive seasonality, focusing primarily on two wild primate populations, chacma baboons (*Papio ursinus*) in Namibia and mandrills (*Mandrillus sphinx*) in Gabon. In the first section, I define reproductive seasonality and highlight its diversity in the animal kingdom. Second, I briefly review the influence of environmental seasonality on reproductive seasonality, considering both ultimate (e.g. resources availability) and proximate (e.g. photoperiod) causes. Third, I envision other potential ultimate determinants of reproductive seasonality, likely to explain the diversity of breeding strategies. In this section, I emphasize the importance of (i) environment (un-)predictability, (ii) species ecology and life history traits, (iii) reproductive (a-)synchrony and (iv) individual variation in reproductive phenology. Finally, I describe the main consequences of reproductive seasonality on individual fitness, considering both offspring and

mothers. I develop these ideas using examples from vertebrates, with a focus on mammals, and in particular on primates.

I°) What is reproductive seasonality?

Reproductive seasonality is defined as the periodic temporal clustering of reproductive events (births, conceptions, etc.) in the annual cycle between individuals of the same species. It can be characterized by two main aspects: (i) the strength (or tightness) of the clustering of reproductive events, later referred as **intensity of reproductive seasonality**, and (ii) the timing in the annual cycle of reproductive events, thereafter referred as **reproductive phenology**.

A high diversity in the intensity of reproductive seasonality is observed in the animal kingdom, in particular in mammals. At one extreme of the continuum, some species breed seasonally, such as mountain goats (*Oreamnos americanus*) that give birth each year in a single month (Côté & Festa-Bianchet, 2001). At the other end, some species are non-seasonal breeders and show no (or very few) variations of monthly birth frequencies, such as humans (*Homo sapiens*) (Bronson, 1995; Ellison, Valeggia, & Sherry, 2005). This diversity is in particular striking among primates (Campos et al., 2017) (See Figure 1): while Verreaux's sifakas (*Propithecus verreauxi*) breed very seasonally, with more than 75% of births occurring in one month, gorillas (*Gorilla beringei beringei*) are non-seasonal breeders, with an absence of seasonal patterns in their monthly birth frequencies. Seasonal breeding is the norm rather than the exception in the animal kingdom, and in particular in mammals (Bronson, 2009), and primates (Brockman & van Schaik, 2005a; Heldstab et al., 2020; C. Janson & Verdolin, 2005).

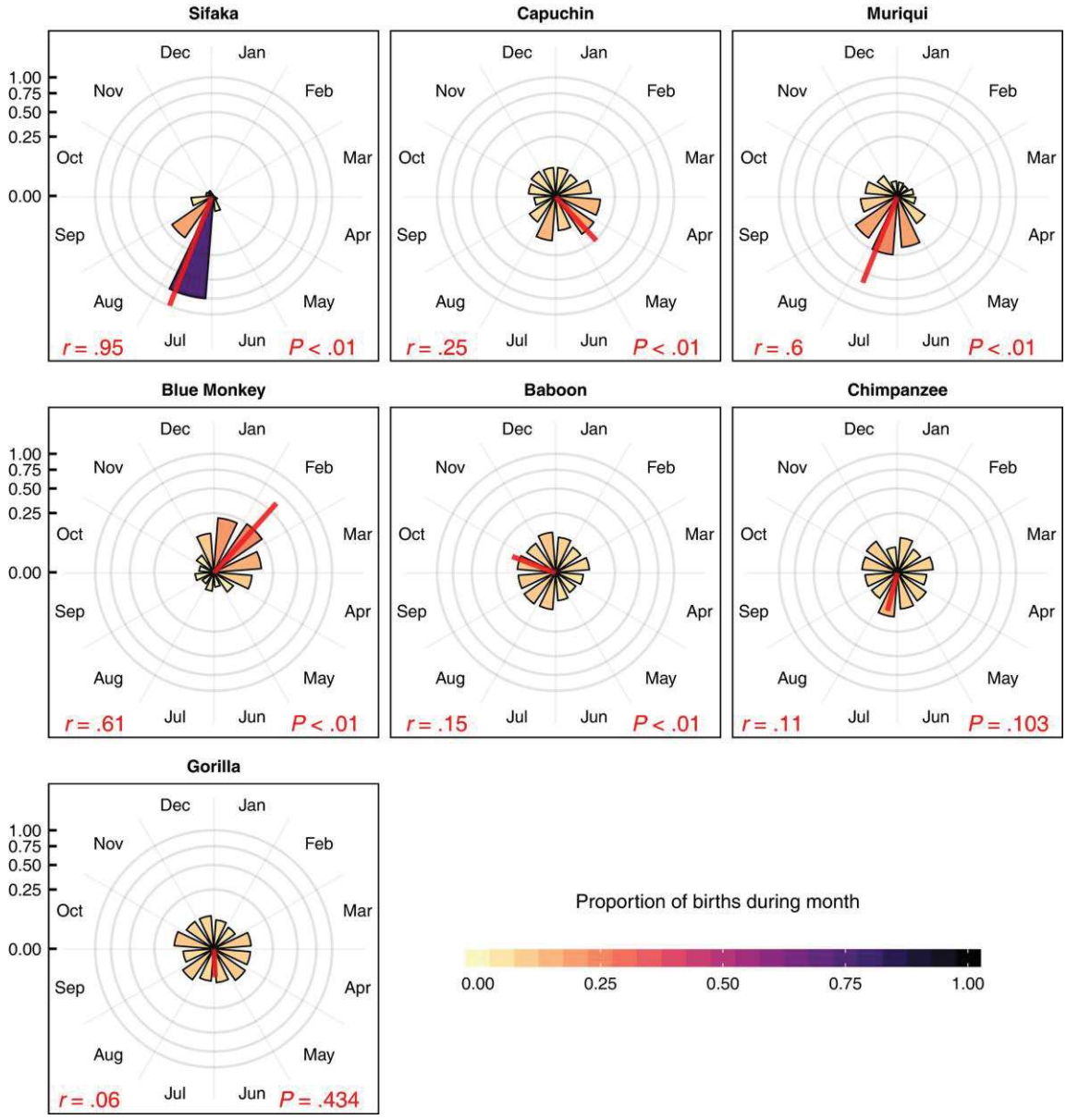


Figure 1: Diversity of reproductive seasonality among primates (from Campos et al., 2017)

Circular histograms showing the proportion of births in each month in each study population. Note that the radial axis is square-root-transformed to exaggerate differences in the lower end of the scale. The red lines show the mean vector (r). The orientation of r indicates the average birth day of year in the population, and the length of r indicates how unevenly observations are spread across the annual cycle. When r=1, all births occur on the same day of year, and when r=0, the births are evenly distributed across the 12 months. The pvalues show the results of a Rayleigh test for non-uniformity of circular data. Significant results (P<0.05) indicate seasonal reproduction. Note that 'baboon' refers here to the Amboseli yellow baboon (*Papio cynocephalus*) population.

The position of each species in this continuum can be refined. A species is indeed considered as a seasonal breeder if there is a season with births, followed by a season without any births at all; whereas a species is considered as a non-seasonal breeder when births occur year-round, i.e. in the absence of interruptions in the occurrence of births. However, a non-seasonal species can still show a seasonal pattern of births if these are not randomly distributed through time, showing one or more birth peak(s) or birth valley(s). Therefore, in order to better describe this diversity in primates, Lancaster & Lee categorized the intensity of reproductive seasonality into 3 main levels (Lancaster & Lee, 1965): high level of reproductive seasonality when more than 66% of births occurred in a 3 months-time period (months with the highest frequencies of births), low level when less than 33% occurred in the same 3 months-time period, and moderate level otherwise.

In addition to the variation in intensity of reproductive seasonality, high variation in reproductive phenology is observed, depending on the species and the environment considered. Indeed, for example, while most ungulates from temperate and arctic regions give birth in spring, in April-July (Owen-Smith & Ogutu, 2013; Post, 2003; Rutberg, 1987); most ungulates from tropical regions have more flexible parturition dates, often occurring more frequently at the onset of the rainy season (Owen-Smith & Ogutu, 2013), i.e. in September-December in the Serengeti National Park, Tanzania (Sinclair, Mduma, & Arcese, 2000).

Reproductive seasonality is highly diverse in vertebrates, both in terms of intensity and phenology. Studies investigating the evolution of reproductive seasonality focused almost exclusively on the role of environmental seasonality as a potential determinant of reproductive seasonality, and mainly in temperate and arctic regions. Here I review how and why environmental seasonality impacts reproductive seasonality, both at the ultimate and proximal level, with a particular interest towards tropical regions.

II°) Environmental seasonality as both ultimate and proximate cause of reproductive seasonality

Within-year periodic variations (of period one year) of climatic factors, such as rainfall, temperature, wind, humidity, ocean currents, are responsible for the existence of seasons. The fluctuations of some of these climatic parameters affect plant phenology, which in turn impact resource availability for a given species in a given environment (Boyce, 1979). Various factors, representative of the environmental seasonality perceived by a given animal species, can affect reproductive seasonality: photoperiod, temperature, rainfall, and more importantly, resource availability. Those factors can be either the ultimate or the proximate cause of reproductive seasonality (or both). I here briefly review the main findings about the impact of environmental seasonality, focusing on vertebrates, and providing some examples from primates in particular.

A- Ultimate causes of reproductive seasonality

Ultimate causation explain traits in term of evolutionary forces acting on them, i.e. here ultimate causes describe how natural selection acted in favour of organisms breeding seasonally in certain environment. Baker (1938) first proposed that the ultimate cause of the seasonal breeding patterns of some birds and mammals might be seasonal variation in food abundance (Baker, 1938). Numerous studies later confirmed that food availability is the major ultimate cause of seasonal reproduction in all mammals (Bronson, 2009). The main reason is that reproduction is a costly period in terms of energy for females, as they need to provide sufficient amounts of energy for their own maintenance but also to insure the survival and growth of their offspring. This is particularly true for mammals during pregnancy and lactation (P. C. Lee, 1996). For example, an adult female shrew (*Blarina brevicada*) weighting 11g must find enough food to produce enough milk to sustain 55 g of offspring in late-lactation on average

(Pearson, 1944). Consequently, shrews can reproduce only during the most energetically favourable season of the year, determined by food availability (and ambient temperature as well). The costs of motherhood are also marked in primates, exhibiting longer lactation periods relatively to their size (Jones, 2011). For example, in humans, the extra cost of pregnancy is about equal to a Mars® chocolate bar a day on average over the 9 months of pregnancy, while during lactation, women must consume around three Mars® chocolate bars a day on average from births to weaning (corresponding to 1.3 times the energy required when not pregnant nor lactating) (P. C. Lee, 1996). Therefore, adjusting reproductive timing according to the annual food peak is adaptive, and reproductive phenology is under strong selective pressure (see IV for consequences of reproductive seasonality on reproductive success).

As a result, several lines of empirical evidences confirm that the more intense the seasonal variations of food availability are (i.e. the level of within-year variation), the more intense the reproductive seasonality should be (i.e. the more concentrated births should be). First, numerous studies on mammals showed that the intensity of reproductive seasonality increased with latitude, which is a proxy of the level of within-year fluctuation of resource availability, both at the species (Di Bitetti & Janson, 2000; Rutberg, 1987) and population level (McNutt, Groom, & Woodroffe, 2019). For example, Rutberg (1987) studied 27 ruminant species living world-wide and found that higher latitudes are associated with shorter breeding seasons (Figure 2). Similar relationship has been found in recent comparative studies among captive species of carnivores (Heldstab et al., 2018) and primates (Heldstab et al., 2020), with higher latitude of origin associated with shorter birth peak breadth. Second, a species' diet also affects its reproductive seasonality, as animals eating mostly seasonal resources (like fruits or arthropods) may be under stronger selective pressure to breed seasonally than those eating less seasonal ones (leaves) (Heldstab et al., 2020; C. Janson & Verdolin, 2005). As such, a

comparative study on New World monkeys found that frugivores and insectivores are more seasonal that folivores (Di Bitetti & Janson, 2000).

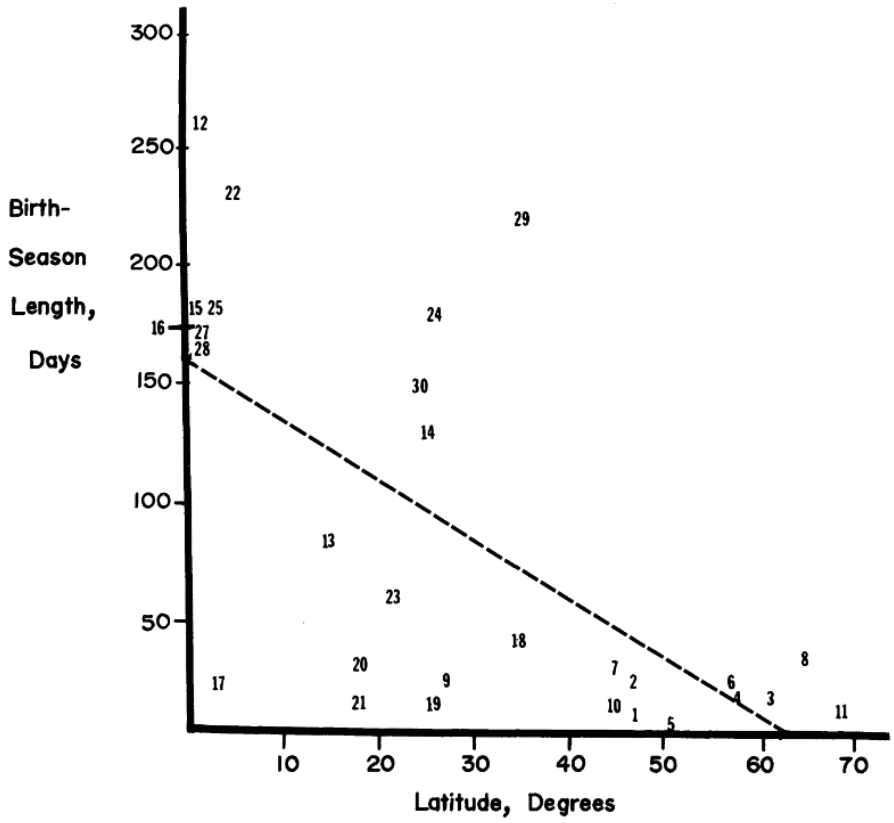


Figure 2: Relationship between birth season length (defined as the number of consecutive days during which 80% of the year's birth occur) among 27 species of wild ruminants, and latitude (north or south) (from Rutberg, 1987).

Each number refers to a ruminant species (see Table 1 from Rutberg, 1987 for correspondences). Note that at high latitudes (>40°), all ruminant species are seasonal breeders, with short birth seasons. In contrast, at low latitudes (<30°), ruminant species exhibit higher reproductive flexibility, with either short or long birth seasons.

In terms of reproductive phenology, all seasonal breeders time a critical stage of their reproduction with the seasonal food peak. In most birds living at high latitudes, reproductive phenology has evolved so that chick-rearing and offspring fledging periods are synchronized with the peak of food availability (Deviche & Davies, 2013). In mammals, lactation is the

costliest period for females in terms of energy expenditure, and hence species tend to time lactation with the seasonal food peak (Bronson, 2009). However, the pattern of reproductive timing is by no means universal, and females can employ widely divergent resource allocation tactics in support of reproductive effort (Brockman & van Schaik, 2005a; Bronson, 2009; Jönsson, 1997), and match either early-lactation, weaning, fledging or laying dates with the seasonal food peak. For example, in New World monkeys, births concentrate before the peak in food availability, allowing either peak lactation (for smaller-sized species) or weaning (for larger-sized species, i.e. capuchins) to take place before the start of the lean season (Di Bitetti & Janson, 2000).

While seasonal fluctuations in resource available affect maternal energy intake, seasonal fluctuations in temperature also affect her energy balance, but through her energy expenditure. Therefore, temperature seasonality can also act as an evolutionary determinant of reproductive seasonality. This is especially true in high latitude and/or high altitude, for warm-blood species (mammals and birds) given their thermoregulation constraints. New-born mammals are smaller than adults, and thus have a higher surface/volume ratio, making them more sensitive to cold temperatures. Consequently, most mammals living in high latitude give birth during the warmest seasons, i.e. in spring and summer (Bronson, 2009; Charmantier & Gienapp, 2014; Rutberg, 1987). Moreover, even for a relatively large mammal living in a warm tropical habitat, the African wild dog (*Lycaon pictus*), temperatures have been shown to be the evolutionary explanation for their seasonal reproduction: wild dogs breed year-round at lower latitudes, while those living at latitudes >7° time their reproductive events so that their pup-rearing periods coincide with the coolest weeks of the year (McNutt et al., 2019). However, most primates live and breed in relatively warm environments (but see the exceptions of geladas *Theropithecus gelada*: Tinsley Johnson, Snyder-Mackler, Lu, Bergman, & Beehner, 2018 ; and Japanese macaques *Macaca fuscata*: Garcia, Huffman, Shimizu, & Speakman, 2011;

Takahashi, 2002), and consequently, temperature is rarely a constraint for them and thus cannot explain the adaptiveness of reproductive seasonality in this taxa.

Lastly, in addition to temperature and food availability seasonal variation, rainfall may be another environmental factor explaining why some species breed seasonally in a few cases. For instance, in an Australian snake, *Tropidonophis mairii*, females nest most intensely soon after the cessation of monsoonal rains when soils are moist enough to sustain optimal embryogenesis (wetter nests produce larger hatchlings that are more likely to survive) but are unlikely to become waterlogged (which is lethal to eggs), explaining why reproductive seasonality is associated with rainfall in this species (Brown & Shine, 2006).

However, in most cases, rainfall by itself, like temperatures, is not the ultimate explanation of reproductive phenology, but is still a crucial parameter to explain both proximally and ultimately reproductive seasonality as within-year variation of temperatures and/or rainfall drive plant phenology and more broadly seasonal variation in resource availability (Boyce, 1979; Carnegie, Fedigan, & Melin, 2011; Van Schaik, Terborgh, & Wright, 1993). Therefore, numerous studies investigating the relationship between reproductive timings and rainfall (in tropical habitats) or temperature (in temperate habitats) seasonal variation used the latter as a proxies of food availability or environment productivity.

B- Proximate causes of reproductive seasonality

The proximate causes of reproductive seasonality correspond to the environmental cues used by females to adjust their reproductive timing depending on the season. The two non-exclusive main proximal causes of reproductive seasonality revealed in the literature are: (i) mother condition (with a threshold) , and (ii) photoperiod (Clauss, Zerbe, Bingaman Lackey, Codron, & Müller, 2020). In mammals, both factors can affect the onset of the period of sexual

receptivity, via several physiological mechanisms (see Paul, Zucker, & Schwartz, 2008 for more details).

i. Condition-threshold

On top of acting as the ultimate cause, within-year variation in resource availability can also act as a proximate cause of reproductive seasonality. It has been argued that regardless of the environmental conditions, if maternal body condition is below a certain threshold, conception (or maintenance of pregnancy) may be prevented. This condition-controlled threshold maximises mothers' condition and survival, as a pre-requisite to raise successfully future offspring. For example, the onset of oestrus in wild Japanese macaques is strongly affected by food quality, occurring almost exclusively during the best fruiting conditions (Takahashi, 2002).

Differences of reproductive seasonality between captive and wild populations of the same species can also be informative about the proximal mechanisms responsible for reproductive timings. Indeed, given the assumption of unlimited resource provision in zoos, more species should show seasonal reproduction in natural habitats (where resource availability may be periodically/seasonally limited so that body condition is below the reproduction-controlling threshold) than in zoos. As such, for example, long-tailed macaques (*Macaca fascicularis*) breed non-seasonally in captivity, where food supply remains constant (Smith, 1984), while they are seasonal breeders in the wild (van Schaik & van Noordwijk, 1985). More broadly, the percentage of primate species (30%) switching their reproductive seasonality (from more to less seasonal in resp. wild *versus* captive individuals) is higher than ruminant and carnivore species, suggesting that primates depend more often on internal triggers for reproduction than other mammalian groups (possibly because a higher proportion of primate species live in tropical environment where a reliable photoperiod cue may not be available) (Heldstab et al.,

2020). Whether and how mammals differ in the magnitudes of body condition threshold controlling reproduction remain unknown.

ii. Photoperiod

Day length, the most accurate natural predictor of annual phase (given its absence of between-year variation), is the predominant environmental cue used by animals to onset their reproduction (Bradshaw & Holzapfel, 2007; Bronson, 2009; Paul et al., 2008). Photoperiodism is the ability of organisms to assess and use the variation in daylight length as an anticipatory cue in order to adjust their life histories, including their reproduction, with their seasonal environment (Bradshaw & Holzapfel, 2007). Various studies on numerous taxa showed the use of a photoperiodic *zeitgeber* ('signal' or 'cue' in German) to adjust reproductive events (Bradshaw & Holzapfel, 2007; Bronson, 2009). For example, in mammals, the reproduction of a marsupial, *Antechinus stuartii*, is inhibited by an artificial long-day photoperiod (Scott, 1986). A photoperiodic stimulus can also be a factor increasing conception probabilities in some African ungulate species, but not in all of them (Spinage, 1973). For primates more precisely, the duration of daily photoperiod has been experimentally proven to be the a proximate factor that triggers reproduction in various lemur species (Rasmussen, 1985). Species with photoperiod-controlled reproduction may maintain the same intensity of reproductive seasonality when kept in captivity at latitudes with detectable photoperiodic cues: this has been shown in various mammal groups, such as ruminants (Zerbe et al., 2012), carnivores (Heldstab et al., 2018) and primates (Heldstab et al., 2020).

However, in tropical regions (where most primate species live), especially close to the equator below latitudes of 11.75° (Clauss et al., 2020; Heldstab et al., 2020), seasonal differences in photoperiod are slight, and are therefore deemed unsuitable as seasonal clues.

iii. Other environmental cues

Other triggers than photoperiod and condition threshold can mechanistically cause the onset of reproduction, but they are species specific, and scarcer (Paul et al., 2008). One of them is temperature. Global warming provides a natural experiment to investigate the effect of temperature on reproductive phenology, emphasizing the importance of annual variations in temperature as a proximate cause of reproductive seasonality, in particular in birds. Indeed, warmer winters cause many bird (review in: Charmantier & Gienapp, 2014), but also some mammal species (in red deers, *Cervus elaphus*: Bonnet et al., 2019), to advance their reproductive phenology in temperate climates. More precisely, the effect of temperature on bird reproductive physiology and phenology has been well described and quantified. For example, wild song sparrow *(Melospiza melodia)* males from a high altitude population, which are exposed to cold temperatures in spring, have later testes development in their annual reproductive cycle than males from a coastal population, which are exposed to milder temperatures (Perfito, Meddle, Tramontin, Sharp, & Wingfield, 2005). Other studies on great tits (*Parus major)* show that increased spring temperatures lead to advanced laying dates (M E Visser, Van Noordwijk, Tinbergen, & Lessells, 1998). It is also likely, even if there is a lack of evidence, that humidity can trigger reproduction in some species, when food availability is tightly linked to rainfall variation (Paul et al., 2008).

C- Potential mismatches between ultimate and proximate causes

Climate change modulates the timing of environmental seasonality (Easterling et al., 2000), and thus potentially causes mismatches between ultimate and proximal causes of reproductive seasonality. Seasonal breeding birds have been well studied to investigate the impact of a change in the timing of seasonal food peak caused by global warming on reproductive phenology (Charmantier & Gienapp, 2014), and in particular one species: great tits, *Parus*

major (see Figure 3). Great tits present a strong breeding seasonality, typical for passerines living in temperate regions, as they synchronize egg hatching with the narrow seasonal peak of caterpillars that constitute their major food source (Blondel, Dervieux, Maistre, & Perret, 1991; Charmantier et al., 2008; Hinks et al., 2015; Marcel E. Visser, Holleman, & Gienapp, 2006). Because of climate change, this tight food peak occurs earlier each year, and some populations have been too slow to adjust their reproductive timing accordingly (Reed, Jenouvrier, & Visser, 2013; Marcel E. Visser et al., 2006). This mismatch between reproductive and environmental phenology has strong fitness consequences and translates into a lower number of fledglings (Reed et al., 2013). Studies on mammalian seasonal breeders, though less common, have also highlighted similar reproductive phenology shifts in response to climate change, in reindeers (Post & Forchhammer, 2008), roe deers (Bonnet et al., 2019), bighorn sheep (Renaud, Pigeon, Festa-Bianchet, & Pelletier, 2019) and marmots (Inouye, Barr, Armitage, & Inouye, 2000). In addition, mismatches between vegetation phenology and birth timings have been found in a roe deer population, slowing its demography (Plard, Gaillard, Coulson, Hewison, Delorme, Warnant, & Bonenfant, 2014).

The ability of one species to exhibit flexible phenology in response to a changing environment depends on the proximate cue used to adjust its reproduction on the short-term: organisms using photoperiodic cues are necessarily less flexible than others (Brockman & van Schaik, 2005a; Clauss et al., 2020). These phenological mismatches are likely to change in the long-term, as it has been shown that seasonal timing, and in particular laying date, is heritable (Charmantier & Gienapp, 2014; Evans, Postma, & Sheldon, 2020; Postma, 2014). This is more generally a pre-requisite for the evolution of reproductive timings, as a non-heritable trait could not evolve by definition.

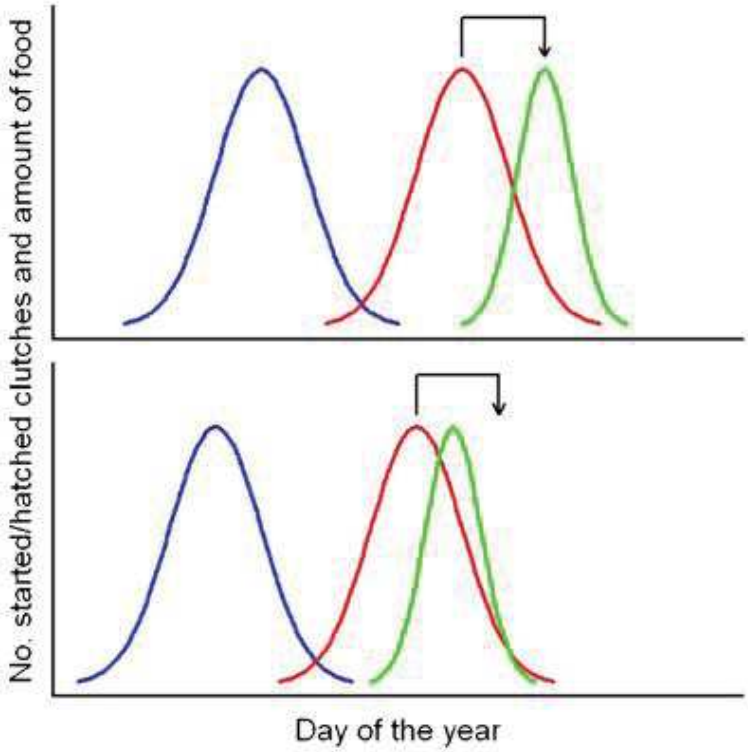


Figure 3: Schematic illustration of phenological 'mismatch' taking great tits and their caterpillar food supply as example (from Charmantier & Gienapp, 2014)

"The curves indicate frequency distributions of first eggs of clutches (blue), hatching (red) and caterpillar abundance (green). Food demands of great tit chicks are highest approximately 9 days after hatching indicated by the black arrow. In the upper panel describing a scenario before climate change, the birds' breeding is well-timed to the caterpillars, and chick demand coincides with caterpillar abundance. In the lower panel, the timing of both the great tits and the caterpillars has advanced–due to climate change–but the caterpillars have advanced twice as fast. This now has led to a 'mismatch' between the chick demands and the phenology of the caterpillars." (from Charmantier & Gienapp, 2014)

As emphasized in this section, the literature mainly focused on environmental seasonality as the primary driver of variations in intensity of reproductive seasonality and in phenology. However, environmental seasonality on its own cannot explain why sympatric species with similar diet exhibit divergent reproductive strategies. A striking example comes from the Serengeti National Park, where the African topi (*Damaliscus korrigum)* is a highly seasonal breeder while the phylogenetically related hartebeest (*Alcelaphus buselaphus)* is not, and where several seasonal breeding herbivores vary widely in the timing and length of their breeding season (Sinclair et al., 2000). In addition, numerous non-seasonal breeding species live in highly seasonal environments (Campos et al., 2017), and, in contrast, many seasonal breeding species live in equatorial environments, with low climatic within-year variations (Hau, 2001; Wikelski, Hau, & Wingfield, 2000). Therefore, other factors must interplay with the intensity of environmental seasonality to account for the evolution of such a wide diversity of reproductive seasonality observed among mammals.

III°) Other ultimate determinants of reproductive seasonality

A- The unpredictability of the environment

Regardless of the intensity of within-year variation, the level of between-year variation in resource availability can affect reproductive seasonality. On top of its impact on reproductive phenology in ecological time (through recent climate change, as shown in IIC), the level of unpredictability of the environment can also affect the intensity of reproductive seasonality in evolutionary time. The more unpredictable the environment, the less seasonal should be the reproduction. Indeed, in theory, in environments where within-year (seasonal) variations are negligible compared to between-year (non-seasonal) variations, individuals adjusting their

reproductive events with relative flexibility might be favoured (van Schaik & van Noordwijk, 1985), in order to exploit the unpredictable food peak opportunistically. This flexibility may cause the absence of reproductive seasonality. The empirical evidence supporting this hypothesis remains scarce (Loe et al., 2005). However, it has recently been shown in 38 ungulate species that the intensity of seasonal breeding decreases with environmental unpredictability, i.e., inter-annual variation in the timing and strength of environmental seasonality (English et al. 2012).

Most studies focusing on the evolution of reproductive seasonality only considered the intensity of within-year variation of resource availability as a driver of reproductive seasonality, while the intensity of between-year variation is likely to similarly affect it, especially in primates living in tropical regions where rainfall unpredictability can be important (Dunham, Erhart, & Wright, 2011; Feng, Porporato, & Rodriguez-Iturbe, 2013). Indeed, in addition to modify the timing of the seasonal food, climate change can also affect its magnitude, as it increases the amplitude, nature and frequencies of El Niño events for example. In primates, the birth season of two ateline primates (*Lagothrix lagotricha* and *Brachyteles hypoxanthus*) tends to be delayed during El Niño event years (Wiederholt & Post, 2011). However, the effects of climate change and environmental unpredictability on primates' reproduction, and more precisely on reproductive timing, are overlooked (Korstjens & Hillyer, 2016). More broadly, most studies focused on the impact of environment unpredictability by studying how climate change affects reproductive phenology in ecological times. In contrast, few studies have focused on the effect of environmental unpredictability on the intensity of reproductive seasonality in evolutionary times.

B- Species life history and physiology

Both external and internal factors, such as life history traits and physiology inherent to a group of species, can interact and affect species adaptation, including the evolution of reproductive seasonality. Such internal factors must also be considered to account for phylogenetic inertia. Species features, such as their ability to store energy, size and life history traits might influence the evolution of different reproductive strategies affecting reproductive seasonality.

The use of energy storage has received a particular interest to understand the diversity of animal strategies in resource allocation during reproduction. The concept of 'income' versus 'capital' breeding was first proposed to depict the role of energy storage in breeding strategies, for seasonal breeding bird species (Drent & Daan, 1980). Income breeders only rely on current energy available in their environment for their reproduction, while capital breeders can use stored (capital) energy to use it later for reproduction (Stearns, 1992). The income-capital dichotomy has been later re-used for mammals (Jönsson, 1997), in particular in pinnipeds (Boyd, 2000), and applied to the case of primates, with an influential paper by Brockman and van Schaik, 2005 (Brockman & van Schaik, 2005a). The goal of the income-capital continuum model proposed in this study is to predict reproductive seasonality in primates, considering their size, life history, energy allocation during reproduction, diet and environment (Brockman & van Schaik, 2005a). Briefly, in one end of this continuum, capital breeders can store energy for later reproduction, and thus tend to be large primate species (>3kg), with long interbirth intervals (> 1 year), sensitive to endogen factors (condition threshold) to onset their reproductive events (Brockman & van Schaik, 2005a). In seasonal environments, their conception should happen only after a food peak, i.e. when the mothers are in good condition with a rising energy balance. At the other end of this continuum, income breeders only use current energy available in their environment for reproduction, and thus tend to be small primates (<1kg), with short interbirth intervals (< 1 year) only sensitive to exogenous factors

(such as photoperiod or temperature) to onset their reproductive events. The reproductive phases should be timed in order to maximize maternal condition with births occurring before or during the peak of food with birth (Brockman & van Schaik, 2005a; Carnegie et al., 2011). Conceptions are therefore not linked with female condition nor seasonal variation in food availability, and might occur during the harsh season. This strategy should be promoted in highly seasonal and predictable environments (Brockman & van Schaik, 2005a; Jönsson, 1997), as income breeders may not pay a number of energetic and demographic costs for their stored resource (as capital breeders may).

However, this model has often been criticized, for several reasons (Lewis & Kappeler, 2005; Stephens, Boyd, Mcnamara, & Houston, 2009). The interpretations of the terms 'income' and 'capital' breeders have diversified, with a lack of rigidity in the definition, leading to subjectivity. For example, what constitutes the reproductive period is inconsistent (onset of reproduction, pregnancy or lactation) (Lewis & Kappeler, 2005; Stephens et al., 2009), and as such, depending on the definition of reproductive period used, Verreaux's sifakas (*Propithecus verreauxi*) can be considered either capital or income breeders (Lewis & Kappeler, 2005). In addition, associations between proximal causes of the onset of reproduction and the ability to store energy are made in this model without any empirical evidence (Clauss et al., 2020). Lastly, several empirical studies do not support assumptions made by this model. A striking example comes from the reproductive phenology of lemur species living in the same environment in Ranomafana National Park, Madagascar. Despite a huge diversity of size, ability to store energy, energy allocation during reproduction, and the fact that they all share the same environment, 13 lemur species all time weaning with their seasonal peak of resource available (Wright, 1999). The capital-income framework fails to explain this particular reproductive phenology, and its predictive power on reproductive phenology is thus limited. Despite these

limitations, the ability to store energy is a crucial adaptation to environmental variation, likely to decrease reproductive seasonality.

Independently of energy allocation strategies, body mass, or more precisely life history parameters correlated with body mass, may affect birth seasonality in mammals (Bronson, 1989; C. Janson & Verdolin, 2005). Very small species (<0.3kg) generally have short reproductive cycles (from conception to weaning/infant independency) and may be able to fit multiples cycles per year. Because these cycles are usually separated by two to six months, they would be produced with relatively low birth seasonality. Species of moderate size (0.3–3 kg) can have an entire cycle only once a year. Therefore, if they rely on seasonal resources, they should show highly seasonal birth patterns. Larger-bodied species (>3 kg) are, in general, not able to fit a reproductive cycle into a single year. In addition, because their energetic expenditure is spread out over a longer period and may necessarily include a period of relative food scarcity, the exact timing of births may be less important to fitness (Bronson 1989). Consequently, larger species are expected to be less seasonal than moderate size ones. However this assumption is controversial. First, it has been argued that it is not the length of interbirth interval per see that matters for reproductive seasonality, but whether IBI are multiple of one year or not. Second, no negative relationship between species size (female body mass) and intensity of reproductive seasonality had been found in primates (Heldstab et al., 2020; Plavcan, van Schaik, & McGraw, 2005), carnivores (Heldstab et al., 2018) or ruminants (Zerbe et al., 2012). Third, empirical studies on large mammals found that they can exhibit some degree of reproductive seasonality and that birth timing can have fitness consequences. For instance, giraffes (*Giraffa camelopardalis*), despite their large size, are sensitive to environmental variation, with higher infant mortality when giving birth in certain seasons: reproductive seasonality can thus be adaptive among large and long-lived mammals (D. E. Lee, Bond, & Bolger, 2017). Even elephant, the largest terrestrial mammal, relies on a combination of

photoperiodic cues and body condition threshold to breed (Hufenus et al., 2018), and therefore exhibit some degree of reproductive seasonality (Mumby, Courtiol, Mar, & Lummaa, 2013).

While controlled for body size, other life history traits have been found to affect the intensity of reproductive seasonality. Indeed, shorter gestation periods have been linked with a higher degree of reproductive seasonality in several mammal taxa (Heldstab et al., 2018, 2020; Zerbe et al., 2012). Gestation length and litter size for example are known to be affected by environmental seasonality: shorter gestation and larger litter size are encountered in cold dry seasonal habitats (Tökölyi, Schmidt, & Barta, 2014). Shorter gestation period could thus have favoured the evolution of reproductive seasonality for some mammal species, allowing them to squeeze their entire reproductive cycle into a single year, so that they do not miss reproductive opportunities in the next year (Kiltie, 1984). However, the causal relationship remains unclear, as shorter gestation periods (or more generally faster life-history paces) may have evolved as an adaptation to strong reproductive seasonality. For example, in Carnivora, it has been shown that reproductive seasonality have led to life-history adaptations, through either a shortening of gestation length or a lengthening of the gestation period using delayed implantation (Heldstab et al., 2018).

Numerous additional overlooked life history traits may affect reproductive seasonality. For example, during hibernation or torpor, metabolic rates may preclude any reproductive activity (mating, conception) during this season and thus tighten conception peak breadth. The influence of species life history traits and physiology on reproductive seasonality remains overlooked and neglected in comparison to environmental factors.

C- Social factors: reproductive synchrony versus seasonality

Reproductive synchrony was defined by Ims (1990) as the 'phenomenon caused by biological interactions to produce a tighter clustering of reproductive events than environmental seasonality alone'. Birth synchrony refers to the close overlap of reproductive events within a group (or between females that live in close spatial proximity of each other) but not between groups. The distinction between birth synchrony and seasonality is often not clearly stated, with some confusion between the two terms (Linnell & Andersen, 1998; Maillard & Fournier, 2004; Ogutu, Piepho, Dublin, Bhola, & Reid, 2010). It is important to distinguish seasonality from synchrony (C. Janson & Verdolin, 2005): a species can have a high birth synchrony if females tend to all give birth in a same period, but without necessarily breeding seasonally if the reproductive period does not always occur at the same season (for instance in a theoretical case where all births occur in February in a first year, and in July the following year). Very strong birth seasonality will inevitably produce high birth synchrony, but birth synchrony can occur without birth seasonality. Social stimuli (on top of external environmental cues or condition-threshold) have been shown to onset reproduction in several mammal species (Bronson, 1989), including primates (Herndon, 1983). Such stimuli are responsible, from a mechanistic perspective, of reproductive synchrony in certain species.

Several social factors might affect reproductive seasonality at the ultimate-level by modulating reproductive synchrony. For instance, the 'hider' and 'follower ' dichotomy, indicating if a species' new-born respectively hide or follow its mother during its first weeks or months of life, has been shown to affect ungulate reproductive seasonality in African ruminants (Sinclair et al., 2000; Zerbe et al., 2012). Indeed, follower species benefit from a high degree of birth synchrony in order to satiate predators (Canu et al., 2015; Ims, 1990; Rutberg, 1987; Sinclair et al., 2000) whereas hider species benefit from asynchronous births in order to avoid predation (Ims, 1990; Sinclair et al., 2000; Zerbe et al., 2012). Indeed, the latter species may

not be sufficiently abundant to satiate predators, and synchrony would result in greater rather than lesser predation (Ims, 1990; Sinclair et al., 2000). It has also been shown, comparing within-group and between-group variation in birth dates, that squirrel monkeys (*Saimiri oesterdi*) from Corcovado National Park (Costa Rica) exhibit strong birth synchrony, presumably as a strategy to reduce predation risk on neonates (Boinski, 1987). Birth synchrony can also minimize inter-litter competition. In lions (*Panthera leo*), cub litters of similar age (with interbirth interval shorter than 2 months) have lower mortality rates than cub litters of dissimilar age, as older cubs can prevent younger cubs from gaining access to nipples (Packer & Pusey, 1983). Birth synchrony can also have fitness benefits on offspring survival and growth, as it may allow female allo-parenting or even allo-nursing. For example, in rats (*Rattus norvegicus*), mothers giving birth simultaneously (i.e. less than 15 days apart) are likely to nurse communally, which is beneficial for their newborn pups, as they are heavier at weaning than other pups from litters that were not nursed communally (Mennella, Blumberg, Mcciintock, & Moltz, 1990).

Sociality could also lead to a staggering or reproductive events (e.g births) and lead to lower synchrony than random. This reproductive asynchrony may aim at decreasing reproductive competition over access to mates, paternal care or food (Beehner & Lu, 2013; Ims, 1990). Indeed, fitness costs of synchronous births have been reported in some polygynous birds where females compete over paternal care for their chicks (Slagsvold & Lifjeldt, 1994; Yasukawa, Leanza, & King, 1993; Yasukawa, Mcclure, Boley, & Zanocco, 1990). In addition, oestrus asynchrony has been reported in both seasonal breeding ring-tailed lemurs (*Lemur catta)* (Pereira, 1990) and non-seasonal breeding chimpanzees (*Pan troglodytes)* (Matsumoto-Oda et al., 2007), allowing females to choose their mate by decreasing female competition over mating opportunities. Female-female competition over reproduction (for different types of resources, such as food, mates, alloparental care, paternal care or burrows) has similarly been

documented in several mammal societies (Stockley & Bro-Jørgensen, 2011), such as meerkats (*Suricata suricatta*) (T. H. Clutton-Brock et al., 2001) and banded mongooses (*Mungos mungo*) (Nichols, Bell, Hodge, & Cant, 2012). More precisely, two social factors in mongooses' large social groups (Gilchrist, 2006) produce birth synchrony rather than asynchrony (64% of females giving birth the exact same night), namely infanticide risk (higher for early-born pups) and between-litter competition (higher for late-born pups) (Hodge, Bell, & Cant, 2011). In numerous primate species, individuals live in large social groups, where female-female competition over food or mates can be intense (Beehner & Lu, 2013; T. Clutton-Brock & Huchard, 2013; Stockley & Bro-Jørgensen, 2011). However, the consequences of female-female competition on reproductive phenology and the intensity of reproductive seasonality in primates remain unknown. This gap in the literature may come from the fact that disentangling synchrony from seasonality is often difficult, especially in seasonal breeders, as it requires the monitoring of multiple groups from the same population. Understanding the evolution of reproductive seasonality now requires an integrative approach investigating the interplay between environmental variation, life history and sociality.

D- Individual-level variation in reproductive phenology

Most studies explored the adaptiveness of reproductive seasonality at the population level, looking at its demographic consequences. However, reproductive phenology, like birth timing for example, is an individual trait, and individual variation in reproductive phenology may affect the intensity of reproductive seasonality and reproductive synchrony at the population level.

Female condition might be influenced by various individual traits regardless of environmental seasonality, such as female age, parity of reproductive history; which may in

turn affect reproductive phenology, especially for species with condition-dependent conception probabilities. For example, in roe deers (*Capreolus capreolus*), female quality (a combination of female longevity and median adult body mass and cohort) largely determines parturition dates: females of higher quality (heavy and long-lived) give birth on average earlier than lower quality ones (Plard, Gaillard, Coulson, Hewison, Delorme, Warnant, Nilsen, et al., 2014). Similarly, very young and very old female moose (*Alces alces*) ovulate later than prime-aged females each year in a Norwegian population (Garel et al., 2009).

The effects of environmental seasonality (both within and between-year variation) and of various social factors (female-female competition, mate choice, etc) can be modulated by individual factors. This is especially true in gregarious species where individuals regularly associate with one another (or even in solitary species with regular interactions between familiar individuals), as females often establish dominant-subordinate relationships (Kaufmann, 1983; Rowell, 1974). In such social systems, dominant females may have privileged access to resources, and higher feeding efficiency (T. Clutton-Brock & Huchard, 2013; Stockley & Bro-Jørgensen, 2011). These advantages of dominant females in terms of energy intake are often associated with higher reproductive success, as dominant females often exhibit earlier age at first reproduction, shorter interbirth intervals, higher offspring survival and increased longevity (Clutton-Brock and Huchard 2013; Stockley and Bro-Jørgensen 2011). However, the consequences of rank-related variation in foraging success and life history traits on reproductive seasonality have not been assessed. Only one study in our knowledge, on reindeers (*Rangifer tarandus*), showed that dominant females tend to have earlier parturition dates, presumably because of their better condition (Holand et al., 2004). In theory, dominant females can better buffer environmental seasonality, and therefore lead to lower reproductive seasonality at the population level. In terms of social competition, dominant females may actively suppress the reproduction of subordinate females, as in banded mongooses (Nelson-Flower et al., 2013),

meerkats (Tim H. Clutton-Brock, Hodge, Flower, Spong, & Young, 2010), marmots (*Marmota marmota*) (Hackländer, Möstl, & Arnold, 2003), African topis (Bro-Jørgensen, 2007) and numerous primate species (Baniel, Cowlishaw, & Huchard, 2018; Beehner & Lu, 2013; Wasser & Barash, 1983). When such competition occurs over access to a sexual or social partner, such as in the case for mating competition or competition over paternal or alloparental care, it may lead to lower intensity of reproductive seasonality (as reproductive events of females competing for a mate would be staggered).

Few studies have attempted to identify whether reproductive phenology may vary across individuals, and which individual determinants are responsible of such variation in mammals. Investigating individual variation in phenology strategies can hence contribute to shed light on variation in the intensity and timing of breeding seasonality across populations.

IV°) Fitness consequences of reproductive seasonality

Reproductive seasonality can strongly affect individual fitness and is therefore under strong selection (Figure 4). By definition, seasonal breeding is costly as it introduces gaps between reproductive cycles, at least when those cycles are not integer years (Brockman & van Schaik, 2005b). Reproductive seasonality is thus a trade-off between benefits to breed seasonally or in synchrony and costs of waiting this optimal breeding season (Brockman & van Schaik, 2005b). I here describe the nature of such benefits and costs in terms of reproductive success, for both mothers and offspring.

Birth timing affects offspring development and survival in many species (Lindström, 1999). Indeed, it has been shown in various seasonal breeding species that infants born outside the optimal seasonal birth peak are more likely to die before being independent. For instance, among seasonal breeders living at high latitudes, earlier birth dates often cause higher survival

likelihood, like in the red deer (*Cervus elaphus*) (T H Clutton-Brock, Major, Albon, & Guinness, 1987), roe deer (Andersen & Linnell, 1997), Alaskan moose (Keech et al., 2000), Scottish red grouse (*Lagopus lagopus scotica*) (Fletcher, Howarth, Kirby, Dunn, & Smith, 2013), mountain goat (Côté & Festa-Bianchet, 2001), bighorn sheep (*Ovis canadensis*) (Festa-Bianchet, 1988) ; and can also be associated with faster growth rates, like in the bighorn sheep (Feder, Martin, Festa-Bianchet, Bérubé, & Jorgenson, 2008). Birth timing can also have affect infant mortality among non-seasonal breeders, even if such studies are scarcer. For instance, giraffes (*Giraffa camelopardalis*) from Tarangire National Park, Tanzania (D. E. Lee et al., 2017), or even humans (*Homo sapiens*) from Burkina Faso (Kynast-Wolf, Hammer, Müller, Kouyaté, & Becher, 2006), have different survival outcomes before weaning depending on their birth dates. Reproductive synchrony can also have fitness consequences. For example, caribou calves born during the peak of births in the Denali National Park (Alaska) are less likely to be killed by predators than those born before or after the peak (Adams, Singer, & Dale, 1995), and a similar pattern is found in hares (*Lepus americanus*) (O'Donoghue & Boutin, 1995). On the opposite, reproductive synchrony can have negative impact on offspring fitness. For example, in blue tits (*Parus caeruleus*), the mean body mass of fledglings is lower for synchronous than for asynchronous broods (Slagsvold, Amundsen, & Dale, 1995), presumably because of reduced sibling rivalry in asynchronous broods. A similar result was found thanks to an experimental design in a social lizard (*Egernia whitii*), albeit the increased mass was associated with increased mortality for asynchronous offspring in this case (While & Wapstra, 2008).

In addition, birth timing may have long-term consequences on an individual fitness, as it can modulate its longevity, its age at first reproduction, its reproductive pace, or its post-independence survival, and so affect population life history traits (Lummaa & Tremblay, 2003) (Figure 4). In humans, it has been shown that birth seasons affect longevity, with people born in Autumn having longer lifespan in Austria, Denmark and Australia (Doblhammer & Vaupel,

2001). Birth dates also affect survival into adulthood (Kynast-Wolf et al., 2006; Moore et al., 1997). The permanent effect of malnutrition on the development of the immune system during fetal growth (and possibly early-life infections that can also have long-term consequences on immune function) seems the more likely hypothesis to explain the influence of pre-natal and/or early post-natal events on lifetime longevity (Moore et al., 1997).

In addition to affect the fitness of offspring, reproductive seasonality (and more specifically birth timing) also affects other maternal fitness components. For instance, earlier clutches are larger in red grouses (*Lagopus lagopus scotica*) from the Scottish Highlands (Fletcher et al., 2013). Similarly, for numerous species of squirrels (all seasonal breeders), late born litters are composed of fewer young than earlier ones (Huber, Hoffmann, Millesi, Dittami, & Arnold Huber, 2001). However, for species producing one offspring per litter (or clutch), litter (or clutch) size is no longer relevant, and the quantity of offspring produced has often been neglected. For example, numerous studies showed, for seasonal breeding primates (producing one offspring per litter), that giving birth outside the birth peak is usually costly for offspring survival (Dietz, Baker, & Miglioretti, 1994; SmaII & Glenn Smith, 1986; Tecot, 2010; Thompson & McCabe, 2013), but none of these studies looked at the effects of birth timing on mother's reproductive pace (i.e. interbirth interval). It is relevant as mothers and offspring evolutionary interests are not closely aligned (Trivers, 1972), because a mother must strategically allocate her energy towards her current but also future offspring. It is obviously in a mother's interest to ensure her current offspring survival, but it is also in her interest to maximise her reproductive pace (Bateson, 1994), in order to increase her own reproductive success. For example, mammalian females can either minimize their own reproductive costs by matching the annual food peak with periods of high energetic demands such as peak-lactation (Emery Thompson, 2013; P. C. Lee, 1996), or alternatively minimize offspring mortality by matching the food peak with periods of offspring vulnerability, such as late weaning (Brockman

& van Schaik, 2005a; C. H. Janson & Verdolin, 2005; van Schaik & van Noordwijk, 1985), but cannot usually do both simultaneously. Most studies were done on short-lived species, such as rodents and passerines, which can squeeze their entire cycles in the same optimal season. However, in long-lived species like most primates, mid-lactation and late-weaning can be separated by several months (van Schaik & van Noordwijk, 1985), leading to maternal trade-off over the optimal birth timing. Such a trade-off has never been tested empirically. Considering the consequences of birth timing on numerous indicators of the fitness of both offspring and mother can thus bring new perspectives in our understanding of the evolution of reproductive seasonality.

To sum up, various factors may interplay to affect reproductive seasonality, at the individual level, but also at the group and population one (Figure 4). While the proximate mechanisms responsible for the onset of reproduction are well characterized (Clauss et al., 2020; Paul et al., 2008), the ultimate causes of such timing are relatively poorly understood (Bronson, 2009; Williams et al., 2017). Indeed, the majority of studies investigating the evolutionary determinants of reproductive seasonality have been performed on either captive species (Heldstab et al., 2020; Zerbe et al., 2012), where various factors likely to affect reproductive seasonality in the wild cannot be considered, or species living at high latitudes (Bronson, 2009), where the intensity of within-year environmental variations is extreme, and likely to obscure other determinants. Nonetheless, most biodiversity hotspots are located in the tropics (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000), and less is known about the evolutionary determinants of reproductive seasonality in the tropics. Furthermore, these habitats are highly affected by climate change, with a dramatic increase of extreme climatic events like cyclones or droughts (Dai, 2013; Easterling et al., 2000).

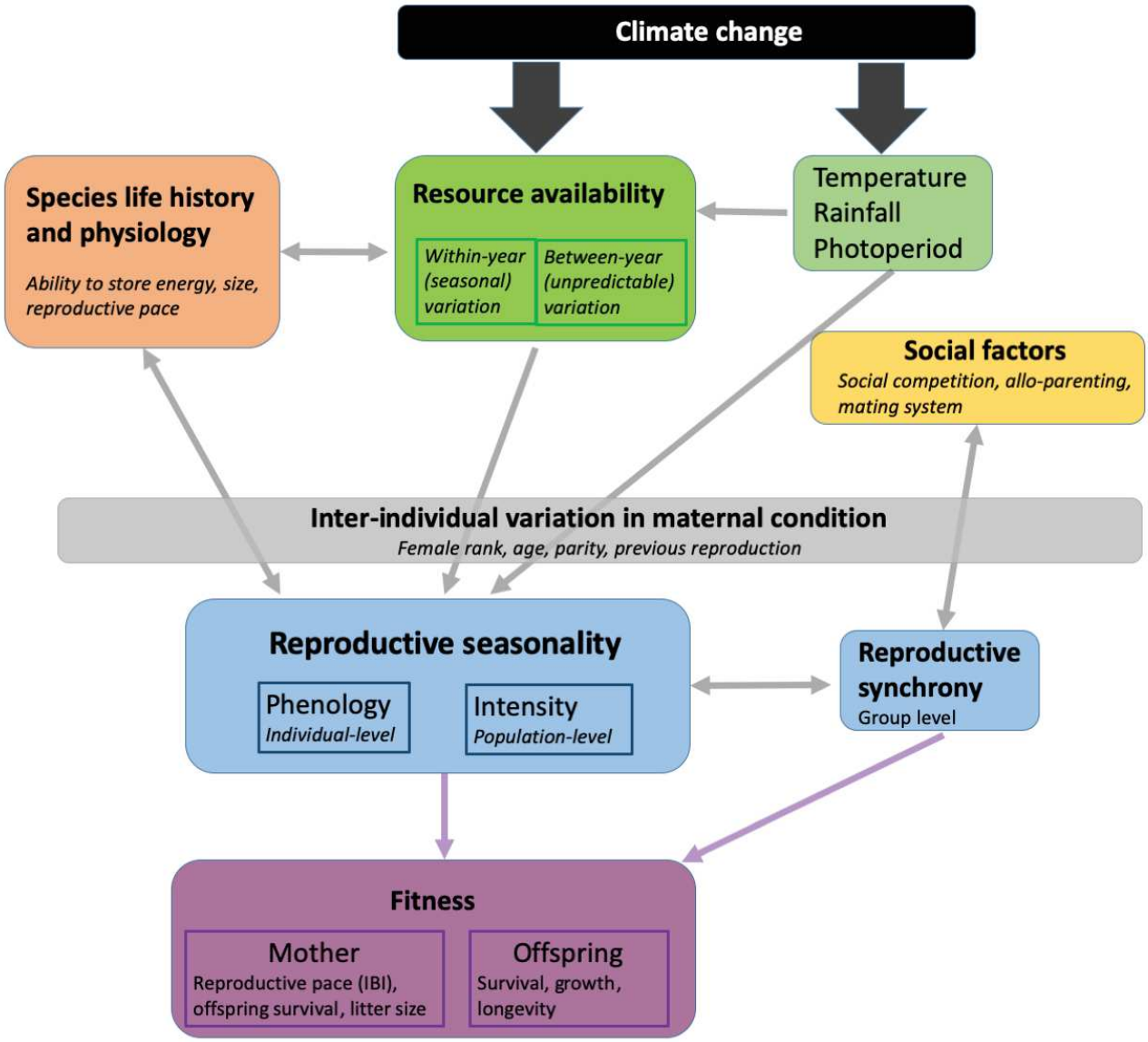


Figure 4: Summary of the main determinants and fitness consequences of reproductive seasonality.

Grey arrows represent causation effects, both proximate and ultimate. Large dark grey arrows show the unilateral large effects of climate change on climatic factors and resource availability. The violet arrows exhibit the fitness consequences of reproductive seasonality and synchrony.

Our knowledge on the consequences of climate change on reproductive seasonality in tropical species, and *in fine* on their demography, is limited. Primates are mostly long-lived

species occurring in tropical environments. Most primates are expected to struggle to adapt to rapid climate change because of their limited dispersal ability, long generation times, and restricted ranges (Dunham et al., 2011; Korstjens & Hillyer, 2016; Zhang et al., 2019). However, how primates adjust their reproductive timing in response to climate change and land use shifts is not well predicted (Korstjens & Hillyer, 2016). A better knowledge of the ecology and evolution of reproductive seasonality can help us to understand the effects of climate change on primates' reproduction and demography. It can further contribute to establish more efficient conservation strategies for these species. Indeed, quantifying the main factors affecting reproductive seasonality (and ultimately, demography) can help us (i) to identify which component(s) of climate change (change in the timing or magnitude of the food peak, increased temperatures, etc.) has the greatest impact on reproduction, (ii) to better predict how primate species would respond to future climate change, and (iii) to identify the species and populations that are most vulnerable to extinctions, in order to target conservation efforts. For example, some primate populations might be more sensitive than others towards environmental unpredictability, depending on their diet, environmental cues to onset reproduction, reproductive rates and ability to store energy. Disentangling the importance of these various factors on reproductive performances and timing thus appears crucial to establish efficient conservation plans, although obviously, other factors than climate change, such as deforestation, land use change, poaching and illegal bushmeat trade threaten often more strongly primate populations than climate change in the short-term.

V°) Study aims

This study is an attempt to investigate the main evolutionary determinants and fitness consequences of variations in reproductive seasonality in two wild primate populations, chacma

baboons (*Papio ursinus*) from Namibia, and mandrills (*Mandrillus sphinx*) from Gabon. We use a combination of long-term life history, morphometric, ecological and behavioural data to investigate individual variation in reproductive phenology and synchrony, and its consequences on various components of fitness for both mothers and infants. Focusing on these populations will contribute to fill some gaps in the literature, as they are two long-lived social species living at low latitudes. Moreover, they exhibit an intriguing reproductive seasonality: chacma baboons breed year-round while living in a highly seasonal environment (Swedell, 2011); and, in contrast, mandrills breed seasonally while living in an equatorial environment, presumably relatively stable across the annual cycle (Hongo, Nakashima, Akomo-Okoue, & Mindonga-Nguelet, 2016).

In the first chapter, I describe in details our two study populations and sites, highlighting their similarities and differences, and how they are relevant for our questions. I also provide a brief overview of the main methods and data used thereafter.

In the second chapter, I develop a field method to assess baboon infant age with accuracy, which is particularly valuable for later chapters considering the birth timing of the Tsaobis baboons. More precisely, I investigate whether the colour transition of infant baboons, from black fur and pink skin to grey fur and skin, can provide an accurate methodology to estimate the age of baboons with unknown birth dates. In addition, colour transition is used as a proxy of developmental pace to test the influence of birth timing on infant morphological development.

The third chapter investigates the reproductive phenology of the Tsaobis baboons. After a characterization of reproductive and environmental seasonality, we test the adaptive significance of birth timing using two fitness indicators, namely mother interbirth interval durations and infant survival before weaning. We also investigate if individual traits mediate

variation in reproductive phenology, and whether maternal care strategies and behavioural manifestations of mother-offspring conflict vary with birth timing.

The fourth chapter asks why chacma baboons are non-seasonal breeders. We test three non-exclusive hypotheses to explain the evolution of non-seasonal breeding in chacma baboons: the absence of reproductive seasonality results from (H1) a population-level selective pressure, where the unpredictability of rainfall and resources selects for year-round reproduction; (H2) a group-level selective pressure, where females within a group stagger their reproductive events to minimize reproductive synchrony in response to reproductive competition over access to paternal care; and (H3) a selective pressure occurring at the individual level, where females of different social ranks are affected differently by seasonal environmental variations, and/or by the reproduction of other female group mates, leading to a loss of reproductive synchrony at the group level and to the absence of reproductive seasonality at the population level.

The fifth chapter attempts to understand why mandrills are seasonal breeders while they are an equatorial, long-lived and social species. We test three non-exclusive hypotheses to answer this question: reproductive seasonality emerged in response to (H1) environmental seasonality affecting mandrills' food availability, (H2) benefits on both females' current and future reproduction and (H3) individual rank-related variation in reproductive phenology.

Lastly, the sixth chapter presents preliminary results on a comparative analysis quantifying inter- and intra-specific variation in the intensity of reproductive seasonality in the genus *Papio* and relatives. We further investigate the main climatic determinants of such variation, and which phase of the female reproductive cycle is matched with the annual peak of food availability.

Chapter 1

Study sites and populations



A- Study species

Mandrills (*Mandrillus sphinx*) and chacma baboons (*Papio ursinus*) are both Old World monkeys, and relatively close relatives in the primate phylogeny (Zinner, Arnold, & Roos, 2009). They are both part of the *Cercopithecidae* family, along with other baboons, macaques, colobines, mangabeys, drills and geladas (Kingdon et al., 2012). Although they were previously thought to be 'forest baboons', mandrills and drills (the two species of the Mandrillus genus) are actually more closely related to *Cercocebus*, i.e. mangabeys than to *Papio* (Kingdon et al., 2012) (Figure 5).

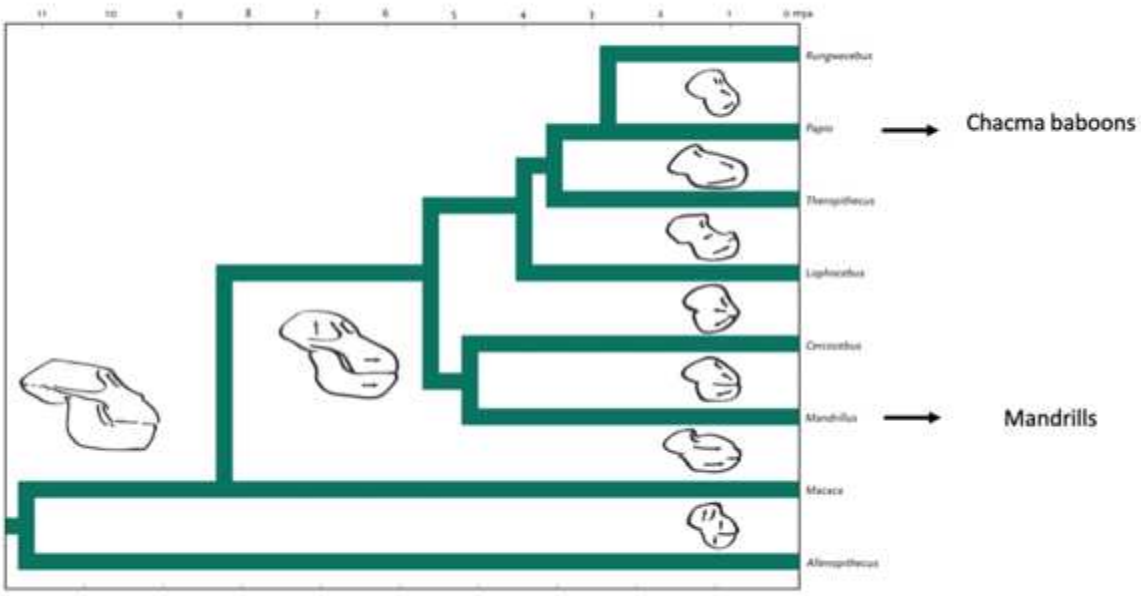


Figure 5: Phylogenetic trees of the *Cercopthecidae* family (from Kingdon et al., 2012)



Figure 6: In case you wonder how mandrills and chacma baboons look like (© pictures: Projet Mandrillus & me)

Panel A: an adult male mandrill, exhibiting bright colours, with style. Panel B: an adult male chacma baboon exhibiting his large canines, with style. Panel C: An adult female mandrill walking, with style. Panel D: An adult female chacma baboon, sitting on her sexual swellings, with style. Both species are highly dimorphic.

Both species have numerous similarities in terms of ecology and social organization (Swedell, 2011). First, they have similar sizes, with striking sexual dimorphism. Chacma baboon is the heaviest baboon species. Male mandrills and chacma baboons both weigh on average 30kg (Figure 6). In contrast, female mandrills weigh only 10 kg on average, versus 15kg for female chacma baboons (Figure 6). Second, both species are mainly terrestrial, with comparable feeding ecology. They are omnivorous and adaptable foragers, including into their diet a combination of fruits, flowers, seeds, pods, leaves, tubers, gum, insects, small preys, and even possibly human-produces food (garbage, crops) (Swedell, 2011). Mandrills exhibit however a clear frugivorous tendency (Nsi Akoue et al., 2017). Baboons are known for their

ability to use fall-back food available in their environment during the harsh season (S. A. Altmann, 2009). Third, they have some similarities in their social systems. They both live in multi-male multi-female groups, ranging from 20 to up to 800 individuals (Abernethy, White, & Wickings, 2002) for mandrills (group size is lower in baboons, and highly variable between populations) (Swedell, 2011). Females are philopatric, i.e. remain in their natal group throughout their life, whereas males often disperse at sexual maturity, in neighbouring groups (although the fate/social environment of adult male mandrills outside the mating season remain unclear). Both sexes have linear dominance hierarchies within groups. In adult males, hierarchy is unstable, established and maintained through fights and aggressions, sometimes lethal (Bulger, 1993). In contrast, in adult females, hierarchy is inherited from the mother (they form matrilines) and relatively stable (Bulger, 1993). In females, social rank strongly affects foraging success (Barton & Whiten, 1993) and reproductive performances: dominant females have shorter interbirth intervals than subordinate ones in both species (Cheney et al., 2004; Setchell, Lee, Wickings, & Dixson, 2002). Fourth, they have similar mating systems. Both species are polygynandrous, and male intra-sexual competition for access to females is intense, resulting in important reproductive skew, with the alpha male monopolizing up to 70% of reproduction (M. Charpentier et al., 2005; E. Huchard, Alvergne, et al., 2010).

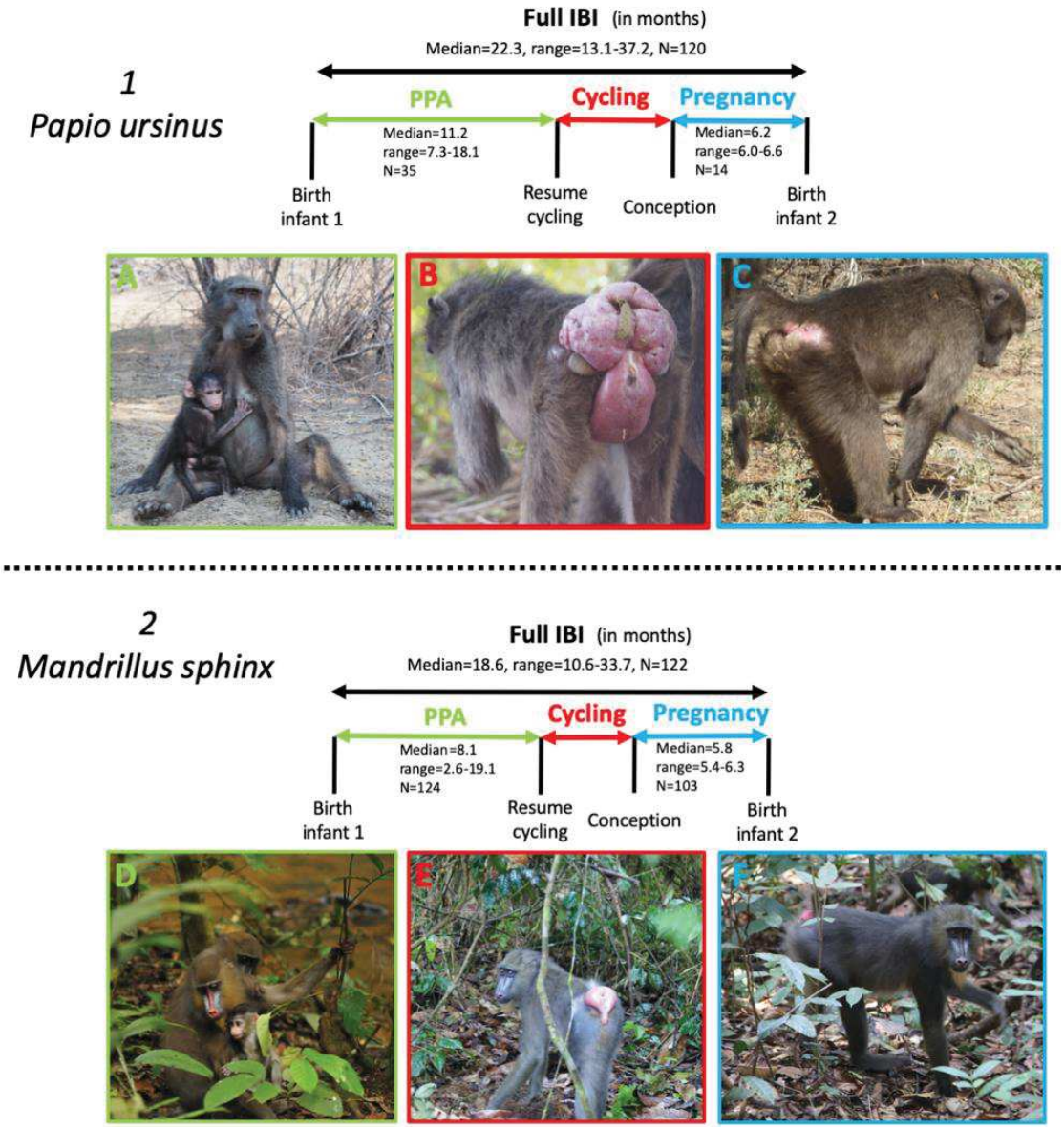


Figure 7: Reproductive states, durations of interbirth intervals (IBIs) and its different phases, for Tsaobis' chacma baboon (Panel 1) and Lékédi's mandrill (Panel 2) adult females (© pictures: Projet Mandrillus & me)

The Panel 1 shows the three phases, and associated durations, of an interbirth interval, in months, computed from data from the Tsaobis Baboon Project, from 2005 to 2019 (N indicates the number of events). The Panel 2 shows the three phases, and associated durations, of an interbirth interval, in months, computed from our data from the Mandrillus Project, from 2012 to 2020 (N indicates the number of events). These values include only IBIs between two livebirths in which the first offspring lived for at least 18 months (for baboons) or 6 months (for mandrills). Following a birth, the female can be seen nursing / lactating, with a dependent infant around her (pictures A and D). During this period after parturition, a female is not cycling or sexually receptive, and this phase is called postpartum amenorrhea (PPA), and is shown in green. Then, a female resumes cycling (indicated in red), as shown by conspicuous sexual swellings (pictures B and E). After conception, during pregnancy (indicated in blue), the paracallosal skin of females turns bright red (panel C) around 3 weeks post-conception in chacma baboons, while a distinctive pink and swollen tumescence is observed a few month after impregnation in mandrills (picture F).

However, mandrills and chacma baboons also have interesting differences in their ecology, social system and life history traits. Even if their gestation lengths (175 days on average for mandrills (Setchell et al., 2002), *versus* 190 days for chacma baboons (Barrett, Henzi, & Lycett, 2006)) and sizes are similar, mandrills tend to have faster life history traits than baboons: they have earlier age at first reproduction, shorter post-partum amenorrhea, and shorter interbirth interval on average (Figure 7). In addition, mandrill societies are characterized by a seasonal influx of males in the group at the onset of the mating season (Abernethy et al., 2002; Hongo et al., 2016). In other words, most adult males do not stay within the group outside of the mating season, in contrast to chacma baboons. This seasonal arrival is likely to be caused by their strong breeding seasonality, and might have strong impact on mandrills' socio-ecology. They also live in different environments: chacma baboons live in the southern part of Africa (Figure 8), in savannah and arid regions, while mandrills live in central Africa, in equatorial forests. Finally, baboons are one of the most-studied primate genus, given their shared evolutionary history with humans (J. Fischer et al., 2019). On the contrary, mandrills remain an enigmatic primate, with most of our knowledge coming from a semi-captive population (Setchell, 2016). For instance, infanticide by males that recently acquire the alpha status have been reported in baboons, and is a major cause of infant mortality in various chacma baboon populations (Ryne A Palombit, 2003), but its occurrence in mandrills remain unknown. Consequently, males and lactating females often form tight social bonds in baboon promiscuous societies, called 'friendships', whose main function seems to be infant protection against infanticide (Lemasson, Palombit, & Jubin, 2008; Moscovice et al., 2010; R. A. Palombit, Cheney, & Seyfarth, 2001; Ryne A Palombit, Seyfarth, & Cheney, 1997). Father-infant associations are also observed later in infant life, during the gradual process of weaning, i.e. up to 2 years. It has been shown to promote access to better quality food during weaning (Huchard

et al. 2012) and to limit aggression from conspecifics (Lemasson et al., 2008; Nguyen, Van Horn, Alberts, & Altmann, 2009), therefore increasing infant developmental pace (M. J. E. Charpentier, Van Horn, Altmann, & Alberts, 2008). However, we do not know if similar forms of paternal care occur in mandrills.

Papio and Mandrillus represent interesting genera, as they live in a wide variety of habitats across Africa (see the wide distribution of the single genus *Papio*: Figure 8) and display a large diversity of social systems and ecological adaptations. In particular, a wide array of strengths of reproductive seasonality can be observed. On the one hand, most baboon populations are non-seasonal breeders (Bercovitch & Harding, 1993; Swedell, 2011), while in the other hand, mandrills (Setchell et al., 2002) and kinda baboons (*Papio kindae*) (Petersdorf, Weyher, Kamilar, Dubuc, & Higham, 2019) are seasonal breeders. In addition, important variation in reproductive seasonality is observed within species, as chacma baboons from the Drakensberg mountains (Lycett, Weingrill, & Henzi, 1999) tend to give birth more seasonally that those from De Hoop Reserve (Barrett et al., 2006) for example. It raises the question of why such a wide diversity in reproductive schedules within and between species among these close relatives.

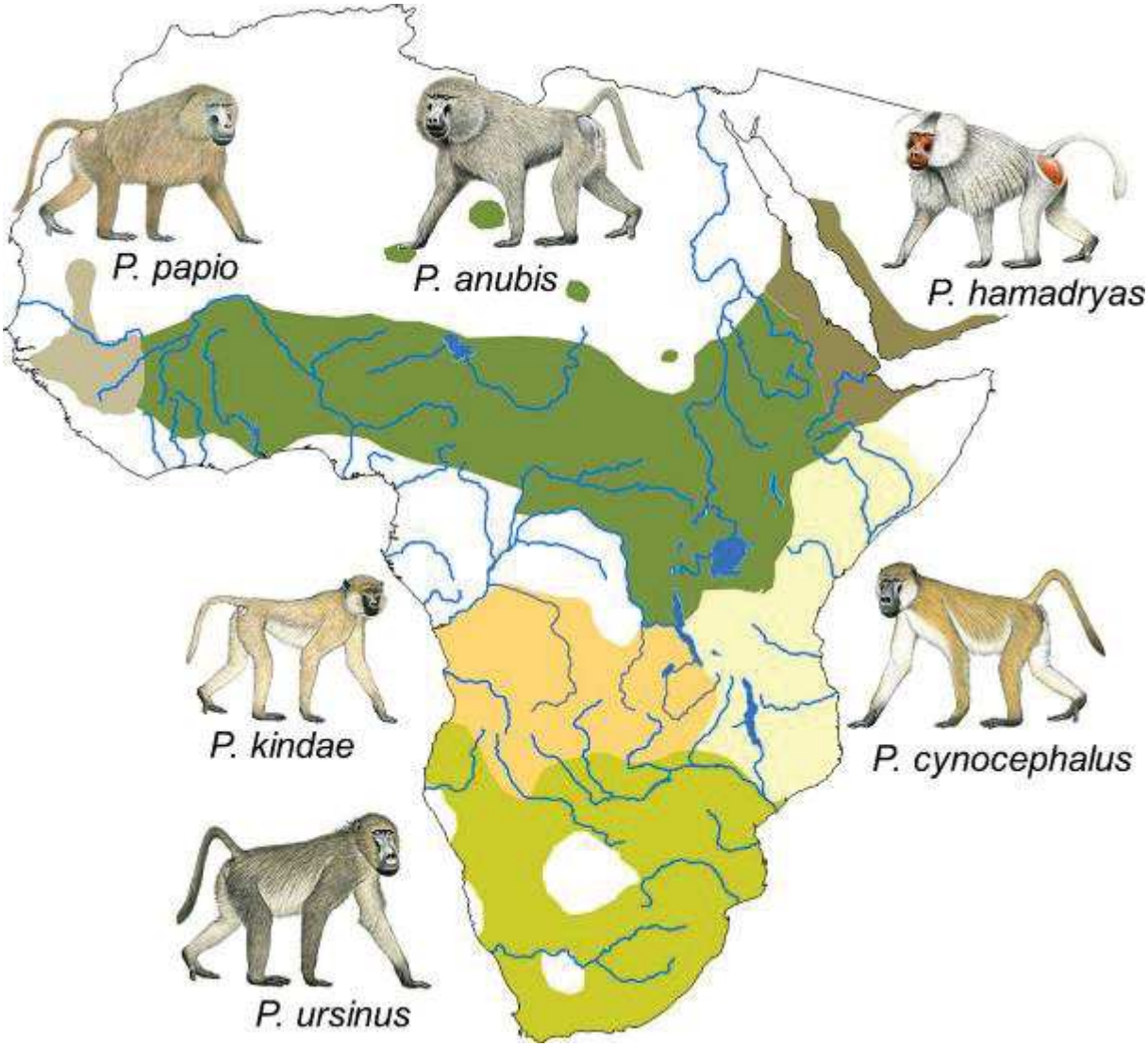


Figure 8: Geographical distribution of the 6 *Papio* species (from Fischer et al., 2017)

B- Study sites and populations

The study population of chacma baboons live at **Tsaobis Nature Park** (22°23S, 15°44'50E) in the Erongo Region in central Namibia (Figure 9). Tsaobis is a semi-desertic area, characterized by steep rocky hills descending towards alluvial plains, and crossed by the ephemeral Swakop riverbed (Cowlishaw & Davies, 1997). The Swakop river is dry most of the time, but still supports permanent patches of trees and bushes where baboons are foraging year-round, which

are *Acacia Erioloba*, *Acacia tortilis*, *Faidherbia albida*, *Prosopis glandulosa* and *Salvadora persica*. It is a strongly seasonal environment: the short perennial bushes and annual grasses present on the hills surrounding the Swakop riverbed respond quickly to the austral summer rains, which usually fall between December and April, and then dies back during the dry winter months (Cowlishaw & Davies, 1997). The annual rainfall is sparse and highly variable between years.

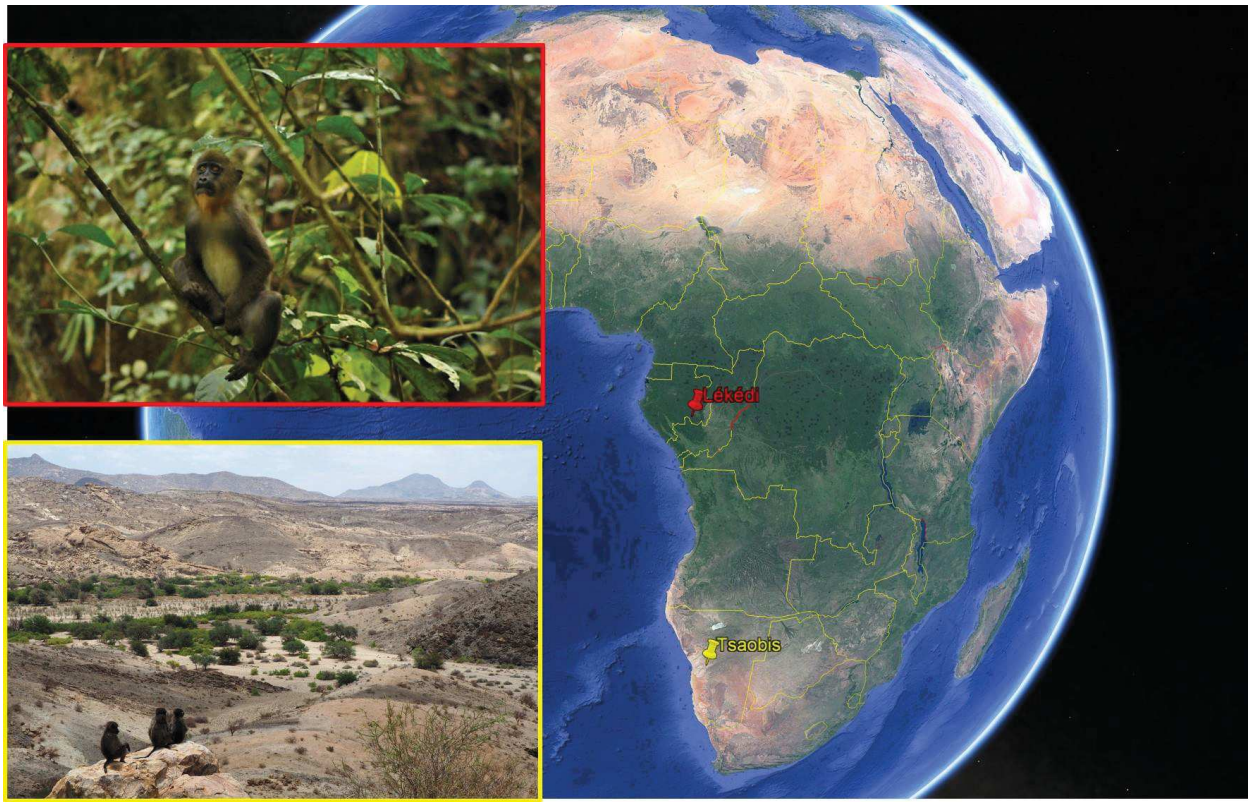


Figure 9: Geographical location of the two primate populations studied in this thesis (© pictures: Projet Mandrillus & me)

The study population of mandrills live in a private park, the **Lékédi Park**, and its vicinity, situated 7 km northwest away from the closest village Bakoumba, in Southern Gabon (Figure 9). The park and surroundings are composed of a mosaic of evergreen forests, grasslands and savannahs (Brockmeyer et al., 2015). The environment is usually characterized by four distinct ecological seasons, driven by variations in rainfall, with a long-rainy season

(February-May), a long-dry season (June-September), a short-rainy season (October-November) and a short-dry season (December-January) (M. J. Charpentier et al., 2018; Nsi Akoue et al., 2017).

Both populations are fully habituated and followed on a daily basis for the past years in the framework of two long-term projects: the Tsaobis Baboon Project and the Mandrillus Project.

The **Tsaobis Baboon Project** was created in 2000 by Guy Cowlishaw, and is now co-directed by Alecia J. Carter, Guy Cowlishaw and Elise Huchard. Since 2005, two troops of chacma baboons, named 'J' and 'L' (which have been habituated respectively in 2000 and 2005), are followed on a daily basis by field observers, though not year round. Each year, a field season is conducted, mainly during winter (between May and October), for a variable number of days (mean=137, range: 57-240). In addition, since 2016, another troop, named 'M', the result of a fission of 'J' troop, is also followed (Figure 10 to see the home ranges of these three troops). Troop size between 2005 and 2019 ranged from 50 to 65 individuals for J and from 20 to 80 individuals for L, while M troop was composed from 20 to 24 individuals between 2016 and 2019. Individuals of J and L troop have been captured in 2005, 2006, 2012, 2016, 2018 and 2019, and the ones of M troop in 2017 (see Huchard et al., 2010 for more details about trapping procedures). Briefly, baboons are provisioned with maize cobs during the baiting process for trapping, but not otherwise. During captures, all non-marked individuals are marked with a unique ear notches combination, making baboons recognizable, including infants and juveniles (see also Figure 11 for more details about the trapping process). Among other samples, tissue and hair samples are taken for genetic and isotopic purposes. Dental examination also allowed the estimation of individual's age using tooth eruption and molar wear patterns (Kahumbu & Eley, 1991) at the onset of the project.

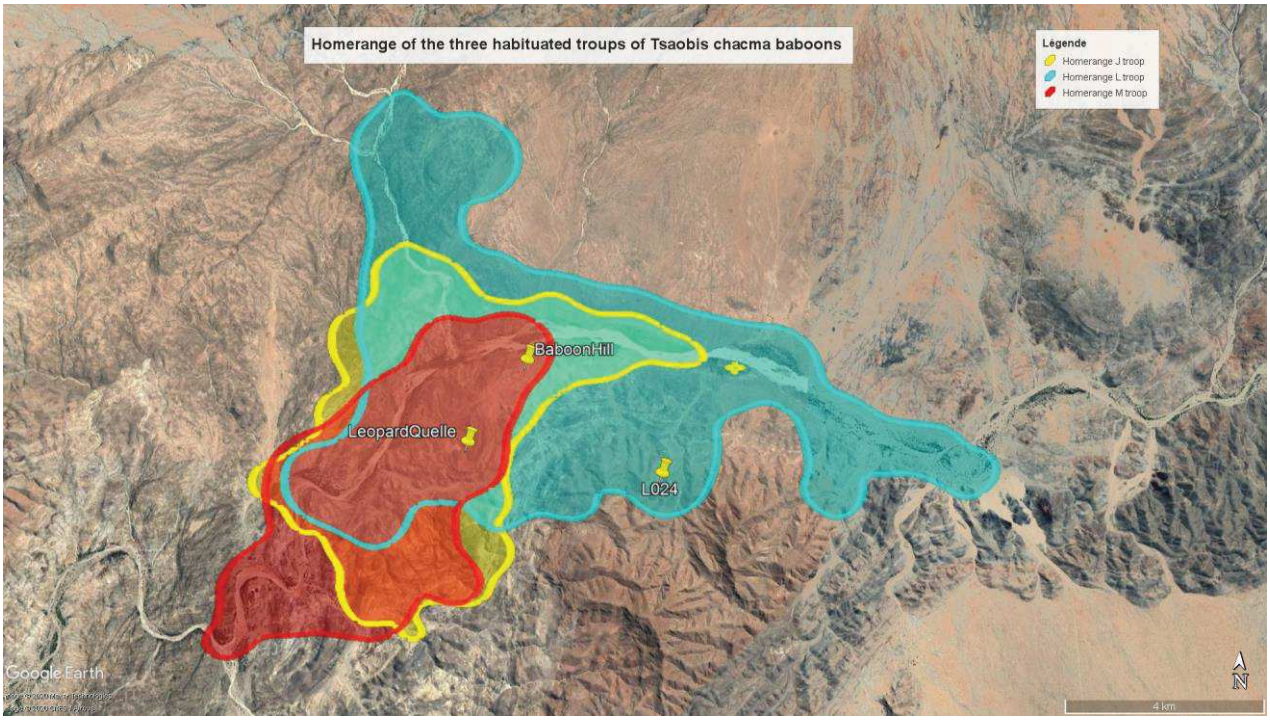


Figure 10: home ranges of the three habituated troops of Tsaobis baboons in 2005-2019

Based on the daily 30-min GPS locations from 2005-2019, we computed 100% isopleth home ranges for each group using kernel density estimates with the adehabitatHR package ('kernelUD' function) (Calenge, 2006). L troop home range is indicated in blue, J troop in yellow and M troop in red

The **Mandrillus Project** was created in 2012 and is directed by Marie Charpentier. This population originated from 65 captive individuals initially housed at the CIRMF (Centre International de Recherche Médicale de Franceville, Gabon), who had been released in the park on two occasions, in 2002 and 2006 (Peignot et al., 2008). During the first months after release, they were provisioned with bananas and monkey chow in low quantities to supplement their natural diet. This food supplementation decreased rapidly (from 2008 to 2012) and stopped in April 2012. It is now the only habituated wild non-provisioned mandrill population. The group was composed of around 120 individuals in June 2012. Group size increases gradually since then, and in early 2020, this study group was composed of approx. 250 individuals, including

ca. 180 of them being individually-recognized. Individuals are recognized thanks to distinctive marks and features: for instance face wrinkles are in particular useful to distinguish adult females. Captures on several individuals have been realized since 2012 each year, in order to fit them with GPS collars for radio-tracking, but also to collect a variety of blood and tissue samples used for genetic or hormonal analyses (see Beaulieu et al., 2014; Beaulieu, Benoit, Abaga, Kappeler, & Charpentier, 2017 for more details about trapping procedures).

In both projects, a variety of data are collected during daily observations in the field with the followed troop. First, all individuals seen during the day are recorded, along with deaths and births, allowing us to have precise demographic data. In addition, the reproductive states of the females are recorded on a daily basis: an adult females could be either lactating, cycling or pregnant (Figure 7). Baboons and mandrill females exhibit conspicuous features allowing us to assess females' reproductive states non-invasively (Figure 7). Females develop exaggerated sexual swellings when they are sexually receptive, and these swellings reach their maximum size as they ovulate (Higham, Heistermann, Ross, Semple, & MacLarnon, 2008; E. Huchard et al., 2009). An oestrus cycle lasts between 35-40 days in both species (Setchell & Wickings, 2004; Wildt, Doyle, Stone, & Harrison, 1977), and is divided in two phases: the turgescent phase, where swellings are increasing in size and females are sexually receptive, and the deturgescent phase, where swellings decrease in size until being absent, when females are not receptive.

Finally, behavioural data can be collected with accuracy as individuals, including infants, are recognizable in both projects. In addition to *focal* observations (which can be specific to a particular project in a given year), *ad libitum* observations are made on a daily basis in both projects (see C for Tsaobis data collection procedures).

C- Data collection at Tsaobis

I spent a total of nine months in the field at Tsaobis. On two occasions, in May 2018 and December 2019, I have been there two weeks in order to make a census of the three troops. These censuses consisted in recording all individuals present in the troops, in particular infants seen for the first time, along with the reproductive states of each adult female.

Moreover, I led two field seasons of around four months-long, one in September-December 2018, and the other in April-July 2019, in order to collect relevant data for my study, and for the long-term data collection of the project. I was with a team of 5 and 6 international volunteers in 2018 and 2019 respectively. We followed the baboons daily on foot, with two teams of 2-3 persons following two different troops. Baboons move from 1 to 20km a day, and sleep on cliffs in order to limit predation risk (Cowlishaw, 1997). They can use different cliffs each night, and we therefore needed to follow troops from dusk until dawn.

The two field seasons started (in October 2018 and May 2019) by the captures of all individuals of our two large habituated troops, J and L. The process of baiting starts three weeks to one month before the trapping date, in order to get the baboons used to forage around and inside cages (see Figure 11 for more details about the trapping procedure). During captures, we marked unmarked individuals, i.e. mainly juveniles, with a unique combination of ear notches: these two captures thus permit me to realize behavioural observations on these newly-notched juveniles.



Figure 11: The different phases of the trapping process at Tsaobis (© pictures: Rémi Emeriau)

The chronological order of the pictures goes from left to right, and from top to bottom. First, we deploy around 60 cages in the same location in the field. During two to three weeks, we bait baboons with corn, starting exclusively outside the cages, and then little by little, within the cages, in order to get them use to go inside the cages without any fear. 1: On the day of trapping, at dawn, a baboon (the adult female Bubonica here), is attracted by the food, and grabs the maize cob inside a cage. 2: She pulls the cob and triggers the mechanism, the door starts to lower down. 3: Once asleep (via anaesthesia), we collect morphological data, dental eruption and wear patterns, biological samples (blood and hair), etc (see also for more details: Elise Huchard, Raymond, et al., 2010). The unmarked individuals are also marked, via ear notching. 4: At the end of day, at dusk, once fully awake, the baboons are released, all together.

Baboons are all well-habituated, and the conditions for observation at Tsaobis are excellent (given the low vegetation density in this arid environment): observers can approach

within 5 meters of any individual without causing any reaction (Figure 12). It allows observers to collect a wide variety of precise and accurate data in the field:

- Every 30 minutes, the spatial location was collected with a GPS point, and scan was performed to measure patterns of troop activity, spread and habitat used. The GPS points collected in 2018-2019, along with the ones since 2005, were used to compute troop home ranges in 2005-2019 (Figure 10)
- Monitoring of individuals present and absent in the troop on a daily basis, along with the reproductive state of each adult female (Figure 7)
- The occurrence of an unusual and/or innovative event in the troop, along with inter-troop interactions. These data were not used in this thesis and are part of the long-term protocols at Tsaobis;
- Collection of faecal samples, on targeted individuals in the three troops. These samples have been or will be used for parasitological and genetic analyses, but not for this thesis.
- Monthly phenology survey, in the hills and riverbed, in order to record food availability for baboons. However, because of the high between-year variation in the data collection procedures, along with the absence of preliminary study investigating the association between actual baboon food availability and phenology survey, these data were not used in this thesis.
- In 2019, onset of a thanatology survey, to observe the variation in 'grieving' behaviour in baboons, following a death in the troop. It consisted in focal observations on a daily basis during the two weeks following a death, on one close relative or friend of the deceased, and on one control individual (not related nor close). These data were not used for this thesis.

- Different behavioural *ad libitum* observations. It included agonistic interactions, to establish dominance hierarchies within a group, grooming interactions, to assess social network within a group, but also copulations, tantrums and masturbations.
- The colours of infant baboons before they turned completely grey (see chapter 2 for the scale and body part considered to assess colour scores).

On top of these data, volunteers and I mainly collected behavioural *focal* observations (J. Altmann, 1974) on juvenile baboons less than 34 months old. Focal observations were spread equally across the day (divided in four blocks of 3-hours) and focal individuals were chosen randomly, and never sampled more than once within a block. Focal observations were 20-minutes long, and lasted at least 10 minutes in all cases.



Figure 12: An observer recording a behavioural focal observation on an infant baboon (© pictures: Rudolf Schipfer)

Rachel Heaphy, volunteer in the 2019 field season, is actually only pretending to collect data here.

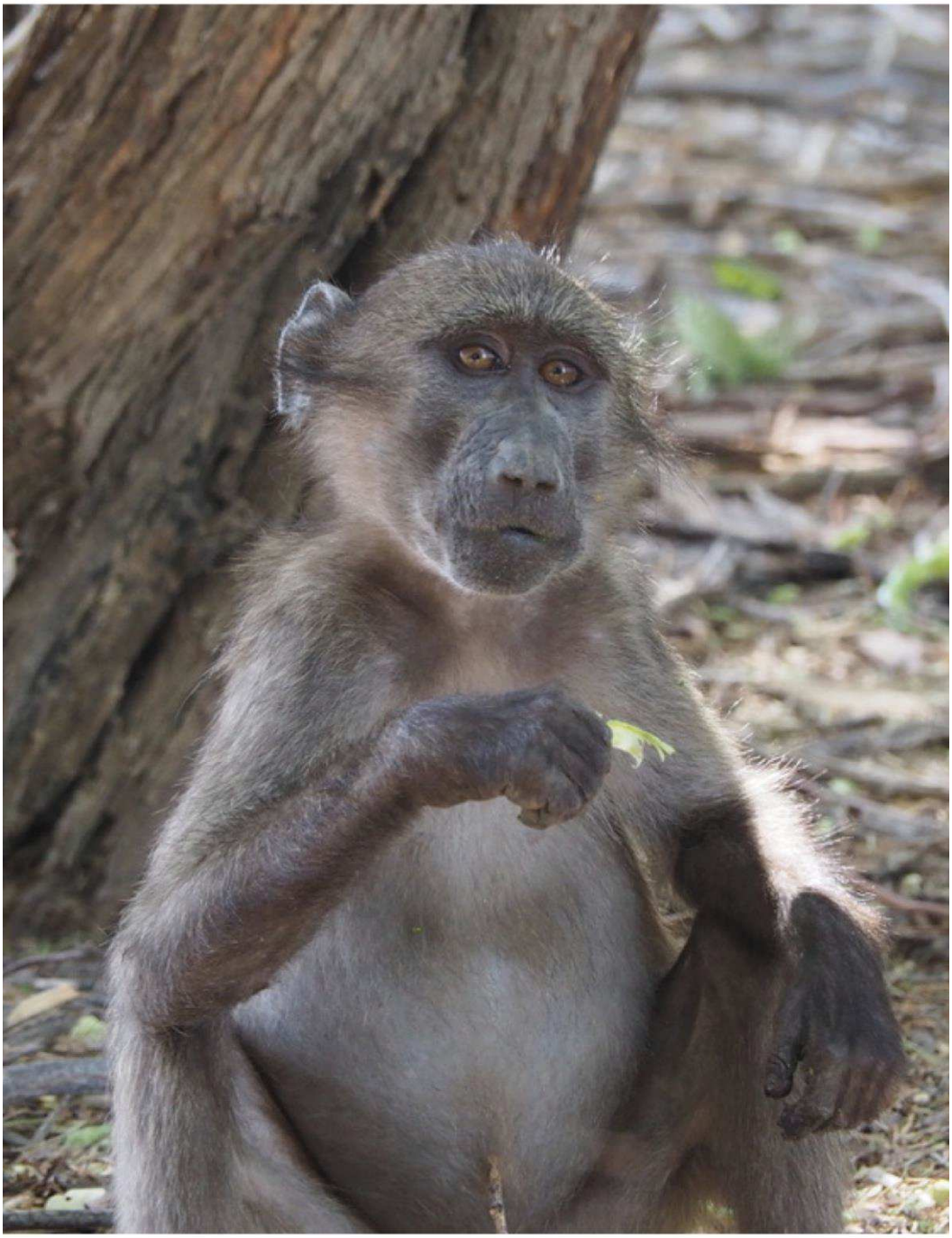
We recorded on a continuous basis the **activity** of the focal individual: feeding (with the nature of the food item), resting/exploring environment, social playing (along with the identity of the playing partner(s), and of the individual who initiated the playing bout), travelling (alone, riding on the mother on dorsal or ventral position), travelling-feeding, suckling (along with the mother activity during the suckling bout, and the identity of the initiator of the end of the suckling bout), grooming (along with the identity of the grooming partner(s) and the direction of the grooming bout), auto-grooming and drinking. We also recorded on a continuous basis mother-focal infant proximity: we collected approaches and leaves with its mother, taking a 60cm distance threshold, and the identity of the individual approaching or leaving.

Every 5 minutes, we realized **scan** observations (J. Altmann, 1974), and every focal observation started and ended with a scan observation. During scans, in addition to the focal's activity, we recorded its distance with its mother, the identity of all individuals within 5 meters of the focal individual, and counted the number of bites per minute if the focal individual was feeding.

Lastly, we collected point **events** during focal observations. It included all agonistic (threats, supplants, displacements, etc.) or affiliative (lipsmacks, carrying, handling, grunt, etc.) interactions with another individual. We also recorded stressed behaviour such as nervous glances, self-scratches, etc. I was in particular interested to record with precision mother-infant relationships, and we therefore collected a range of behavioural events specific to mothers and infants, such as: ask nipple, ask grooming, grab nipple, reject from nipple, prevent access to nipple, infant vocalizations (gecking, 'mooh' grunting, loud screams) and behaviours ('electric shock', 'helicopter tail') during a tantrum.

We collected a total of 3325 focal observations from 48 juveniles aged between 1 and 34 months old, corresponding to 1136 hours of observation in 2018-2019. These behavioural data are used in Chapter 3.

Lymphoma



Chapter 2

Developmental transitions in body color in chacma baboon infants: implications to estimate age and developmental pace

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ABSTRACT

Objectives: In many primates, one of the most noticeable morphological developmental traits is the transition from natal fur and skin color to adult coloration. Studying the chronology and average age at such color transitions can be an easy and non-invasive method to (i) estimate the age of infants whose dates of birth were not observed, and (ii) detect inter-individual differences in the pace of development for infants with known birth dates.

Materials and Methods: Using a combination of photographs and field observations from 73 infant chacma baboons (*Papio ursinus*) of known ages, we (1) scored the skin color of six different body parts from pink to grey, as well as the color of the fur from black to grey, (2) validated our method of age estimation using photographic and field observations on an independent subset of 22 infants with known date of birth, and (3) investigated ecological, social and individual determinants of age-related variation in skin and fur color.

Results: Our results show that transitions in skin color can be used to age infant chacma baboons less than seven months old with accuracy (median number of days between actual and estimated age = 10, range=0-86). We also reveal that food availability during the mother's pregnancy, but not during lactation, affects infant color-for-age and therefore acts as a predictor of developmental pace.

Discussion: This study highlights the potential of monitoring within- and between-infant variation in color to estimate age when age is unknown, and developmental pace when age is known.

***Keywords**: ageing method, primate, inter-individual variation, food availability*

INTRODUCTION

The relationship between age and physical maturation has been a major topic of interest in behavioral and evolutionary ecology. Across species, different developmental paces shed light on between-species life-history variations (Sibly, Grady, Venditti, & Brown, 2014). For example, primates, including humans, have longer periods of lactation, associated with slower postnatal growth and smaller litter size compared to other mammals of similar sizes (Dufour & Sauther, 2002). Across populations and individuals of a same species, variation in infant developmental pace can have important fitness consequences on later survival and future reproduction (Lindström, 1999) as well as on maternal reproductive success, via a trade-off balancing investment in current versus future progeny (Lee, Majluf, & Gordon, 1991; Maestripieri, 2002; Trivers, 1972).

Developmental pace may vary in relation to various environmental, social, maternal and individual traits. Specifically, and as for all mammals, the quantity and quality of milk represent a primary influence on infant growth trajectory (Lee, 1996). For example, a positive impact of exclusive breastfeeding in the first 3-5 months of life on growth rates is observed among children in Bangladesh (Arifeen, Black, Caul, Antelman, & Baqui, 2001). In non-human primates, food availability between conception and weaning is an important source of variation in developmental pace, which is likely mediated by maternal condition for young infants who do not yet feed independently (Lee, 1996). As a result, the seasonal timing of birth, as well as maternal traits that may affect the nutritional status of mothers, may affect growth and development (Lee, 1996; Lummaa, 2003; Vandeleest & Capitanio, 2012). For example, in hierarchical societies, dominant females often have a better access to food, which may lead to higher reproductive rates and faster offspring development (Clutton-Brock & Huchard, 2013; Stockley & Bro-Jørgensen, 2011). Individual traits, like infant sex, may also impact the developmental pace of sexually dimorphic primates (Lonsdorf, 2017). Finally, selective

pressures such as predation risk (Coslovsky & Richner, 2011; Fontaine & Martin, 2006), infanticide risk (Bădescu et al., 2016) or group size (Borries, Larney, Lu, Ossi, & Koenig, 2008) may further impact developmental trajectories, depending on the species considered.

In more than 30% of primate species, one of the most noticeable and widespread morphological developmental traits is the transition from natal fur and skin color to adult coloration (Ross & Regan, 2000; Treves, 1997). Neonatal fur coloration may have evolved to promote allomaternal care, infant attraction and protection by other group members, or in response to infanticide risk (Ross & Regan, 2000; Treves, 1997). Even if the ultimate function of neonatal fur color remains unclear (Hrdy, 1976; Treves, 1997), careful monitoring of such developmental transitions at the individual level could have at least two important applications. First, if the age at which such transitions occur does not vary excessively across individuals, it can be an easy and non-invasive method to estimate individual ages in transitional infants for whom the date of birth is unknown (Altmann & Altmann, 1981). Such a method relies on the detailed description of age-related changes in body coloration for a cohort of infants of known ages. This approach, which can be applied using observational data only, has significant advantages over many other common methods, such as body weight or dental eruption patterns, which rely on invasive measurements (Hohn, 2009; Morris, 1972).

Second, for infants of known ages, inter-individual differences in the age of color transitions may reflect broader individual variation in developmental pace, if they correlate with physical growth or other indicators of behavioral development, such as social, feeding and locomotor development, or the temporal dynamics of the mother-offspring relationship (Barthold, Fichtel, & Kappeler, 2009; Treves, 1997). Few studies have investigated such correlations. Across species, the loss of natal pelage of 138 primate species is partially correlated with the temporal dynamics of mother-offspring spatial proximity, i.e. this color change begins around the period when the infant spends a considerable amount of time (25%)

out of the mother's arm-reach (Treves, 1997). Within species, the transition from natal to adult fur coincides with advanced physical independence, such as independent locomotion and feeding on solid food as is the case in red-fronted lemurs (*Eulemur fulvus rufus*) (Barthold et al., 2009). In such cases, recording infant color changes at particular ages may represent one easy way to quantify individual differences in developmental pace, and an early-life indicator of weaning age, which is a crucial life history trait affecting maternal fitness.

Baboons are among the most studied of the non-human primates, but our ability to estimate infant age and our understanding of the determinants of infant developmental pace in this species are still limited. Little work has been done to estimate infant age based on color transitions since two seminal papers on yellow baboons (*Papio cynocephalus*) forty years ago (Altmann & Altmann 1981; Rasmussen 1979) - although a short preliminary study has also been published on chacma baboons (*Papio ursinus*) (Whitehead, Henzi, & Piper, 1990). These studies report that the fur and skin of infants of both species show different coloration compared to adults. When they are born, the fur is black and the exposed skin on the face, ears, hands, and feet are pink, and they gradually acquire the physical traits of adults, grey skin and dark grey fur for chacma baboons (yellow fur for yellow baboons) in their first year of life. This transition may operate following a specific chronology, with some parts of the body turning grey before others (Altmann & Altmann, 1981). However, those studies have only described the chronology of the color transitions, while the accuracy of a method based on such transitions to estimate infant ages has never been assessed.

More is known about developmental pace in baboons, but few studies have focused on the specific pace of developmental transitions in coloration. High levels of individual variation can be seen across various indicators of development including changes in fur and skin color, as well as in growth rate and behavioral development, with some infants maturing faster than others (Altmann 1980; Altmann and Alberts 2005; Altmann and Altmann 1981; Johnson 2003).

Food availability in the environment is a major factor influencing individual variation in growth rate (Altmann & Alberts, 2005). The timing of the birth in the annual cycle could thus impact infant developmental pace, as seasonal variation in food availability largely occur across tropical Africa (Feng, Porporato, & Rodriguez-Iturbe, 2013). Moreover, maternal traits are also known to affect baboon infant development: yellow baboon infants of dominant females have faster growth rates and reach sexual maturity earlier than those of subordinates (Alberts & Altmann, 1995; Altmann & Alberts, 2005; Charpentier, Tung, Altmann, & Alberts, 2008). In this same population, offspring of multiparous females are larger for their age than offspring of primiparous females (Altmann & Alberts, 2005). Overall, while the determinants of individual variation in growth trajectories have already been explored, less is known about color transitions in baboons. Examining such variation may contribute to a better understanding of processes affecting growth and physical maturation, and changes in the color of certain body parts could be used as indicators of developmental pace in baboon species.

Using the skin and fur coloration of wild infant chacma baboons, we first characterize in detail the temporal sequence of physical maturation from natal to adult-like coloration to compare the chronology of these coloration transitions with other baboon populations and species. Second, we assess the accuracy of the developed method by using these dates of coloration transitions to estimate the ages of infants, and comparing age estimates with their known birth dates. We then examine the main determinants of individual variation in body color transitions for a cohort of infants of known ages, focusing on the influence of ecological factors (food availability during pregnancy and early lactation, timing of infant birth in the annual cycle), maternal traits (rank and parity) and individual traits (sex) on the age at transitions.

Material and Methods

1 Study site

Data were taken by different field observers each year between 2005 and 2019 from three habituated groups of chacma baboons (J and L since 2005, and M, a fission of group J, since 2016) living in Tsaobis Nature Park (22°23S, 15°44'50E). Chacma baboons at the Tsaobis Baboon Project live in a semi-arid region of Namibia, on the edge of the Namib Desert. Annual rainfall is low and variable which leads to relatively low, and highly unpredictable food availability (Cowlishaw & Davies, 1997). Nonetheless, rainfall occurs most years, and peaks between January and April, resulting in an annual food peak of variable intensity and duration from February to May. The groups were followed daily on foot from dawn to dusk, allowing observers to collect a variety of demographic, life-history, behavioral and group spatial data. Each group member was known individually through ear notches and identifying marks, and each new birth in a group was recorded. Reproductive states of adult females were recorded every day in the field, and they were classified as: (i) pregnant, where pregnancy was determined *post hoc* following infant birth, and encompassed the six months between the conceptive cycle and the birth; (ii) lactating, for the period from infant birth until the resumption of cycling; and (iii) cycling, including both swollen females (i.e., sexually receptive with a perineal swelling) and non-swollen females between two swelling phases. Groups were not followed year-round, and each year a field season of variable length was conducted (median=126 days, range: 57-240 days).

2 Ecological and individual traits

To investigate the determinants of individual variation in physical development, we considered both ecological and individual traits. We estimated food availability with the normalized

difference vegetation index (NDVI). This measure has previously been used as a proxy of food availability in our population (Baniel, Cowlishaw, & Huchard, 2018) and other baboon populations (Zinner, Peí Aez, & Torkler, 2001). We extracted the mean NDVI per 16-day period on a 500 m resolution from 2004 until 2019 on the NASA website (MOD13A1 product) (Didan, Barreto Munoz, Solano, & Huete, 2015) within the home ranges of the three habituated groups. Using the GPS locations recorded every 30 minutes by the observers during daily group follows, between 2005 and 2019, we computed 100% isopleth home ranges for our three groups separately using kernel density estimates ('kernelUD' function, h set to 'href') implemented in the adehabitatHR package (Calenge, 2006). We then computed a daily NDVI value for each group on its given home range using a linear interpolation between two known NDVI values of 16 days-intervals.

The social rank of adult females was established each year for each group separately using *ad libitum* and focal observations of dyadic agonistic interactions (supplants, displacements, threats, chases and physical attacks). We computed a linear hierarchy among adult females using Matman 1.1.4 (Noldus Information Technology, 2013), and then calculated a relative rank for each female controlling for group sizes. This relative rank was computed using the formula (N-r)/(N-1), where N was the number of adult females in the group in a given year, and r was the absolute rank of the female (ranging from 1 to N, 1 being the most dominant). Although adult females' ranks are relatively stable through time, individuals' relative ranks change as females enter and leave the hierarchy through maturation and death, respectively. Each female was assigned one relative rank per year, ranging from 0 (for the lowest ranking female) to 1 (for the highest-ranking), as hierarchy is inherited and stable for female baboons. For analyses of infant development, we considered the mother's rank during the year her infant was born.

The mother's parity was assigned using long-term life-history data. Females were considered primiparous between the birth of their first and second infant, and multiparous after the birth of their second infant.

3 Infant color scoring

Infant coloration was scored using photographs and direct field observations. An observation, which could be either from a photograph or from the field, was a set of scores of different body parts on a given day for a given infant baboon. We used photographs opportunistically taken by field observers between 2005 and 2018 of infant baboons aged between 0-19 months old (N=255 pictures of 109 infants in total, median=2 pictures per individual, range: 1-11 pictures per individual). We discarded photographs when luminosity or quality were too poor to give a color score. In addition, in 2018 and 2019, infant baboons were scored every two weeks using direct field observations, until they finally turned completely grey. We obtained 158 field observations on 28 infants in this way, i.e. with no photograph (median=5.5 observations per individual, range: 1-10 observations per individual). Infant baboons were scored on photographs by one observer (Author 2), and in the field by one observer (Author 1). We determined the inter-individual consistency of scores by scoring independently the same set of 60 pictures, and compared score similarity with the intra-class correlation coefficient for each body part (Koo & Li, 2016). To do so, we computed intra-class coefficient looking at the absolute agreement of a single-fixed rater with a two-way mixed models, using the ICC function of the 'psych' package in R (Revelle, 2020). The scoring reliability was excellent for each body part (mean ± SD, ICC = 0.92 ± 0.06, see also Table S1 of the Supporting Information). Thus, in total, we scored coloration for 134 infants between 2005 and 2019.

In addition to determining the color of the fur covering the whole body, we scored the skin color of the following body parts: ears, eye contours, hands and feet, muzzle, muzzle tip, and ischial callosities (see Figure 1 for locations of these body parts). For each body part, we attributed a score between 1 and 5 following previous work (Altmann & Altmann, 1981; Rasmussen, 1979), such that 1 is fully pink, 2 is distinctively pinker than grey, 3 is a mixture of pink and grey, 4 is distinctively greyer than pink, and 5 is fully grey (Figure 2). For the fur, 1 is fully black, 3 is a mixture of black to grey, and 5 is fully grey; we did not use scores 2 and 4 because the color transition for the fur is less obvious than for other body parts (Figure 2). We scored all the body parts that were visible in each photograph. The data that support the findings of this study are openly available in Mendeley data: http://dx.doi.org/10.17632/65vk9tck25.1.

4 Accuracy of age estimations based on fur and skin coloration

To describe the physical transition in fur and skin coloration and further test whether it is a reliable method to estimate the age of an infant, we focused on scores from a sample of 73 infants of known age, that is, whose date of birth was known with a maximum uncertainty of 10 days. These dates of birth were determined from having been present on either the day of birth (51 infants, hereafter called Sample 1) or the day of conception (22 infants, called Sample 2). The conception day was identified as the exact day of deturgescence of the sexual swelling in the conceptive cycle, which was the cycle followed by a pregnancy and by no other cycle. We then estimated the dates of birth of these 22 infants by adding 190 days to the conception date, based on the fact that the mean gestation length is 190 days at Tsaobis with little variability (range: 181-200 days, SD = 5, N = 13 pregnancies where both conception and birth were observed). We considered only baboons aged less than 8 months, as older baboons, from 8 to 19 months old, were all fully grey. We thus restricted our dataset to this Cohort 1, comprising

242 observations from 73 infants: 148 photographs on 59 infants and 94 field observations on 16 infants (including 2 infants that were both photographed and observed in the field in 2018). Specifically, we obtained 238 scores for ears, 201 for eye contours, 238 for fur, 203 for hands and feet, 239 for muzzle, 91 for muzzle tip and 143 for ischial callosities.

To determine the body parts that showed the most reliable timing in color transition to predict ages, we computed a correlation matrix using the Spearman's rank correlation coefficient between infant age (in months) and color scores for each body part of individuals in Cohort 1. We also examined pairwise correlation coefficients between the different coloration scores to determine whether some body parts provided redundant information because they changed color at the same age. It is important to note that the dataset used to generate these correlations is pseudoreplicated to some extent given that some individuals contribute multiple observations. These correlation coefficients are nevertheless useful to compare values across body parts, but should be interpreted with caution to evaluate the statistical significance of any single correlation.

To determine the accuracy of coloration scoring as an estimate of infants' ages, we computed the difference between the actual known age and the estimated age of another, independent subset of 70 observations on 22 infants. To do so, we divided our Cohort 1 in two sub-samples, namely Sample 1, including 172 observations of 51 infants with precisely known dates of birth (less than 10 days of uncertainty), and Sample 2, including 70 observations on 22 infants (with exactly 10 days of uncertainty on their date of birth, since it had been inferred from conception date). We use Sample 1 as the reference for age estimation at color transitions, and Sample 2 to validate our method on a fully independent sample.

With Sample 1, we first conducted a principal component analysis (PCA) taking into account the color scores of the seven body parts considered, using the function 'PCA' of the 'FactoMineR' package (Husson, Josse, Le, & Maintainer, 2020). We had a considerable

number of missing values in our dataset as it was generally impossible to score all body parts from a single picture. To conduct a PCA with missing values, we performed imputations to complete the dataset using the 'imputPCA' function of the 'missMDA' package (Josse & Husson, 2016), which uses an iterative algorithm taking into account similarities between observations, as well as relationships between the scores of different body parts. The first dimension of the PCA (PC1) explained 86.6% of the variance of the color scores (versus 8.8% for the second dimension), and was the only PC retained for downstream analyses. We then investigated the relationship between PC1 and infant age (in days). To do so, we compared several linear models, all with PC1 as response variable, and containing as fixed effects a polynomial function of age modelled with variable degrees (from 1 to 8). We selected the best model of this subset as the one minimizing the Akaike Information Criterium (AIC), and a polynomial function of age of degree 4 was retained in our model.

Next, we followed four steps to quantify the accuracy of age estimation from Sample 2. First, we estimated the missing values of the Sample 2 dataset on color scores using the method described above ('missMDA' package) (Josse & Husson, 2016). Second, we predicted the values of PC1 using the color scores of the seven body parts, using the 'predict.PCA' function of the 'FactoMineR' package, that took into account the PC1 values computed from Sample 1 (Husson et al., 2020). Third, we used the linear model (that was computed on Sample 1) to calculate one age estimate for each of these predicted values of PC1, i.e. for each observation of Sample 2. More precisely, we used the 'uniroot' function in R to solve the equation of 4 degrees linking each PC1 value with infant age. Fourth, we computed the absolute difference, in days, between the actual known age (± five days of uncertainty) and this estimated age to quantify the accuracy of our method of age estimation.

In order to investigate the effect of the number of body parts that were scored on the accuracy of our age estimates, as well as which body part was the most informative in this

context, we repeated this process with a variable number of body parts. From the seven body parts initially considered, we first removed the fur scores from Samples 1 and 2, as the scores of this body part had the lowest correlation with PC1. We then repeated this process by progressively removing one body part at a time, based on the relative values of the correlation between PC1 and the raw scores of that body part, removing first those parts for which scores were least correlated to PC1. Chronologically, we first removed fur, followed by hands and feet, ischial callosities, muzzle and eye contours. Our last round of analyses contained only scores from ears and muzzle tip.

We also tested whether the 5-level scale for color scores produced more accurate age estimations than a simpler 3-level scale with the following levels: (1) pink (score 1 in our 5-level scale), (2) transitional (pooling scores 2, 3, 4 in our 5-level scale), (3) grey (score 5 in our 5-level scale). Using only one score instead of three for transitional colors can facilitate data collection in the field, and be less subjective across observers. We then repeated the same processes described for Samples 1 and 2, to quantify the accuracy of the age estimation under a 3-level scale of color scores for different number of body parts considered.

We also tested the effect of the number of observations per individual on the accuracy of age estimates. In Sample 2, there were 70 observations from 22 infants (range = 1-8, median=2 observations per infant). For all infants with more than one observation, we computed one estimated birth date by averaging the different birth date estimates from each observation. We then computed the difference, in days, between the actual and estimated birth dates as an indicator of estimation accuracy to compare the accuracy of age estimates obtained from a variable number observations of a given infant.

Moreover, we investigated the potential effects of the actual age of an infant on the accuracy of age estimations per observation, to test whether the accuracy of our age estimates may decrease for older juveniles. To do so, we ran a linear mixed model, with the accuracy of age

estimates per observation (i.e. the absolute number of days between actual age and estimated age) as a response variable, the actual age as the only fixed effect, and infant identity as the only random effect (to control for repeated observations). For this analysis, we used all observations available from Sample 1, for all 7 body parts scored on a 5-level scale.

Finally, we were interested in quantifying the effects of observation types, i.e. field or photographic observations, on the accuracy of age estimation per observation. To do so, we ran a linear mixed model, with the accuracy of age estimates per observation as a response variable, the observation type as the only fixed effect, and infant identity as the only random effect (to control for repeated observations). For this analysis, we used all observations available from Sample 1, for all 7 body parts scored on a 5-level scale to estimate ages of Sample 2 (Sample 2 contained 38 field observations from 5 infants and 32 photographic observations from 17 infants).

5 Determinants of individual variation in the pace of color changes

To identify the main determinants of developmental pace, we used 242 observations from the full sample of 73 infants with known ages (Cohort 1), and ran general additive mixed models (GAMMs). We first computed a weighted mean color score for each observation, where the score of each body part was given a different weight depending on its correlation with infant age (see above). More precisely, we attributed less weight to body parts that were less correlated with age by dividing their color score by their correlation coefficient, on the basis that the developmental pace of these body parts was less variable across individuals for a given age, and so presumably less affected by environmental and individual factors. We thus obtained a general score of color development across all body parts for a given observation. Our response variable was the weighted mean color score per observation (continuous variable).

GAMMs allow to fit non-linear relationships between the response variable and one or more fixed effect(s), using thin plate splines (Wood, 2003). We first determined the best model describing the age effect on mean color scores, with the identity of infant set as random effect to take into account the lack of independence between multiple observations of a same individual. To do so, we compared GAMMs containing either (1) a simple, continuous effect of age; (2) age modelled as a polynomial of degree 2; (3) a polynomial of degree 3; or (4) age modelled using a thin plate regression spline. We selected the best model as the one minimizing the Akaike Information Criterium (AIC). We found that the age modelled using a thin plate regression spline was retained in all our models (See Table S2 in the Supporting Information for model selection on the weighted mean color score response variable for an example). We then ran our global GAMMs, with age modelled with a spline, infant identity as random effect, and including the following additional fixed effects:

- *Food availability during infant growth*. We expected infants whose gestation and birth occurred during periods of high food availability to develop faster for their age (Altmann & Alberts, 2005; Johnson, 2003). To test which time period of infant development (prenatal versus postnatal) was most sensitive to variations in food availability, we investigated the effects of both food availability during pregnancy (approximated by the mean NDVI daily values between conception and birth date for a given infant) and early lactation (approximated by the mean NDVI daily values between birth and observation date for a given infant). As these two indicators of food availability were highly correlated (Pearson correlation = 0.39, confidence interval: [0.28; 0.49], t=6.58, P-value$<10^{-4}$), leading to collinearity, we included them separately in two different models.

- *Date of birth*. We expected infants born at particular times of the year to develop more quickly. The NDVI is only a partial proxy of food availability, and other components of seasonal variation that are not necessarily captured by NDVI (such as temperature, photoperiod,

or particular plant phenologies) may further affect developmental pace. As a given date in the annual cycle is a circular variable (at least when considering environmental seasonality), we used a sine fixed effect expressed as follows to introduce the infant's date of birth, converted in radians, into our multivariate linear model:

$$\sin(Infant's\ date\ of\ birth + \varphi)$$

Where φ is the phase value. We changed the phase value φ (to 0, π/6, π/3, π/2, 2*π/3, 5*π/6) to account for potential phase shifts across the year, i.e. to consider all the months of the year as possible birth months maximizing faster development. For example, a positive effect of the sine phase of π/6 would maximize February, and a negative effect will maximize August. We ran sequentially six different multivariate models (GAMMs with the six different phase values) containing all other fixed effects, and we selected the best phase as the one minimizing the AIC (which is π/3 for the weighted mean color score model).

- *Mother's dominance rank*. We expected infants from dominant females to develop more quickly, following studies on other aspects of baboon developmental pace (Altmann & Alberts, 2005; Cheney et al., 2004; S. Johnson, 2003).

- *Mother's parity*. We expected infants from primiparous mothers to develop more slowly, following studies on other aspects of baboon developmental pace (Altmann & Alberts, 2005).

- *Infant sex*. We did not expect any sex difference in the pace of early morphological development, following studies on other aspects of baboon developmental pace (Altmann & Alberts, 2005; Altmann & Altmann, 1981; Johnson & Kapsalis, 1995). Nevertheless, we included this variable to control for potential unexpected sex differences.

- *Group identity,* to control for possible differences between social groups.

We further considered each body part separately (seven models) to test whether the same determinants affected all body parts or only some of them, and to evaluate which body parts

were most sensitive to ecological, individual and maternal traits. Here, our response variables were the scores of one given body part, and were coded as ordinal, with five categories for each body part (except for the fur, with only three categories). We ran all the GAMMs using the 'gam' function of the 'mgcv' package (Wood, 2003), in R version 3.5.0 (R Core Team, 2018). Ordinal response variables for each body part were specified with the family 'ocat' of the 'mgcv' package (Wood, 2003). We computed parameter estimates for each fixed effect, with Wald statistic tests (X^2) and P-values associated. For smooth effects, we computed the effective degrees of freedom, with the Wald statistic test and the P-value. We considered an effect to be significant when its P-value was < 0.05. We were also interested in quantifying the importance of inter-individual variation in developmental pace, and so tested the significance of the random intercept, looking similarly at its P-value. For each model, we also checked graphically the normality of the residuals' distribution and the accuracy of the number of knots used for the age thin plate spine (this parameter constrains the 'wiggliness' of the smooth, i.e. the number of bow points in the fitted curve) (Wood, 2003) using the 'gam.check' function of the 'mgcv' package (Wood, 2019). Graphical representations were made using the 'mgcViz' package (Fasiolo, Nedellec, Goude, & Wood, 2018).

RESULTS

1 Characterization of fur and skin color changes in chacma baboon infants

All results associated with the characterization of fur and skin color changes in relation to age are summarized in Figure 3. All baboons were fully grey (i.e., at all body parts) after 8 months of age, with similar fur and skin coloration as adults. The fur, muzzle or hands and feet were the first body parts to turn grey, on average between 1 and 2 months of age. Hands and feet, as well as the muzzle, started to transition around 1 month old until becoming fully grey at approx.

4 months of age. Ears started to turn grey after 2 months and were totally grey by 5 months. The last body parts to change color were the eye contours, the ischial callosities, and the tip of the muzzle, which started to transition at approx. 3 months of age, and finished after 5 months. The qualitative chronology of the transition was apparent in the correlation matrix (Table 1): hands and feet scores were highly correlated with muzzle scores, and eye contours scores were highly correlated with muzzle tip scores. Nonetheless, the order in which body parts change color was not always consistent across individuals. For some infants, we observed ears turning grey before muzzles and hands, or ischial callosities turning grey before the muzzle tip and ears. Overall, a chacma baboon infant with entirely pink skin and black fur was almost always younger than 2 months old, as at least the hands and feet started to turn grey after this age. An infant with entirely grey skin and fur was at least 4 months old, as no infant was observed with a grey tip of the muzzle before this age. Finally, a transitional infant was aged between 1 and 6 months old.

2 Accuracy of age estimates based on color scores

The color scores were strongly correlated with the known ages of infants for all body parts, though correlation coefficients were slightly lower for the fur and the ischial callosities (Table 1). This means that the scores of these two body parts produce less precise age estimates, probably due to higher inter-individual variation in the age of transition of these parts compared to others. For example, a 3-month-old baboon could exhibit the full range of colors for ischial callosities, from fully pink to fully grey; and a 1-month-old baboon could exhibit a fully black or a fully grey fur (Figure 3).

In order to test the accuracy of infant body coloration as a method of age estimation, we computed a composite score (using PCA) from 172 observations of all body parts from 51

infants of known ages (births observed, Sample 1), and then predicted this composite score to estimate ages on an independent sample of 70 observations from 22 infants of known ages (Sample 2). We obtained a median difference of 12 days between the actual age and the estimated age using 70 observations, 7 body parts and a 5-level scale of color scores (Table 2). We also investigated the effects of the number of body parts considered, and the number of levels of the color scale. Decreasing the number of body parts considered only slightly decreased the accuracy of age estimates (Table 2), and the same conclusion applied for using a 3-level color scale instead of a 5-level one – though using a 3-level scale in combination with few body parts decreased accuracy more substantially (Table 2). Our best age estimations per observation were computed when considering the skin across all 6 body parts but excluding the fur, and using a 5-level color scale (absolute number of days of between actual and estimated ages: median = 10.7, range = 0.1–86.4). We also investigated the effect of the number of observations per infant on the accuracy of age estimates: the more observations, the more accurate were the estimates (Figure S1, Supporting Information). Finally, the accuracy of age estimates significantly decreased with age (X^2 = 10.0, P-value = $1.54x10^{-3}$) (Figure S2, Supporting Information), and were lower for photographic compared to field observations (Figure S3, Supporting information), albeit the latter effect did not reach significance (X^2 = 3.63, P-value =0.06).

3 Determinants of individual variations in the pace of color changes

Finally, we investigated the determinants of inter-individual variations in age-related color scores, looking at ecological (food availability during pregnancy or during early-lactation, birth timing), maternal (parity, rank) and individual (sex) predictors using GAMMs controlling for age with a spline regression (Figure 4). The model explained 93% of the variation in the weighted mean color scores. We detected significant inter-individual differences in mean color

scores (Table 3), and in most body parts (except for the muzzle tips, for which we had fewer infants scored compared to other parts, see Table S3 in Supporting Information). Our index of food availability during pregnancy influenced the weighted mean color score (controlled for age): infants turned grey earlier considering all their body parts together when food during pregnancy was abundant (Table 3, Figure 5). In contrast food availability during lactation did not (Table S4, Supporting Information). We did not detect any effect of maternal (rank and parity) nor individual (birth date and sex) traits on variation in infant mean color scores controlled for age (Table 3). Looking at individual variation in color transitions for each body part separately, we found a positive effect of food availability during pregnancy on the score of ischial callosities only (Table S3, Supporting Information). We also found a positive effect of the timing of birth on the scores of muzzle tips (maximizing scores for infants born in December-January) but not for other body parts (Table S3, Supporting Information). We did not detect any effect of food availability during lactation, maternal traits, i.e. maternal rank and parity, on variation in infant color for any body part (Table S3, Supporting Information).

DISCUSSION

Our purpose in this study was twofold: (1) to assess how well infant chacma baboons with unknown ages can be aged on the basis of their skin and fur color, and (2) to explore potential environmental, maternal, and individual predictors of variation in the pace of infant color development for infants with known ages. The age estimates obtained using infant color scores were generally accurate (median number of days between actual age and estimate age per observations = 10, range=0-86 days). All the tools required for estimating ages in a chacma baboon population are provided in this paper. Figures 1 and 2 can be used to score baboon coloration directly in the field (or using photographs), and the methods section details how the

first dimension of a composite score (using PCA), derived from these color scores, can be computed to estimate ages. Various recommendations can be made to improve the accuracy of age estimates:

1. Use the color scores from all body parts except fur, as age estimates were most accurate with this configuration. However, decreasing the number of body parts considered does not decrease the accuracy of age estimations dramatically. For example, considering only two body parts (ears and muzzle tip) instead of six reduces the accuracy of age estimations by only 4.5 days. Nonetheless, such a result may vary across primate species, and one should establish the relevant body parts to be considered in different species.
2. Score the same individual repeatedly, as an infant with 8 observations had a birth date estimation error of 5 days in average, compared to more than 30 days for infants with only a single observation. Ideally, infants should be scored as early as possible (as accuracy decreases as infants age) and regularly until it turns fully grey.
3. Prioritize field observations. Photographic evidence can be less accurate because color scores may be influenced by fluctuating light conditions. If necessary, photographic approaches should exploit multiple high-resolution photographs of the same individual on a given day at different times and angles to control for light variation.
4. Consider using a 3-level color scale, which is slightly less accurate than a 5-level scale but also more practical, and may maximize inter-observer reliability. However, such choice depends on the trade-off between the accuracy targeted and the conditions of data collection (e.g., single versus multiple observers).

In addition, this study opens the possibility of a similar application for machine learning where an algorithm could predict the age of an infant based on pictures, as long as a large set of high-quality pictures (see recommendation #3) of known-age individuals is available to initialize the

algorithm. This relatively recent method is based on mathematical and statistical approaches through which computers can 'learn' from data to then make predictions. Such methods have been used in a wide range of field applications, and are becoming increasingly common (Al-Jarrah, Yoo, Muhaidat, Karagiannidis, & Taha, 2015).

Changes in the pigmentation of infants' ears and muzzles at Tsaobis follow a similar pattern to that observed in another population of wild chacma baboon living in Mkuzi Game Reserve (South Africa), with an onset of grey coloration appearing around 1-2 months, and the full transition completed around 4-6 months of age (Whitehead et al., 1990). Our detailed characterization of the age at which fur and skin turn grey indicates that infant chacma baboons' coloration develops faster than yellow baboons (Altmann & Altmann, 1981; Rasmussen, 1979). Whilst chacma baboon infants have all turned grey by 8 months of age, most yellow baboon infants are still in the transition phase at this age, and only exhibit adult color around 12 to 14 months of age, depending on the population (Altmann & Altmann, 1981; Rasmussen, 1979). In addition, in contrast to yellow baboons, the order in which body parts change color was not always consistent across individuals in this study. Discrepancies observed in the age and chronology of transition between baboon species highlight that such patterns are species-specific, and that the methodology presented here should be developed and validated separately for each species.

Inter-individual variation in the rate of maturation was high for each body part considered in this study, as found in yellow baboons (Altmann & Altmann, 1981; Rasmussen, 1979). Specifically, the change in fur color was a less accurate indicator of age, as fur turned grey relatively early and showed marked individual variation. Failure to derive accurate age estimates remains non-negligible (we had a maximum of 86 days difference between actual and estimated age when relying on 6 body parts), due to the existence of outlier individuals with very fast or slow development. This suggests that, whilst this method of age estimation is not

perfect, infant coloration can provide a simple and non-invasive proxy to detect individual variation in developmental pace on a semi-quantitative scale. Nevertheless, despite their utility for tracking other developmental factors (Barthold et al., 2009; Treves, 1997), studies linking age-related changes in color to other indicators of developmental pace are very rare in baboons. Only one study on Amboseli yellow baboons recorded that late changes in paracallosal skin color can be seen as a first sign of developmental abnormality, being followed by delayed maturation, locomotor disability and finally death (Altmann & Altmann, 1981).

Regarding the determinants of individual variations in color-for-age considering all body parts together, we found that higher food availability during pregnancy, but not during early-lactation, accelerated the transition towards adult coloration. In line with this, infant yellow baboons from a food-enhanced group grew more rapidly than individuals from wild-foraging groups (Altmann & Alberts, 2005). Similarly, in Phayre's leaf monkeys (*Trachypithecus phayrea*) infants in larger groups transitioned from natal to adult fur color later, suggesting that food competition affects infant color maturation and development (Borries et al., 2008). Here, we distinguished pre-natal from post-natal food availability, and our results emphasize the importance of maternal condition during pregnancy for infant post-natal color development. In capital breeders like baboons or humans, females can store energy to use it later, and conception likelihood generally peaks during periods of high food availability to increase the success of their reproductive attempt (Brockman & van Schaik, 2005). Numerous human studies similarly show that maternal nutritional status during pregnancy has a significant impact on infant birth weight, early-life development, health and survival (Emery Thompson, 2013; Martorell & Gonzalez-Cossio, 1987). This study, by highlighting the effect of prenatal food availability on inter-individual variations in color-for-age, suggests that similar effects could occur in baboons, and that color-for-age may thus be a reliable indicator of other developmental dimensions.

Studies on various primates including baboons have also shown that the infants of dominant females exhibit faster development in terms of growth rate and age at weaning (Altmann & Alberts, 2005; Fedigan, 1983; Pusey, 2012). Yet, surprisingly, maternal rank did not affect individual variation in infant color in this study. Given that color scores reflect inter-individual variation in maternal nutritional condition (see above), it is possible that rank does not capture such differences at Tsaobis, perhaps because most food resources are not monopolizable, or because subordinate females adopt foraging and social strategies that help to mitigate the costs of their low rank (Marshall, Carter, Ashford, Rowcliffe, & Cowlishaw, 2015; Sick et al., 2014).

Interestingly, looking at the color development of each body part separately, we found that the only body part affected by prenatal food availability was the ischial callosities. This suggests that the color scoring of different body parts could be used for different purposes; for example, ischial callosities are a better indicator of developmental pace than of age. Further investigations of the determinants of color changes at specific body parts showed that infants born in December-January have greyer muzzle tips for their age than others. However, the muzzle tip was scored on the lowest number of infants (N = 16), and such a small sample size questions the robustness of this result that was not replicated using other body parts. Using a larger dataset will be necessary to reach conclusive results.

Our study of the determinants of inter-individual variation of color-for-age is preliminary for several reasons. First, we were not able to explore the impact of other factors that are known to influence infant color transitions, like variation in social dynamics and infanticide risk (Bădescu et al., 2016) that are probably of considerable evolutionary significance for young chacma baboons (Cheney et al., 2004; Palombit, 2003). Second, further studies are needed to explore the correlation between age-related changes in coloration and developmental milestones like weaning age for chacma baboons. Testing whether color development co-varies with other dimensions of development would indicate if it could be used as a reliable indicator

of developmental pace that may ultimately be connected to fitness. In line with this suggestion, the transition from natal to adult fur coloration of wild ursine colobus (*Colobus vellerosus*) infants has been used as a proxy of developmental pace to show that high infanticide risk accelerates infant development (Bădescu et al., 2016). Finally, examining the potential effects of infant coloration on protective behavior from other group members, and on the level of alloparenting care received wherever it is relevant (Brent, Teichroeb, & Sicotte, 2008; Ross & Regan, 2000) could be an interesting perspective to test other hypotheses proposed to account for the evolution of natal coat in primates.

Our study demonstrates that monitoring the skin color transition of infant baboons is a non-invasive and accurate method to estimate age up to 8 months old, with a median accuracy of 10 days, which can decrease further if the same individual is scored repeatedly. Our study additionally highlights inter-individual variability in the ages of color transitions. This suggests that scoring the change in infants' body coloration can also be used to detect individual variation of developmental pace, and certain body parts are more variable than others for a given age, and thus represent promising candidates in this respect. In this context, food availability during prenatal life affected infant color-for-age in our population, suggesting that maternal nutritional condition during pregnancy plays a central role in infant color development. Further research is necessary to determine whether such scores correlate with broader aspects of development (morphological, behavioral, and physiological), and which body parts are most useful.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Mendeley data: http://dx.doi.org/10.17632/65vk9tck25.1

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FIGURES

Figure 1: Picture of an infant chacma baboon showing the different body parts scored in this study.

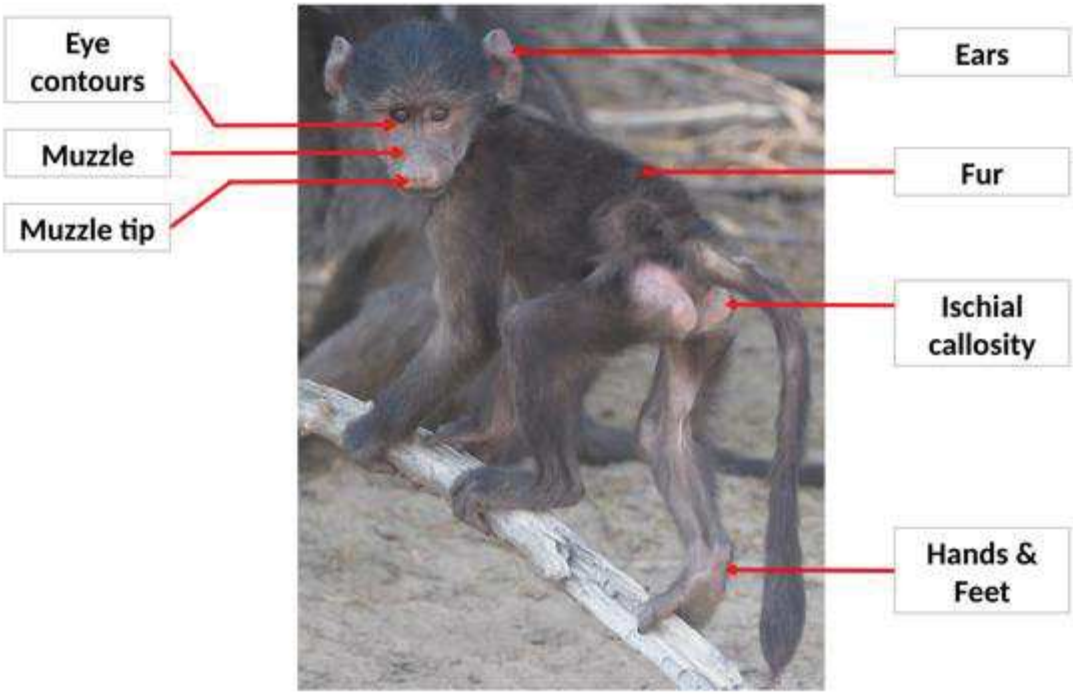


Figure 2: Pictures showing examples of color scores for different body parts.

The first column refers to score 1, i.e. pink skin for each body part, and black fur. The second column refers to score 2, i.e., body parts that are pinker than grey (this score did not exist for fur). The third column refers to score 3, i.e., body parts that are just as pink as grey (and for fur, just as black as grey). The fourth column refers to score 4, i.e., body parts that are greyer than pink (this score did not exist for fur). The last column refers to the score 5, i.e. grey for all body parts as well as for fur.

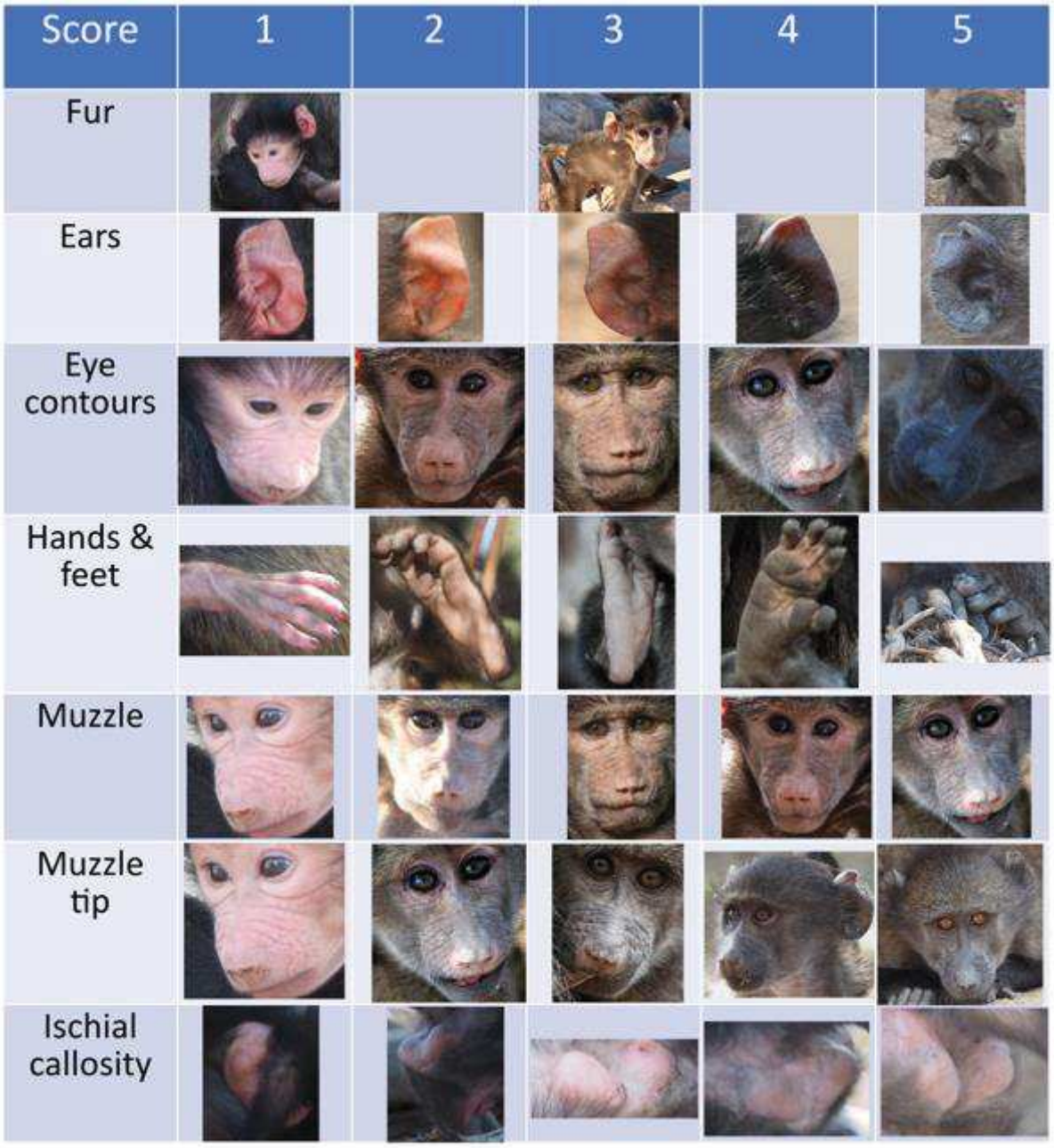


Figure 3: Color scores (from 1 to 5) of the different body parts of an infant according to its age (in months), using 242 observations on 73 infants with known birth date (Cohort 1).

Month 0 indicates an infant less than 1 month old, Month 1 indicates an infant aged between 1 and 2 months old, etc. Each boxplot color represents a body part (see legend for details, ISC refers to ischial callosities). The median value for each boxplot is represented by a diamond, and outlier points are indicated by dark red dots.

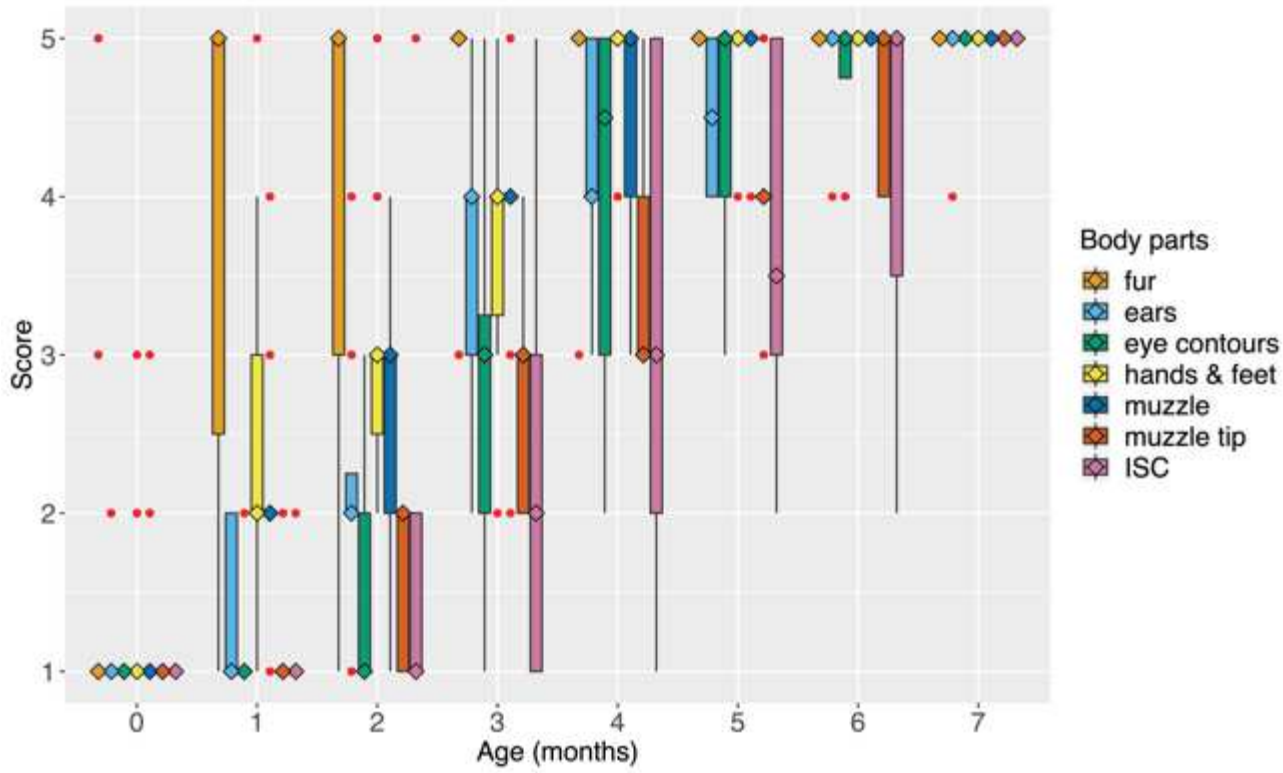


Figure 4: Weighted mean color score according to infant age (in days).

Each dot represents the age component smooth function of the weighted mean color score according to individual age. The red curve shows the fitted smooth effect, and the 95% upper and lower confidence intervals are represented by the dashed blue curves.

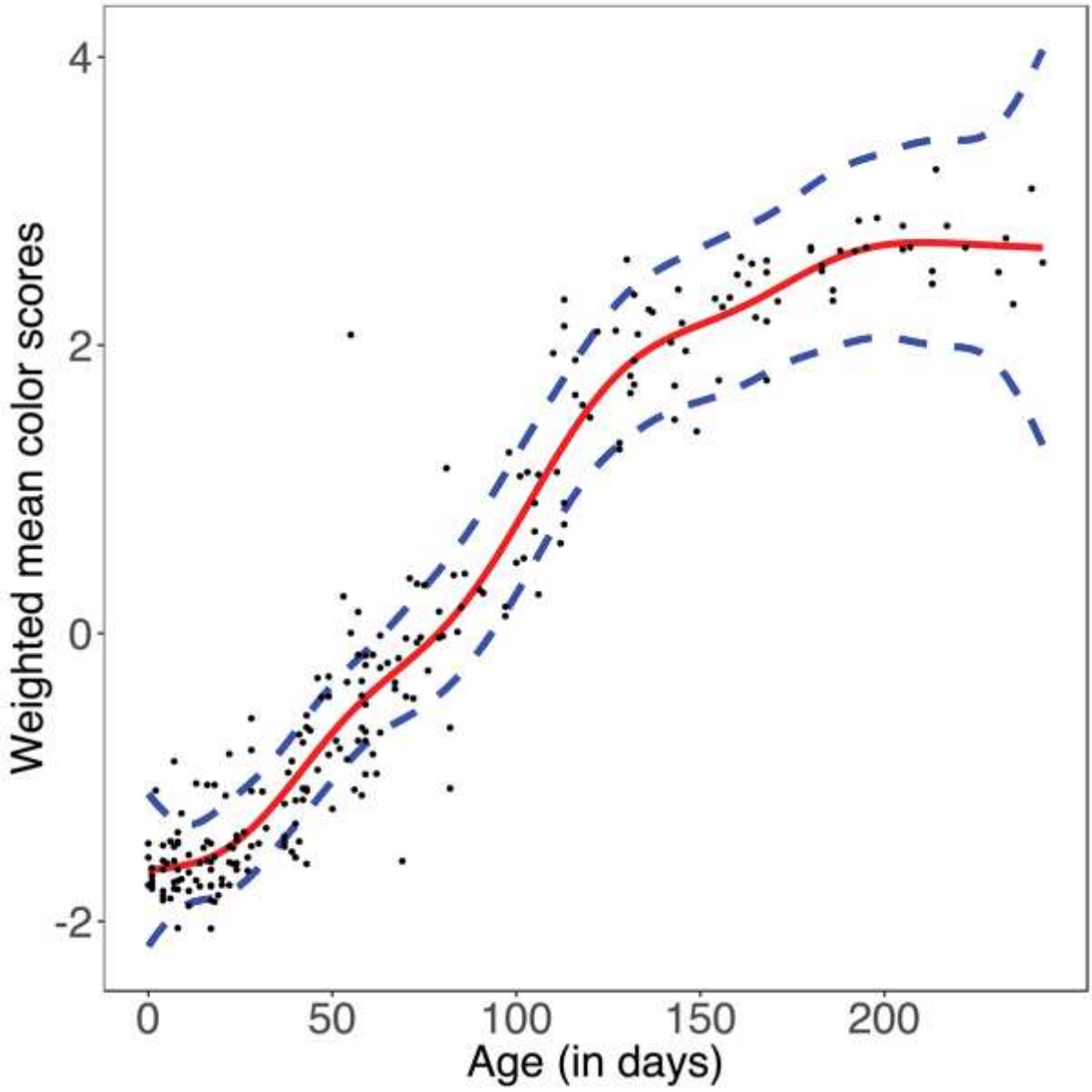
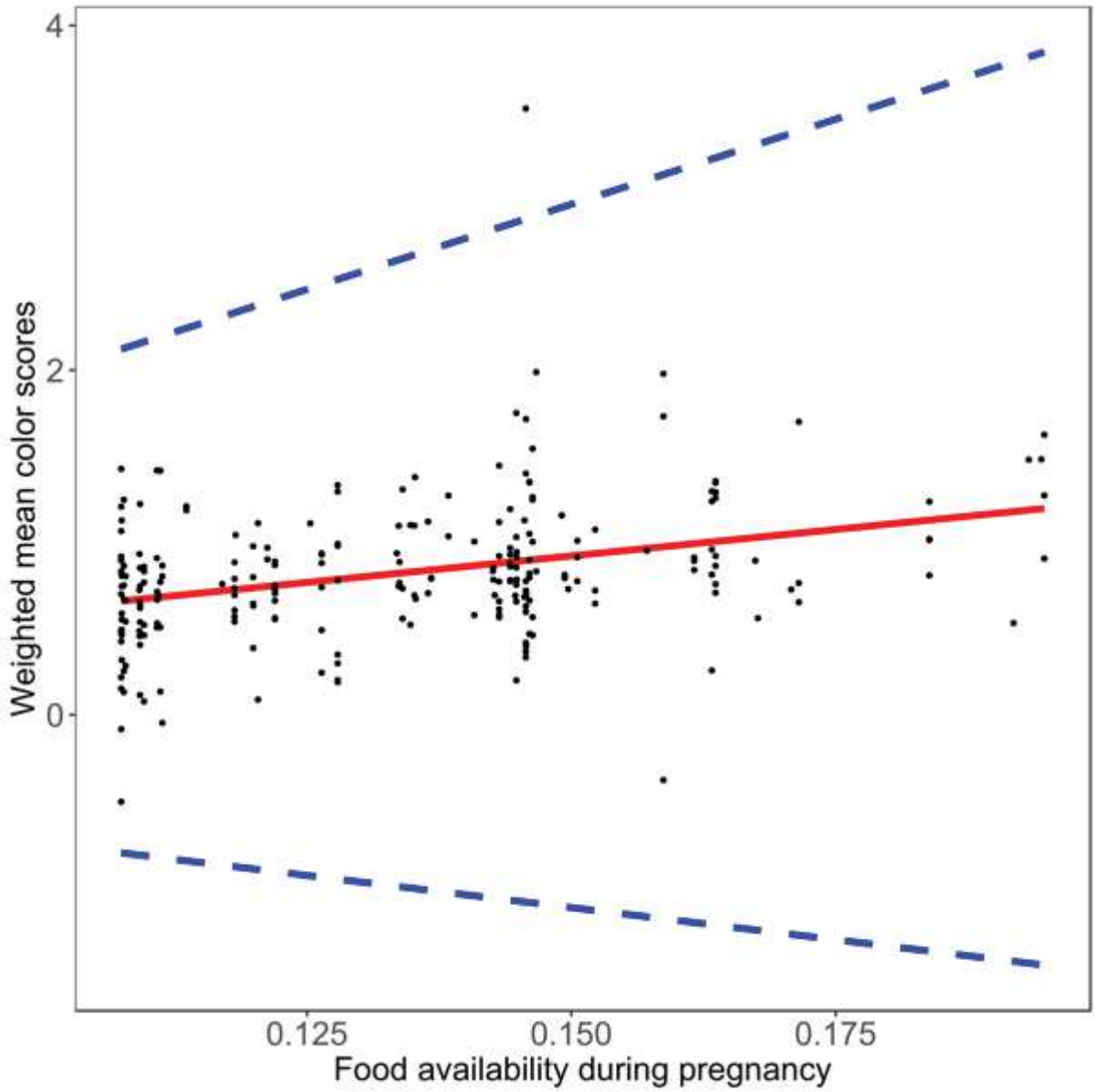


Figure 5: Effect of food availability during pregnancy on infant weighted mean color scores, controlled for infant age, identity and all other fixed effects included in our GAMM.

Each dot represents an observation (raw values). The red curve shows the fitted linear effect of food availability, and the dashed blue curves represent the 95% upper and lower confidence intervals.



Tables

TABLE 1: Correlation table between known ages and age estimates for each body part.

The correlation matrix was built using Spearman rank coefficients and using the full sample (242 observations from 73 infants).

Variable	Age (Months)	Fur	Ears	Eye contours	Hands & feet	Muzzle	Muzzle tip
Fur	0.86						
Ears	0.93	0.86					
Eye contours	0.90	0.84	0.92				
Hands & feet	0.95	0.89	0.94	0.92			
Muzzle	0.93	0.88	0.94	0.92	0.97		
Muzzle tip	0.91	0.85	0.93	0.95	0.92	0.93	
Ischial callosity	0.81	0.78	0.82	0.88	0.82	0.82	0.87

TABLE 2: Accuracy of age estimates using 70 observations from 22 infants (Sample 2), depending on the number of body parts considered, and on the number of levels of the color-scoring scale (3 or 5).

Accuracies were measured by the absolute number of days between actual and estimate age for each observation, which are given with their median and range.

Number of body parts considered †	7	6	5	4	3	2
5-level color scale						
Median	12.2	10.7	12.9	10.9	16.4	15.2
Range	0.1 - 95.3	0.1 - 86.4	0.1 - 79.2	0.5 - 87.3	0.5 - 82.4	1.4 - 70.8
3-level color scale						
Median	11.5	11.9	12.8	15.5	17.0	18.5
Range	0.1 - 93.2	0.2 - 95.0	0.1 - 97.0	0.6 - 70.9	1.2 - 74.5	0.1 - 70.2

†: We considered respectively the scores of the ears, muzzle tips, eye contours, muzzles, ischial callosities and hands and feet when 6; of the ears, muzzle tips, eye contours, muzzles and ischial callosities when 5; ears, muzzle tips, eye contours and muzzles when 4; ears, muzzle tips and eye contours when 3; and finally ears and muzzle tips when 2.

TABLE 3: Determinants of inter-individual variation in weighted mean color scores.

We computed parameter estimates (with their standard deviations) for each fixed effect, the Wald statistic (X^2) test, and P-values. For categorical parameters, the tested category is indicated between brackets. Food availability was indexed by the mean daily NDVI during pregnancy and an infant's birth timing in the annual cycle was represented by a sinusoidal term (with a phase of π /3). For smooth effects, we gave the effective degrees of freedom (Edf), the residual degree of freedom (Ref.df), the Wald Statistic (X^2) and the P-value. Significant effects are indicated in bold. Similar models were run on each body part separately, and corresponding results are presented in the electronic supplementary materials (Table S3).

Fixed effects	Estimate	Standard error	X^2	P-value
Intercept	**2.88**	**0.11**		
Food availability during pregnancy	**0.13**	**0.06**	**5.10**	**0.025**
Birth timing	0.06	0.10	0.33	0.57
Sex (Male)	0.03	0.12	0.08	0.77
Rank	0.10	0.06	2.63	0.11
Parity (Primiparous)	0.10	0.18	0.31	0.58
Group (L)	0.15	0.12	1.60	0.21
Smooth effects	Edf	Ref.df	X^2	P-value
Age	**7.10**	**8.03**	**219.9**	**$<1.10^{-3}$**
Infant identity	**40.9**	**66**	**1.88**	**$<1.10^{-3}$**

SUPPORTING INFORMATION

Table S1: Intra-class coefficients (ICC) for each body part.

We also computed the 95% confidence limits for ICC of each body part (ICC lower and upper limits), and indicated the number of observations used for this test (N), which varies across body parts.

Body Part	ICC	ICC lower	ICC upper	N
Fur	0.8	0.71	0.86	60
Ears	0.96	0.93	0.97	58
Eye contours	0.96	0.93	0.97	55
Hands & Feet	0.93	0.89	0.96	38
Muzzle	0.94	0.90	0.96	58
Muzzle tip	0.96	0.93	0.97	54
Ischial callosity	0.9	0.66	0.97	8

Table S2: Model selection performed to identify the best age fit to predict weighted mean color scores.

We ran four GAMMs with infant identity set as random effect and different functions of age as fixed effects. For each model, we computed the log likelihood, degrees of freedom, Akaike Information Criterion (AIC) and ΔAIC which is the AIC value between a given model and the model with the lowest AIC (indicated in bold).

Age effect	Log Likelihood	Model degrees of freedom	AIC	ΔAIC
Age	-140.9	52.9	387.7	53.6
Age + Age²	-141.7	46.5	376.5	42.4
Age + Age² + Age³	-118.2	51.6	339.5	5.4
spline(Age)	**-112.91**	**54.1**	**334.1**	**0**

Table S3: No significant effects of food availability during early-lactation on variation in weighted mean color scores.

We computed parameter estimates (with their standard deviations) for each fixed effect, Wald statistics (X^2) and P-values. For categorical parameters, the tested category is indicated between brackets. For smooth effects, we gave the effective degrees of freedom (Edf), the residual degree of freedom (Ref.df), the Wald Statistic (X^2) and the P-value. The food availability was indexed by the mean daily NDVI between infant birth and observation date (i.e. during lactation), and an infant's birth timing in the annual cycle was represented by a sinusoidal term of its date of birth, with a phase of $\pi/3$. Significant effects are indicated in bold.

Fixed effects	Estimate	Standard error	X^2	P-value
Intercept	**2.89**	**0.11**		
Food availability during lactation	0.07	0.05	1.91	0.17
Birth timing	-0.05	0.10	0.22	0.64
Sex (Male)	0.03	0.12	0.08	0.78
Rank	0.10	0.06	2.54	0.11
Parity (Primiparous)	0.12	0.19	0.43	0.78
Group (L)	0.12	0.12	1.02	0.31
Smooth effects	Edf	Ref.df	X^2	P-value
Age	**7.10**	**8.04**	**221.2**	**$<1.10^{-3}$**
Infant identity	**41.5**	**67**	**2.04**	**$<1.10^{-3}$**

Table S4: Determinants of variation in color scores for each body part.

We computed parameter estimates (with their standard deviations) for each fixed effect, Wald statistics (X^2) and P-values. For categorical parameters, the tested category is indicated between brackets. For smooth effects, we gave the effective degrees of freedom (Edf), the residual degree of freedom (Ref.df), the Wald Statistic (X^2) and the P-value. We indicated the number of observations (Nobs) and of scored individuals (Nind) for each response variable, i.e. for each body part. The food availability was indexed by the mean daily NDVI between infant conception and birth (i.e. during pregnancy), and an infant's birth timing in the annual cycle was represented by a sinusoidal term of its date of birth (with a phase of 0 for fur, $\pi/6$ for eye contours, $\pi/3$ for hands and feet and muzzle, and $\pi/2$ for ears, muzzle tips and ischial callosities). Significant effects are indicated in bold. Note that given the number of models (n=7), the significance threshold falls to $\alpha=0.007$ when applying a Bonferroni correction.

Scores of body part (response variable)	Fixed effects	Estimate	Standard error	X^2	P-value
Fur (Nobs=239 on Nind=73)	Intercept	-3.68	3.96		
	Food availability	40.1	26.8	2.25	0.13
	Infant date of birth	0.57	0.81	0.49	0.48
	Group (L)	-0.07	1.10	0.01	0.95
	Sex (Male)	-0.09	1.07	0.01	0.93
	Rank	0.58	1.68	0.12	0.73
	Parity (Primiparous)	-0.72	1.73	0.17	0.68
	Smooth effects	EDF	Ref.df	X^2	P-value
	Age	**3.75**	**4.58**	**73.8**	**$<1.10^{-3}$**
	Infant identity	**32.8**	**66.0**	**75.4**	**$<1.10^{-3}$**
Ears (Nobs=238 on Nind=73)	Intercept	-0.55	2.54		
	Food availability	9.35	16.67	0.31	0.58
	Infant date of birth	1.10	0.66	2.79	0.09
	Group (L)	1.19	0.71	2.84	0.09
	Sex (Male)	-0.19	0.71	0.07	0.79
	Rank	1.06	1.09	0.94	0.33
	Parity (Primiparous)	-0.15	1.13	0.02	0.89

	Smooth effects	EDF	Ref.df	X^2	P-value
	Age	**2.94**	**3.65**	**455.4**	**$<1.10^{-3}$**
	Infant identity	**21.96**	**66.0**	**49.9**	**$<1.10^{-3}$**
Eye contours (Nobs=202 on Nind=64)	Intercept	-11.4	5.11		
	Food availability	59.3	30.3	3.83	0.05
	Infant date of birth	1.02	1.25	0.66	0.42
	Group (L)	1.28	1.51	0.72	0.40
	Sex (Male)	3.19	1.56	4.21	0.04
	Rank	1.91	2.33	0.68	0.41
	Parity (Primiparous)	-1.39	2.24	0.38	0.54
	Smooth effects	EDF	Ref.df	X^2	P-value
	Age	**3.24**	**4.00**	**260**	**$<1.10^{-3}$**
	Infant identity	**24.0**	**57.0**	**96.7**	**$<1.10^{-3}$**
Hands & feet (Nobs=204 on Nind=66)	Intercept	4.14	3.24		
	Food availability	6.97	21.8	0.10	0.75
	Infant date of birth	0.89	0.90	0.96	0.33
	Group (L)	0.49	1.00	0.24	0.62
	Sex (Male)	-0.49	1.01	0.24	0.63
	Rank	1.67	1.60	1.08	0.30
	Parity (Primiparous)	-1.21	1.53	0.63	0.43
	Smooth effects	EDF	Ref.df	X^2	P-value
	Age	**3.33**	**4.11**	**325**	**$<1.10^{-3}$**
	Infant identity	**33.9**	**59.0**	**120**	**$<1.10^{-3}$**
Muzzle (Nobs=240 on Nind=73)	Intercept	-1.88	3.84		
	Food availability	46.7	24.8	3.55	0.06
	Infant date of birth	1.81	1.00	3.24	0.07
	Group (L)	0.98	1.09	0.81	0.37
	Sex (Male)	2.25	1.11	4.07	0.04
	Rank	1.57	1.70	0.86	0.35
	Parity (Primiparous)	-0.40	1.62	0.06	0.81
	Smooth effects	EDF	Ref.df	X^2	P-value

	Age	**3.83**	**4.67**	**451**	**$<1.10^{-3}$**
	Infant identity	**42.7**	**66.0**	**184**	**$<1.10^{-3}$**
Muzzle tip (Nobs=92 on Nind=16)	Intercept	3.74	9.47		
	Food availability	-26.0	79.4	0.11	0.74
	Infant date of birth	**3.59**	**1.16**	**9.65**	**2.10^{-3}**
	Group (L)	0.50	0.98	0.26	0.61
	Sex (Male)	-0.31	1.01	0.09	0.76
	Rank	1.46	1.53	0.91	0.34
	Parity (Primiparous)	-0.69	2.30	0.09	0.76
	Smooth effects	EDF	Ref.df	X^2	P-value
	Age	**1.00**	**1.00**	**138**	**$<1.10^{-3}$**
	Infant identity	0.76	9.00	0.89	0.31
Ischial callosity (Nobs=144 on Nind=47)	Intercept	-9.66	3.24		
	Food availability	**65.1**	**20.2**	**10.4**	**1.10^{-3}**
	Infant date of birth	2.06	0.83	6.18	0.01
	Group (L)	-0.59	1.00	0.35	0.00
	Sex (Male)	0.00	1.02	0.00	0.99
	Rank	1.44	1.68	0.73	0.39
	Parity (Primiparous)	1.60	1.52	1.12	0.29
	Smooth effects	EDF	Ref.df	X^2	P-value
	Age	**1.00**	**1.00**	**98.8**	**$<1.10^{-3}$**
	Infant identity	**17.9**	**40.0**	**42.0**	**$<1.10^{-3}$**

Figure S1: Decreased inaccuracy of infant estimated birth dates (in days) in relation to the number of observations per infant.

The inaccuracy is the absolute number of days between an infant actual birth date and its estimated birth date. The red curve shows the linear fit, and the shaded area indicates the 95% confidence interval around it.

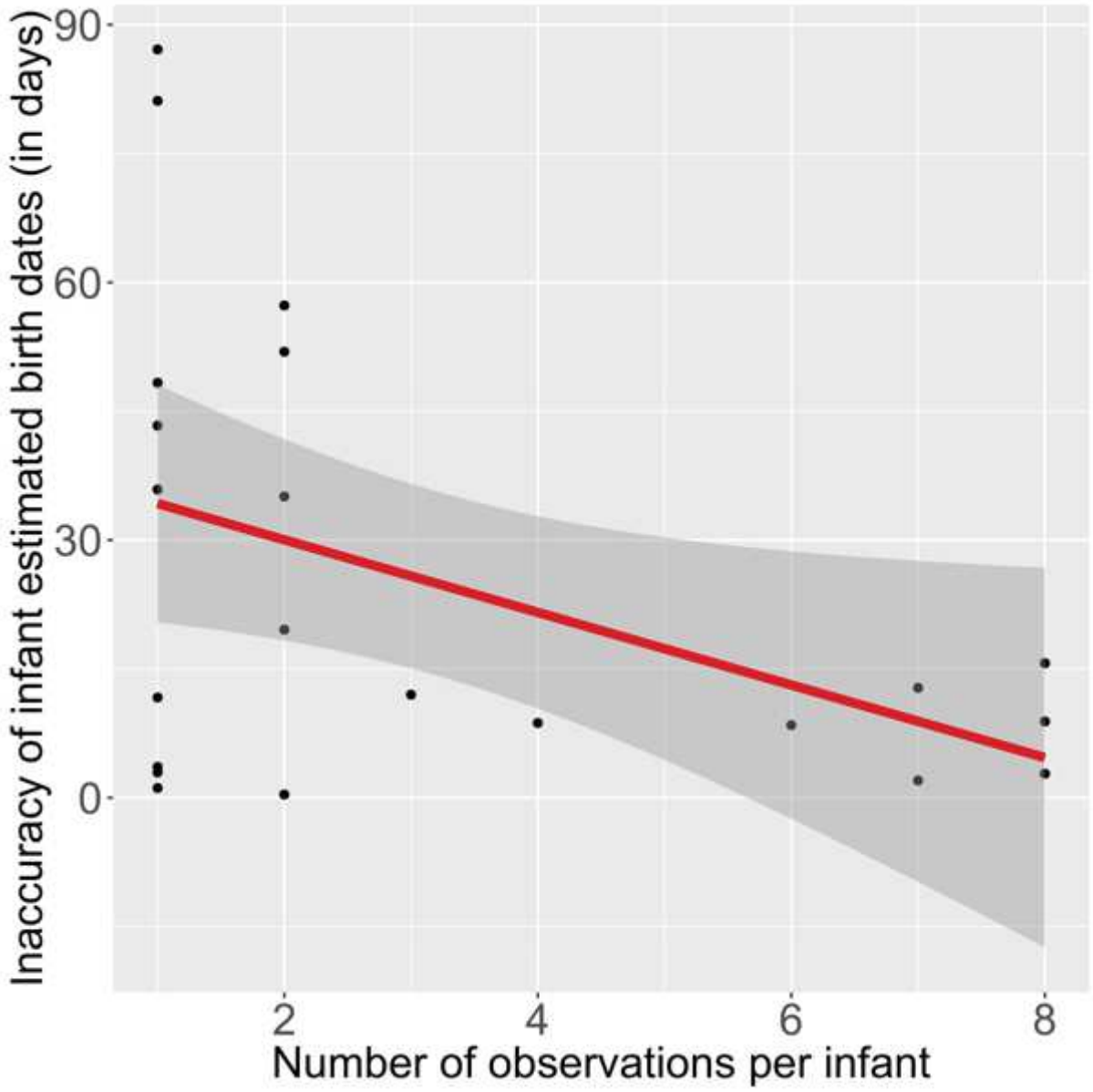


Figure S2: Increased inaccuracy of age estimation (in days) in relation to the actual age of the infant (in days).

The inaccuracy is the absolute number of days between an infant actual and estimated age per observation. The red curve shows the linear fit, and the shaded area indicates the 95% confidence interval around it.

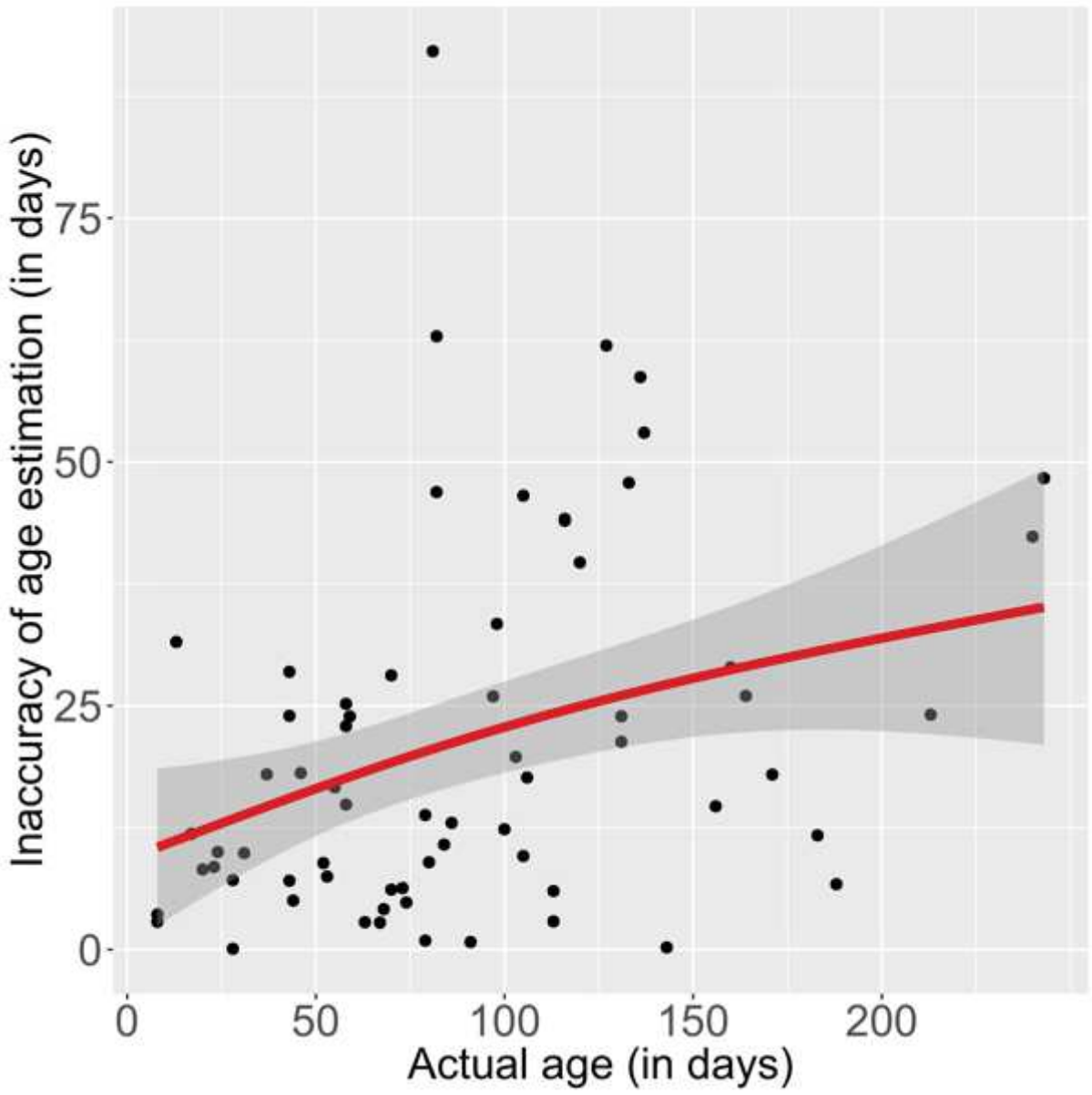
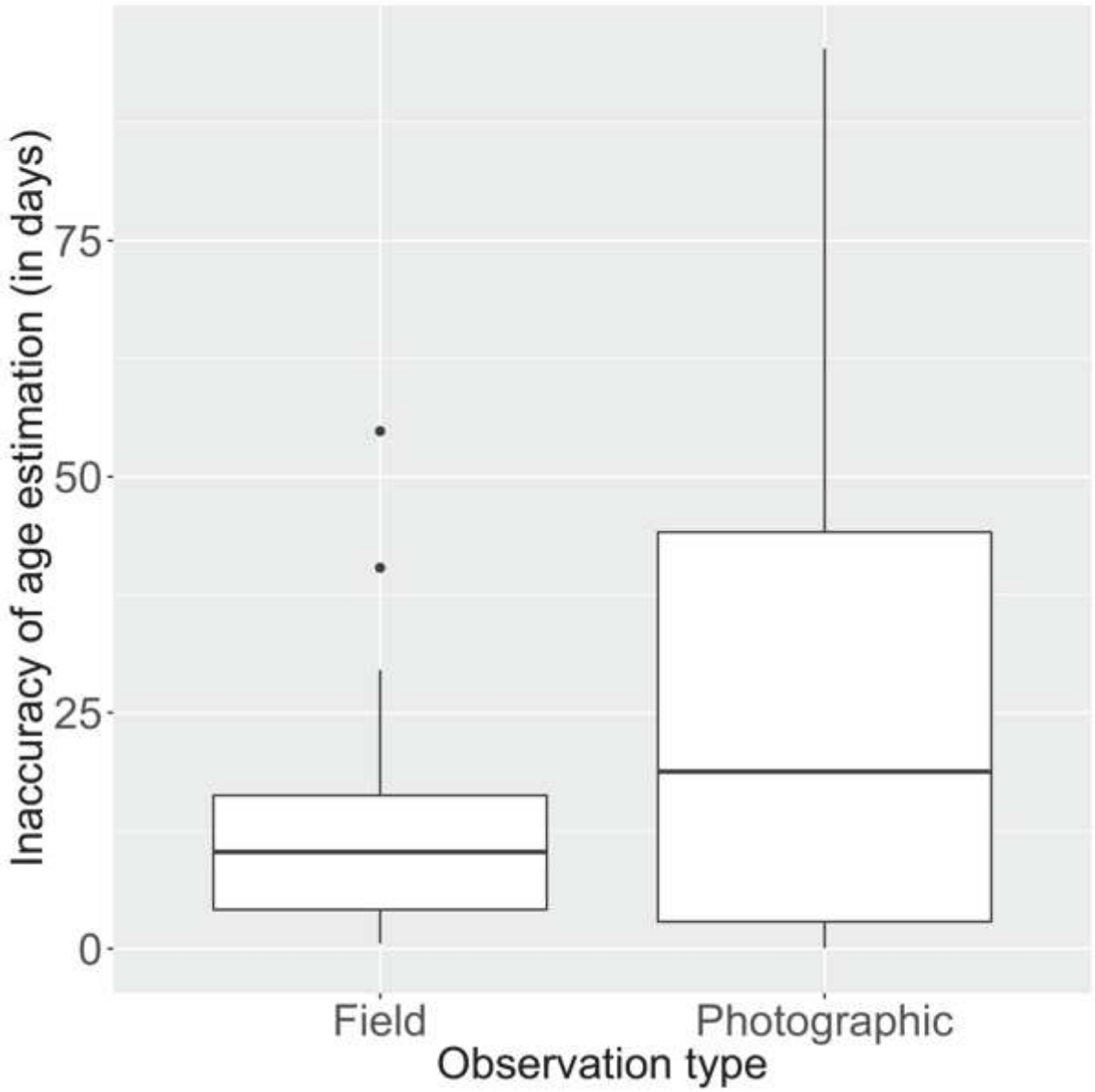


Figure S3: Inaccuracy of infant age per estimation (in days) according to the observation type, i.e. field of photographic observation.

The inaccuracy is the absolute number of days between an infant actual and estimated age per observation.



Keats



Chapter 3

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

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(Article ready to be submitted)

SUMMARY

The evolutionary benefits of reproductive seasonality are usually measured by a single fitness component, namely offspring survival to nutritional independence [1]. Yet different fitness components may be maximised by dissimilar birth timings. This may generate fitness trade-offs that could be critical to understanding variation in reproductive timing across individuals, populations and species. Here, we use long-term demographic and behavioural data from wild chacma baboons (*Papio ursinus*) living in a seasonal environment to test the adaptive significance of seasonal variation in birth frequencies. Like humans, baboons are eclectic omnivores [2], give birth every 1-3 years to a single offspring that develops slowly [3,4], and typically breed year-round [5]. We identify two distinct optimal birth timings in the annual cycle, located 4-months apart, which maximize offspring survival or minimize maternal interbirth intervals (IBIs), by respectively matching the annual food peak with late or early weaning. Observed births are most frequent between these optima, supporting an adaptive trade-off between current and future reproduction. Furthermore, infants born closer to the optimal timing favouring maternal IBIs (instead of offspring survival) throw more tantrums, a typical manifestation of mother-offspring conflict [6]. Maternal trade-offs over birth timing, which extend into mother-offspring conflict after birth, may commonly occur in long-lived species where development from birth to independence spans multiple seasons. Such trade-offs may substantially weaken the benefits of seasonal reproduction, and our findings therefore open new avenues to understanding the evolution of breeding phenology in long-lived animals, including humans.

RESULTS

Empirical studies investigating variation in reproductive timing have mostly focused on fast-lived seasonal breeders, whose development from birth to independence generally occurs within the most productive season [1]. In long-lived mammals, the reproductive cycle from birth to weaning cannot similarly be squeezed into one annual food peak, and consequently, females must choose which stage(s) of the reproductive cycle to synchronize with one or more food peak(s). For example, female mammals could match the annual food peak to coincide with either late-weaning or mid-lactation, but usually not both. The reproductive timing strategy is likely to depend on how females trade-off the survival of their offspring (mortality risks tend to peak at the end of weaning) [7–9] with their own reproductive costs (energetic demands tend to peak around mid-lactation) [10,11]. Whether such reproductive timing strategies can vary within populations is largely unknown. In addition, while evolutionary trade-offs between offspring quality and quantity have been described both within and across species, through associations between birth spacing and infant growth and survival [12–16], the existence of maternal trade-offs over birth timing have only been suggested theoretically [8] and never tested empirically in mammals (but see for a bird species, *Fulica atra*: [17]).

Here, we investigate variation in maternal reproductive success and mother-offspring relationships associated with variable birth timings in the annual cycle of wild chacma baboons (*Papio ursinus*), living in a seasonal semi-arid savannah (Tsaobis, Namibia). Baboons are African primates distributed across a wide latitudinal range, and a classic model for understanding how early humans adapted to seasonal savannahs [18,19]. In particular, baboons typically breed year-round [5], and are therefore considered non-seasonal breeders, though the distribution of births shows moderate seasonality (i.e. varies along the annual cycle) in some species and populations [20–22]. In addition, infant baboons, like many young primates including human toddlers, commonly perform tantrums, a manifestation of mother-offspring

conflict [6,23–25]. Using a combination of detailed long-term life-history and behavioural data collected over 15 years (2005-2019), we first characterize the reproductive and environmental seasonality of the Tsaobis baboons. Second, we quantify the consequences of birth timing on two components of female fitness: offspring survival and maternal inter-birth intervals (IBIs), and identify two distinct birth timing optima. We further test whether individual traits predict whether a female is more likely to give birth around one or the other optimum. Third, we investigate if compensatory maternal care mitigates the costs of suboptimal birth timing for offspring, and whether infants born, and subsequently weaned, in suboptimal timings increased their tantrum frequency.

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

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

Environmental seasonality was pronounced at Tsaobis (Figure 1A). Mean annual rainfall was low and variable (mean ± SD = 192 ± 143mm), falling mostly between January and April (Figure 1A). Following previous baboon studies [26,27], we quantified food availability for baboons using the Normalized Difference Vegetation Index (NDVI), a satellite-based proxy of primary productivity with higher values corresponding to a higher degree of

greenness [28]. Seasonal variation in NDVI followed a similar, but slightly lagged pattern, to rainfall (Figure 1A). The highest birth frequency occurred in October-November, preceding the peak in rainfall (February) and NDVI (March-April, Figure 1A).

2. Distinct birth timings optimize current versus future reproduction

There was an influence of birth timing on two indicators of maternal fitness. First, birth timing affects offspring survival (Table S1): infants born between November 15th and January 1st were the most likely to survive until weaning (Table S2), indicating an optimal birth timing for offspring survival in the annual cycle (Figure 2A). Second, the duration of maternal IBI is influenced by the timing of the birth opening the IBI (Table S1): females giving birth between August 1st and September 15th had the shortest IBIs (Table S2), indicating another different optimal birth timing for maternal reproductive pace in the annual cycle (Figure 2B). In the first case, the birth timing that maximises offspring survival synchronizes the seasonal food peak with the end of weaning, a highly vulnerable life stage for mammals [2,3,29], which occurs between 12 and 18 months after birth in this population (Figure 1B). In the second case, the birth timing that maximizes maternal reproductive pace synchronizes the food peak with the peak of lactation (occurring around 6 months after birth) (Figure 1B), which is the most energetically-costly reproductive stage for mothers [3,8], and may therefore help to alleviate the costs of lactation and enhance maternal condition during the second half of lactation. The observed moderate birth peak (Figure 1A), with 28.4% of births occurring in October-November and a mean annual birth date of Nov 18th, falls between these two birth optima, indicating a maternal reproductive trade-off over birth timing (Figure 2C).

This result raises the possibility that some females might be more likely to time their births to maximise current over future reproduction, or vice versa. In particular, dominance rank

and parity can affect various aspects of individual reproductive performance, including offspring survival and IBI [30–32], and may influence birth timing strategies accordingly. Similarly, mothers conceiving close to the optimal timing for maternal IBIs, which alleviates the energetic costs of lactation, may subsequently favour male over female embryos, which are more costly to produce in sexually dimorphic mammals [30,33,34]. However, we failed to detect any significant variance associated with maternal identity on the deviation between observed birth and the optimal birth timing maximizing offspring survival (LRT=0.66, p=0.42) versus maternal IBI (LRT=0.00, p=0.99). This suggests that females did not consistently target one timing over the other across successive births. Moreover, female parity, rank and infant sex did not influence the proximity of birth timing in relation to each optimum (Table 1).

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

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

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

DISCUSSION

Our results further our understanding of the evolution of vertebrate reproductive timing in several ways. First, we identify two distinct optimal birth timings in the annual cycle, respectively favouring current reproduction (offspring survival) versus future reproduction (maternal reproductive pace). These are separated by four months, and the highest birth frequency occurs between these optima, indicating that mothers trade-off current and future reproduction. Trade-offs over birth timing may be widespread in long-lived species with slow life histories, for which development from birth to independence spans several months, therefore exceeding the length of the most productive season. In such cases, different stage(s) of the reproductive cycle may be synchronized with one or more seasonal food peaks, with the specific pattern dependent on the trade-offs females make among different fitness components. Such variation could account for empirical cases where the observed birth peak fails to coincide with the birth timing expected on the basis of a single fitness measure. For example, in humans from pre-industrial Finland, births did not concentrate in the months with the highest infant survival expectations [35]. More generally, such trade-off may contribute to explain the partial or total lack of breeding seasonality observed in some large mammals [36], such as social primates including apes [22] and humans [37,38].

Second, this study challenges the idea according to which non-seasonal breeding has evolved in response to an absence of optimal birth timing in the annual cycle, especially in species with ecological or physiological traits that buffer seasonal environmental variation [39]. For example, chacma baboons and humans share a generalist diet [2], a capacity to extract fall-back foods at times of food scarcity [40], and an ability to store energy [7,9], which have likely played a critical role in their adaptation to breed year-round in seasonal environments [38,41]. The few studies that have investigated the effects of birth timing on early survival of offspring in non-seasonal breeders such as geladas (*Theropithecus gelada*) [42] have indeed failed to

detect any effect. In modern humans, fitness variation associated with seasonal birth timing is rare [38,43], and where detectable, only has mild effects on adult longevity [44,45]. The fitness consequences of seasonal birth timing detected here were therefore unexpected, and surprisingly reveal that non-seasonal breeding can be favoured even where reproductive success depends on birth timing. Future work will usefully test the generality of these patterns in other species or populations that breed year-round to shed more light on the conditions favouring evolutionary transitions towards non-seasonal breeding.

Third, while different species synchronize different stages of their reproductive cycle with the seasonal food peak [1,7,46,47], this study reveals variations in breeding timing within the same population. However, while mothers experience a trade-off between reproductive pace and offspring survival in their birth timing, it does not appear that they make a strategic choice about where they sit along the trade-off continuum, as we did not detect any effects of female identity, parity or rank on parturition timing. The duration of IBIs - 22 months on average but with extensive variation - prevents females from giving birth every two years at the same season. In addition, other factors, such as maternal reproductive history, may further constrain individual birth timing. Ultimately, the costs of waiting for the next optimal timing may outweigh the costs of giving birth at suboptimal timings.

Fourth, this study underlines the importance of weaning to understand the evolution of mammalian reproductive schedules. Late-weaning is most critical for infants who must learn to ensure their own provisioning. Matching that stage with the most productive season may substantially enhance infant survival [2,3,48,49]. Moreover, the peak of lactation typically coincides with the onset of weaning, and matching it with abundant resources can help to accelerate the transition to feeding independence by granting infants access to a wealth of weaning foods (Figure 1B) [3]. Earlier weaning, in combination with better maternal nutritional condition, will likely promote the resumption of cycling [50–52], and may contribute to explain

the shorter interbirth intervals associated with this birth timing. Such patterns may be very general. In the lemur radiation, for instance, despite a variety of life-histories, ecologies and societies, and the fact that different species mate and give birth at different times of year, all species synchronize weaning with the food peak [48]. Our understanding of the ultimate causes of mammalian reproductive seasonality may gain from granting more consideration to the dynamics and consequences of weaning, which may have been underappreciated in comparison to the energetic costs of pregnancy and lactation [1,7,9].

Fifth, our results show that the trade-off over birth timing faced by mothers may subsequently translate into mother-offspring conflict after birth. Although mothers adjust maternal care seasonally, they do so regardless of the offspring's age. Offspring born at suboptimal periods face the dry season in a critical developmental window (i.e., the end of weaning), and maternal care is insufficient to buffer them entirely from the adverse consequences that lead to higher mortality. Consequently, baboon infants respond by throwing more tantrums, which may be an honest signal of need [24,53], just as children do in similar situations [25]. More generally, these results shed light on the potential influence of environmental fluctuations, and specifically seasonality, on mother-offspring conflicts over maternal care. While the literature focusing on optimal birth spacing has mainly examined trade-offs between current and future reproduction for an implicitly stable level of resources [12,54], such a stability may rarely be encountered by mothers in the wild [55,56], who typically face extensive, but partly predictable, fluctuations in food availability. Taking into account the intensity and predictability of resource fluctuations may largely re-draw the landscape of strategic decisions available to mothers confronted with trade-offs between current and future reproduction in natural environments [56,57].

Our findings open new perspectives to understand the evolutionary drivers of vertebrate reproductive seasonality, by revealing the occurrence of a maternal trade-off between current

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

METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental Models: Organisms/Strains		
chacma baboons (*Papio ursinus*)	N/A	N/A
Software and Algorithms		
R v.3.5.2.	[58]	https://www.r-project.org
Package CircStats	[59]	https://cran.r-project.org/web/packages/CircStats/CircStats.pdf
Package lme4	[60]	https://cran.r-project.org/web/packages/lme4/lme4.pdf
Package blme	[61]	https://cran.r-project.org/web/packages/blme/blme.pdf
Package mgcv	[62]	https://cran.r-project.org/web/packages/mgcv/mgcv.pdf
Package car	[63]	https://cran.r-project.org/web/packages/car/index.html
Package ggplot2	[64]	https://cran.r-project.org/web/packages/ggplot2/index.html
Package adehabitatHR	[65]	https://cran.r-project.org/web/packages/adehabitatHR/index.html
Package DHARMa	[66]	https://cran.r-project.org/web/packages/DHARMa/index.html
MatMan 1.1.4	N/A	http://www.noldus.com/knowledge-base/matman

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources and protocols should be directed to and will be fulfilled by the Lead Contact, Jules Dezeure (dezeurejules@gmail.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

All data and codes to analyze them are available in the following GitHub repository: https://github.com/JulesDezeure/Maternal-trade-off-over-birth-timing-in-baboon.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Three habituated groups of wild chacma baboons were followed between 2005 and 2019: J and L since 2005, and M, a fission group from J, since 2016. They live in a desert-edge population at Tsaobis Nature Park (22°23S, 15°44’50E) in Namibia, in a strongly seasonal environment: the desert vegetation responds quickly to the austral summer rains, which usually fall between December and April, and then dies back during the dry winter months [67]. Water is always available through the presence of both natural seeps and artificial water points for wildlife and livestock. A field team was present each year, mainly during winter (between May to October), for a variable number of months (mean = 4.5, range: 1.9-7.9), that collected daily demographic and behavioural data, as well as GPS locations, while following the groups on foot. All individuals, including infants, are individually recognizable thanks to small ear markings performed during capture and/or other distinctive features.

METHOD DETAILS

Environmental data

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

Daily rainfall in a 0.25 × 0.25 degree grid cell resolution (corresponding to 28 × 28 km at this latitude) was extracted using satellite data sensors from the Giovanni NASA website (product TRMM 3B42) [68], from a rectangular geographic area encompassing the global ranging area of the Tsaobis baboons, computed using GPS locations collected by observers every 30 min when following the study groups. We used the minimal and maximal latitude and longitude recorded between 2005 and 2019. Monthly cumulative rainfall (summed across daily values) were computed between 2005 and 2019.

We used the Normalized Difference Vegetation Index (NDVI) as an index of food availability. NDVI is computed using the near-infrared and red light reflected by the surface of an area and measured with satellite sensors; it produces a quantitative index of primary productivity with higher values corresponding to a higher degree of vegetation cover [28]. It has previously been used as an indicator of habitat quality for the Tsaobis baboons [27] and other baboon populations [26]. We further confirmed that temporal variation in NDVI reflected temporal variation in rainfall: mean cumulative rainfall over the past three months explained between 60-72% of the NDVI variation (Appendix 2). To index food availability using NDVI for each troop, we first computed 100% isopleth home ranges for each group using kernel density estimates with the adehabitatHR package (‘kernelUD’ function) [69], based on the daily 30-min GPS locations from 2005-2019 (from 2016-2019 for M group). We obtained one home

range per group for the entire study period. We then extracted the mean NDVI per 16 day-period on a 500 m × 500 m resolution across these periods using MODIS data (MODIS13A1 product) provided by NASA [28] within these home ranges for each group. Daily NDVI was computed by linear interpolation and then averaged to obtain a monthly value. In contrast to rainfall, NDVI was measured with greater resolution and for each group separately because baboons finely adjust their ranging behaviour in relation to food availability [70].

Individual data

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

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

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

Fitness data

We tested the influence of birth timing in the annual cycle on two fitness measures, namely offspring mortality before weaning and the duration of the maternal interbirth interval. For each infant born between 1st January 2005 and 1st August 2018, we investigated whether it died (yes/no) before weaning. The weaning age was identified as 550 days on the basis of the maximum length of post-partum anoestrus (n = 33 cases for which both birth and cycle resumption were known with accuracy, see also Appendix 4), and presumably reflected the upper threshold of weaning age in our population, assuming that females who resumed cycling had weaned their offspring, as lactation has suppressive effects on ovulation among primates [50,51,72]. Death was recorded when a corpse was observed or when the infant had been missing in the group for five consecutive days. Infants born later than August 2018 were not considered as their survival outcome was unknown. Four infants that disappeared between consecutive field seasons were omitted because we could not establish whether the age of death was before or after 550 days. In our final dataset, a total of 39 infants out of 195 died before

reaching 550 days of age, with mortality occurring at a median age of 74 days (range 1-284 days, n=17 known dates of death).

We defined interbirth intervals (IBI) as the number of days between two consecutive live births of the same female. We only considered IBIs for which the first infant reached weaning, i.e. survived until 550 days old [30]. We discarded other IBIs as females resumed cycling rapidly after their infant's death when unweaned (median=21 days, range=9-51, n=9 observed death), and their IBIs would have been shortened regardless of environmental seasonality. We computed a total of 120 interbirth intervals from 43 adult females, ranging from 397 to 1132 days with a mean of 678 days (SD=128).

Behavioural observations

In order to characterize variation in maternal care and in mother-offspring conflict, we used three behavioural indicators: suckling, infant carrying and tantrum frequencies. We also used these behavioural data, along with life history data, to assign different developmental stages, including the different stages of weaning and the peak of lactation after an infant's birth (see Appendix 4). In addition to life-history data, field observers collected behavioural data on infants aged between 2 and 24 months on a daily basis from dawn until dusk over four periods: from October to December 2006, from July to August 2017, from September to December 2018, and from April to July 2019. We collected a total of 1185 hours of focal observation on 69 infants across four field seasons (mean ± SD = 17.1 ± 7.8 hours of observations per infants, range = 6.3–34.6), with a mean of 40.7 focal observations per individual (SD=29.4). Focal observations were spread equally across the day (divided in four 3-h-long blocks) and focal individuals were chosen randomly, and never sampled more than once within a block. Focal observations durations were 1 h in 2006 and 20 min in 2017-2019, with a minimum of 10 min

in all cases. We recorded the following activities on a continuous basis: suckling (when the focal individual had its mouth on its mother's nipple; we could not distinguish comfort from nutritive suckling), travelling alone, infant carrying (carried by the mother, either ventrally or dorsally) and other activities. We also collected events related to mother-offspring conflicts (see below). In addition, we collected scan observations every 5 minutes (n=16702 scans across 3081 focal observations), including the activity of the focal individual.

Maternal care during weaning

Maternal care was quantified through two measures: suckling frequency and infant carrying frequency, which represent the two main energetic costs of maternal care before weaning [10,73]. First, for each scan observation (taken every 5 min), we considered whether the infant was suckling (1) or not (0) to investigate the effect of birth timing on variation in suckling frequency. In order to determine the best age window to consider, we explored age-related variation in suckling frequency, and found that suckling decreases gradually from 2 to 18 months old, before stabilizing to ca. 2% of the scans from 18 to 24 months old (Figure S2). In addition, the maximum length of post-partum amenorrhea, often used as a proxy for the end of weaning, lasted 550 days (i.e. 18.1 months) in this population (see above). Therefore, we considered only infants aged 2- to 18-months-old for this analysis, using 11687 scans from 55 infants. The birth date uncertainty for these 55 infants ranged from 0 to 130 days (with a median birth date uncertainty of 16 days) and was taken into account in subsequent models (see Appendix 5).

Second, for each scan observation during which an infant was travelling, we determined whether the infant was carried by its mother (1) or travelled on its own (0). This variable allowed us to monitor the gradual decrease from full maternal dependence to full independence

during travelling. When looking for the best age window to consider, we observed that the proportion of infant carrying gradually decreases during the first year of life in our population (Figure S2), as in other baboon populations [73–75]. Therefore, we considered infants aged from 2 to 12 months old for this analysis, using 924 scans from 35 infants.

Mother-infant conflicts during weaning

We considered infant tantrums as a behavioural measure of mother-offspring conflicts, reflecting when an infant's request to access resources from its mother was not initially satisfied [6]. Tantrum occurrence started in early-life, peaked when infants were aged around 6-9 months, and then gradually decreased during the end of their first and second year of life (Figure S2). Therefore, we considered only infants aged 2 to 18 months old for this analysis, using 2221 focal observations from 55 infants. During each focal observation, we determined if a tantrum occurred (1) or not (0), based on a range of distinctive offspring vocalizations (gecks, moans and loud screams) and behaviours (frenzied behaviour when infants hurl themselves to the ground, sometimes accompanied by rapidly rotating their tail) that were recorded on a continuous basis and are characteristic of baboon tantrums [24,75]. A tantrum was considered to occur when at least two of these behaviours or vocalizations were recorded, separated by at least 30s (isolated complaints, and complaints that lasted fewer than 30 seconds, were thus not considered as tantrums here). Tantrums were usually caused by maternal refusal of access to the nipple or to carrying, and more rarely by maternal absence.

QUANTIFICATION AND STATISTICAL ANALYSIS

Characterization of the reproductive seasonality of the Tsaobis baboons

First, to assess the strength and direction of reproductive seasonality, we used a Rayleigh test, from circular statistics, which characterizes the deviation of circular data from a uniform distribution, via the mean direction μ and length R of the vector summing all observed events across the annual cycle (R=0 when the event is evenly distributed, and R=1 when all events are synchronized, i.e. occurs the same day) [76]. Our sample comprised 241 conceptions, 215 births and 171 cycle resumptions which occurred between 2005 and 2019. Uncertainties in those dates were taken into account using 1000 randomized reproductive events for each variable (Appendix 5).

Birth timing effects on two fitness traits

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

In both models, we used a sine term to describe the timing of an infant's birth in the annual cycle. Sine waves allow the introduction of a circular variable into a multivariate model as a fixed effect: the possible effects of the date of birth are circular with a period of one year, as January 1st is equally close to December 31st than to January 2nd. This sinusoidal term was as follows:

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

The date of birth in the formula above was converted in a radian measure, so that the period, i.e. one year, equalled to 2*π, ranging from 2*π/365 for January 1st to 2*π for December 31st. We tested 12 different phase values φ (0, π/12, 2*π/12, 3*π/12, 4*π/12, 5*π/12, 6*π/12, 7*π/12, 8*π/12, 9*π/12, 10*π/12, 11*π/12), to account for different potential optimal periods for the event of interest across the year [27], as offspring mortality and IBI could be minimized for

different birth dates (and so tested all potential dates as minimal). For example, a phase of 0 could maximize April 1st or October 1st depending on the sign of the estimate (see Table S2). We ran sequentially these 12 multivariate models, containing all other fixed and random effects (see below), and selected the best phase as the one minimizing the Akaike Information Criterion (AIC) in this full model set: the phase of $7*\pi/12$ was retained for offspring mortality probability, and of $2*\pi/12$ for IBI (Table S2). We controlled for birth date uncertainty in both models using a set of 1000 randomized birth dates within the interval of uncertainty (see Appendix 5 for more details).

In both models, we included as random effects year of infant birth and identity of the mother to control for repeated observations. In both models, we also included maternal parity, rank (in the birth year of the focal infant) and infant sex as fixed effects, because maternal parity and rank often affect reproductive traits in primates, including baboons [4,30,77], while infant sex can affect both the mother's subsequent interbirth interval [78] and the probability of infant survival in sexually dimorphic primates [3,33]. We also control for group identity as a fixed effect in both models, as data were collected from only three groups in this study [79].

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

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

offspring survival. IBIs are minimised on September 1st (Table S2), and we thus computed, for each birth date, the deviation in days from September 1st (the maximum value of the deviation being 182 for March 1st). We used this deviation as a response variable of an LMM (Model 4), to investigate the individual determinants of giving birth close to, or away from, the timing that minimizes the maternal IBI.

For both Models 3 and 4, we tested the influence of infant sex, female parity and rank (as fixed effects) on the proximity of birth to the optimal timing for offspring survival (Model 3) or for maternal IBI (Model 4). We also controlled for the identity of the mother and birth year as random effects, and for group identity as fixed effects (as there was only three levels for this factor [79]). We tested the significance of maternal identity using a likelihood-ratio test (LRT), comparing the model with and without this random effect. We controlled for birth date uncertainty in these models using a randomization procedure described in Appendix 5.

Birth timing effects on maternal care and tantrum probability

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

In order to investigate the potential effect of birth timing on maternal care and tantrum probability, we used a sine wave term for infant birth date as a fixed effect, following the method explained for Models 1-2. We did so to examine natural minimums or maximums in the frequency of each of these traits along the annual cycle, without making any *a priori*

hypothesis on which periods were minimized or maximized, in order to test whether the observed maximums or minimums would match the periods previously identified as the optimal timings favouring current versus future reproduction. We therefore tested 12 different phases in each full model and retained a phase of $9*\pi/12$ for suckling, 0 for infant carrying, and $2*\pi/12$ for tantrum probabilities. We controlled for birth dates uncertainty in all three models using the randomization procedure described in Appendix 5.

We included, as random effects, the identity of the infant (Models 5-7) to control for repeated observations. We also added the focal observation as a random effect for Models 5-6. We controlled for group identity and year of observation as fixed effects in all models, as there were less than five levels for both factors [79]. In all models, we included maternal parity, rank (in the year of birth of the focal infant) and infant sex as fixed effects. Such parameters are likely to affect reproductive performances as well as the probabilities of maternal care and mother-offspring conflict [3,75]. For Model 7, we also controlled for the duration of focal observation as a fixed effect.

For Models 5-7, we further controlled for the effects of infant age, which modulates the amount of maternal care and probability of tantrums throughout early development [3,6]. We considered four different possibilities for the form of the relationship between infant age and the response variable, using a regression thin plate spline (general additive model), a simple linear effect, and a polynomial regression (of 2 or 3 degrees), respectively [80]. To determine the best fit, we ran these different preliminary models with no other fixed effect but including all random effects (and the duration of focal observation for Model 7), and selected the model minimizing the AIC. The age effect was linear for suckling and infant carrying probabilities (Model 5 and 6), and a second-degree polynomial for tantrum probability (Model 7).

Lastly, mothers might be expected to invest more, and similarly infants might be expected to have more requests for maternal care, during the lean season, irrespective of the

developmental trajectory of the infant, i.e. regardless of its age and birth timing (whether it was born in the optimal period or not). Therefore, we also investigated the potential effect of seasonality by assessing the influence of the observation date on suckling, infant carrying and tantrum probabilities (see Appendix 1 for more details). We did not include in the same model observation date and birth date, as they give redundant information (observation date is, by definition, the sum of birth date and infant's age, and infant's age is already included as a fixed effect). We present our models of birth date effects in the main text (Models 5-7, see also Table S3), and our models of observation date effects in the Supplementary Information (Models 5bis-7bis, Table S4).

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

Statistical methods

All statistical analyses were conducted in R version 3.5.0 [58]. For the Rayleigh test, we used the function 'r.test' from the R package 'CircStats' [59]. To run mixed models, we used 'lmer' (for LMMs) or 'glmer' (for binomial GLMMs) function on the lme4 package [60]. To run general additive mixed models (GAMMs) when investigating the best age effects on suckling, infant carrying and tantrum probabilities, we used the 'gam' function of the 'mgcv' package [80]. All quantitative fixed effects were z-transformed to facilitate model convergence. When we obtained singular fits, we confirmed the results by running the same models with a Bayesian approach, using the 'bglmer' and 'blmer' functions of the 'blme' package [61]. To diagnose the presence of multicollinearity, we calculated the variance inflation factor for each predictor in each full model using the 'vif 'function of the R 'car' package [63]. These were lower than 2.5 in all cases. To assess the strength of the fixed effects in each model, we used the Wald chi-

square tests with associated P-values computed with the 'Anova' function of the R package 'car' [63], and calculated the 95% Wald level confidence intervals. We further checked the distribution of residuals with 'qqPlot' function of the car package for LMMs [63], and with 'simulateResiduals' from DHARMa package for binomial GLMMs [66].

DATA AND CODE AVAILABILITY

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

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AUTHOR CONTRIBUTIONS

J.D. and E.H. designed the study, and J.D. ran the analysis. J.D., A.B., A.C., G.C. and E.H. collected the data, and all authors contributed to the drafting of the manuscript. E.H. acquired the funding for the project leading to this publication.

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TABLES

Table 1: Predictors of female reproductive timing.

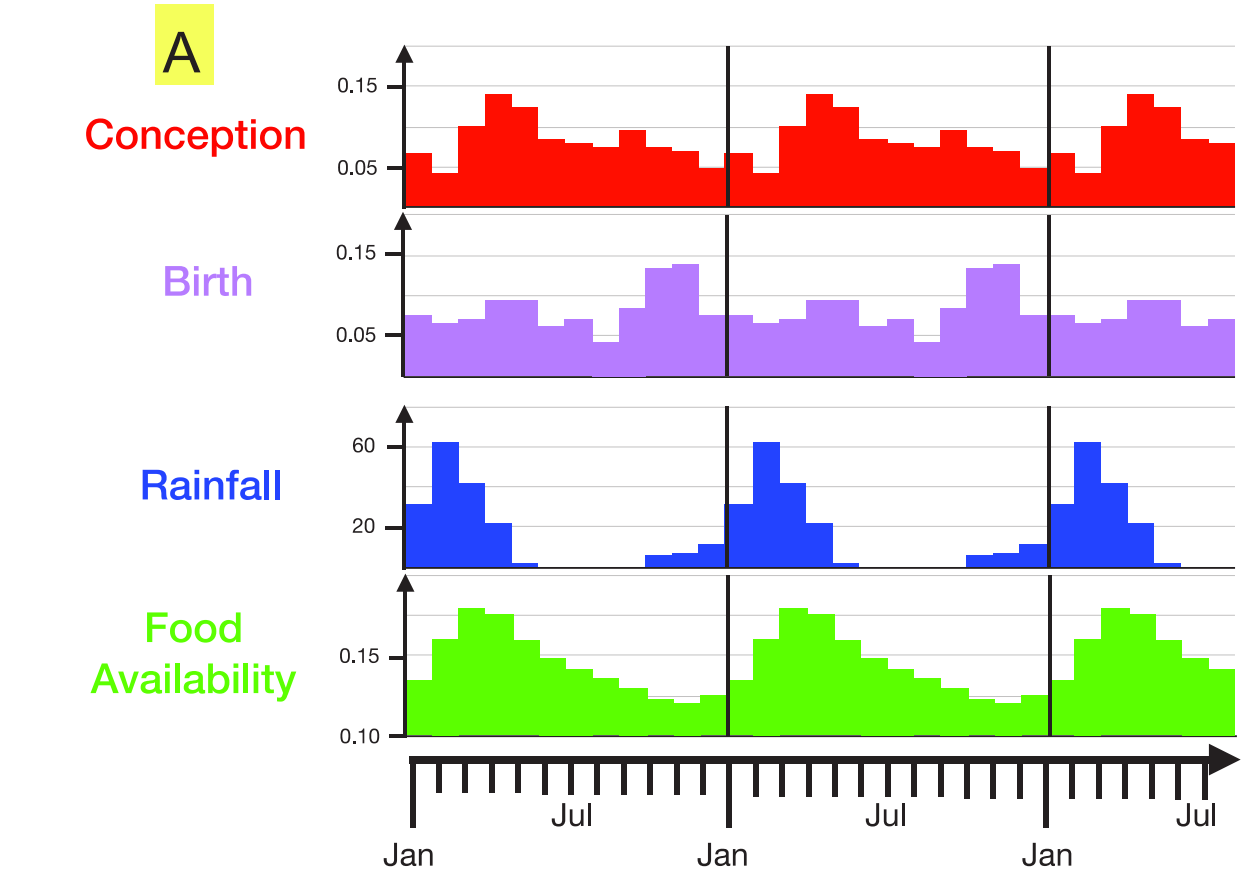
Estimates, confidence intervals, X^2 statistics and P-values of the predictors of the two linear mixed models (Models 3 and 4). The response variables are respectively the deviation from the offspring survival optimal birth timing, i.e. from December 15th (Model 3), and the deviation from the maternal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

Fixed effect		Estimate	IC		X^2	P-value
			Lower	Upper		
Model 3: Deviation from the offspring survival optimal birth timing						
Infant sex	(Male)	6.61	-6.70	19.92	0.95	0.330
Female parity	(Primiparous)	-12.73	-29.97	4.51	2.09	0.148
Female rank		2.58	-4.81	9.98	0.47	0.494
Group	(L)	5.22	-10.29	20.74	1.33	0.515
	(M)	-12.5	-44.53	19.53		
Model 4: Deviation from the maternal IBI optimal birth timing						
Infant sex	(Male)	-3.65	-16.91	9.61	0.29	0.590
Female parity	(Primiparous)	9.63	-7.52	26.78	1.21	0.271
Female rank		-3.41	-10.74	3.92	0.83	0.362
Group	(L)	10.63	-4.73	25.99	1.91	0.384
	(M)	0.87	-30.98	32.71		

FIGURES

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

In Panel A, we plotted the proportion of conceptions (N=241, in red) and births (N=215, in violet) recorded in 2005-2019 per month (Jan for January, Jul for July). We plotted the mean monthly cumulative rainfall (in mm) per month in blue and the mean NDVI value per month in green between 2005 and 2019. In Panel B, we aimed to represent the different phases of the female reproductive cycle, when the birth date occurs within the offspring survival (December 15th) or maternal IBI (September 1st) optimal timing, according to seasonal variation of NDVI. The green bar plot in the background indicates the mean NDVI per month (see y-axis). Pregnancy, indicated with grey arrows, occurs the 6 months prior a birth. Early-weaning, indicated with pink arrows, occurs from 6 to 9 months after a birth. Lactation peak, indicated with black stars, occur around 6 months after a birth. Weaning end, indicated with blue arrows, occurs from 12 to 18 months after a birth (see Appendix 4 for the characterization of these different reproductive stages).


A
Conception
Birth
Rainfall
Food Availability
0.15
0.05
0.15
0.05
60
20
0.15
0.10
Jan
Jul
Jan
Jul
Jan
Jul

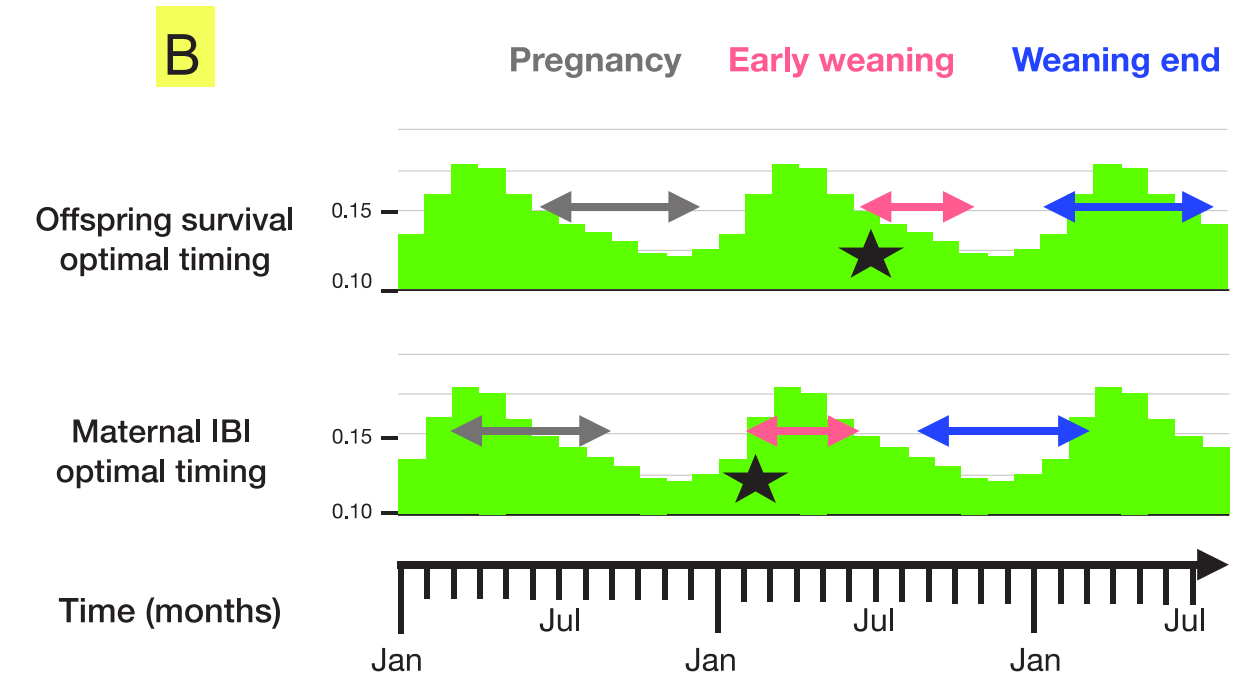

B
Pregnancy
Early weaning
Weaning end
Offspring survival optimal timing
Maternal IBI optimal timing
Time (months)
0.15
0.10
0.15
0.10
Jan
Jul
Jan
Jul
Jan
Jul

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

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

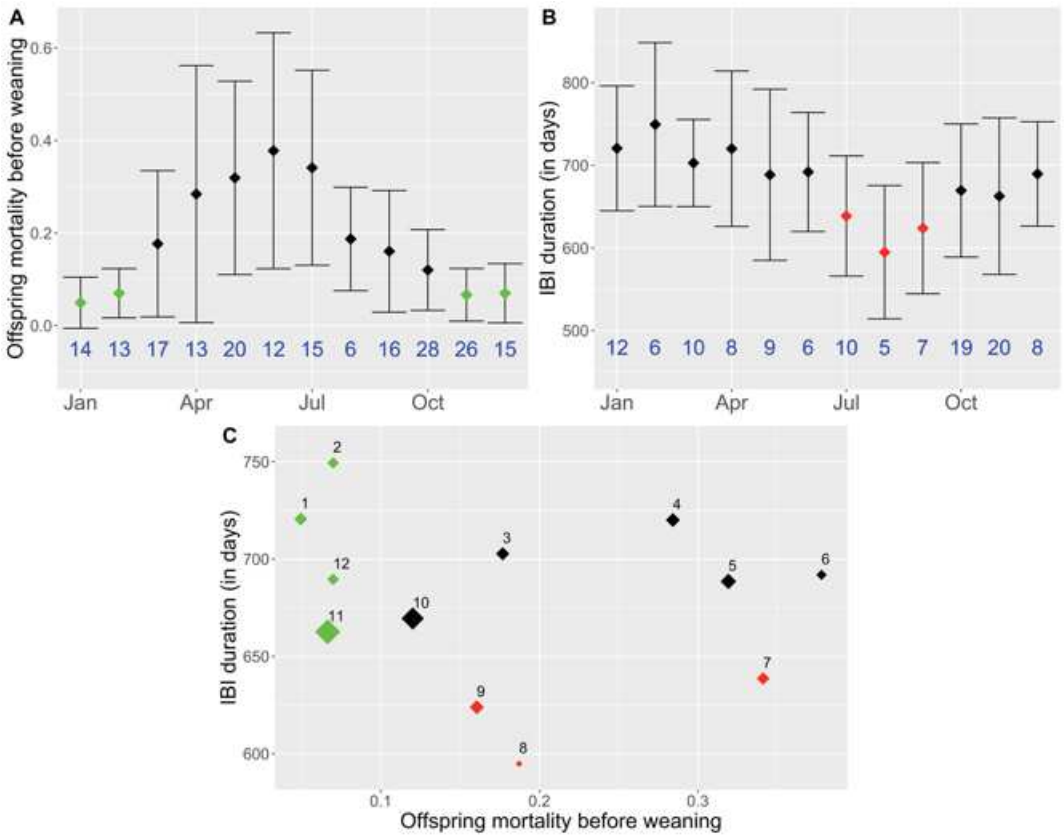
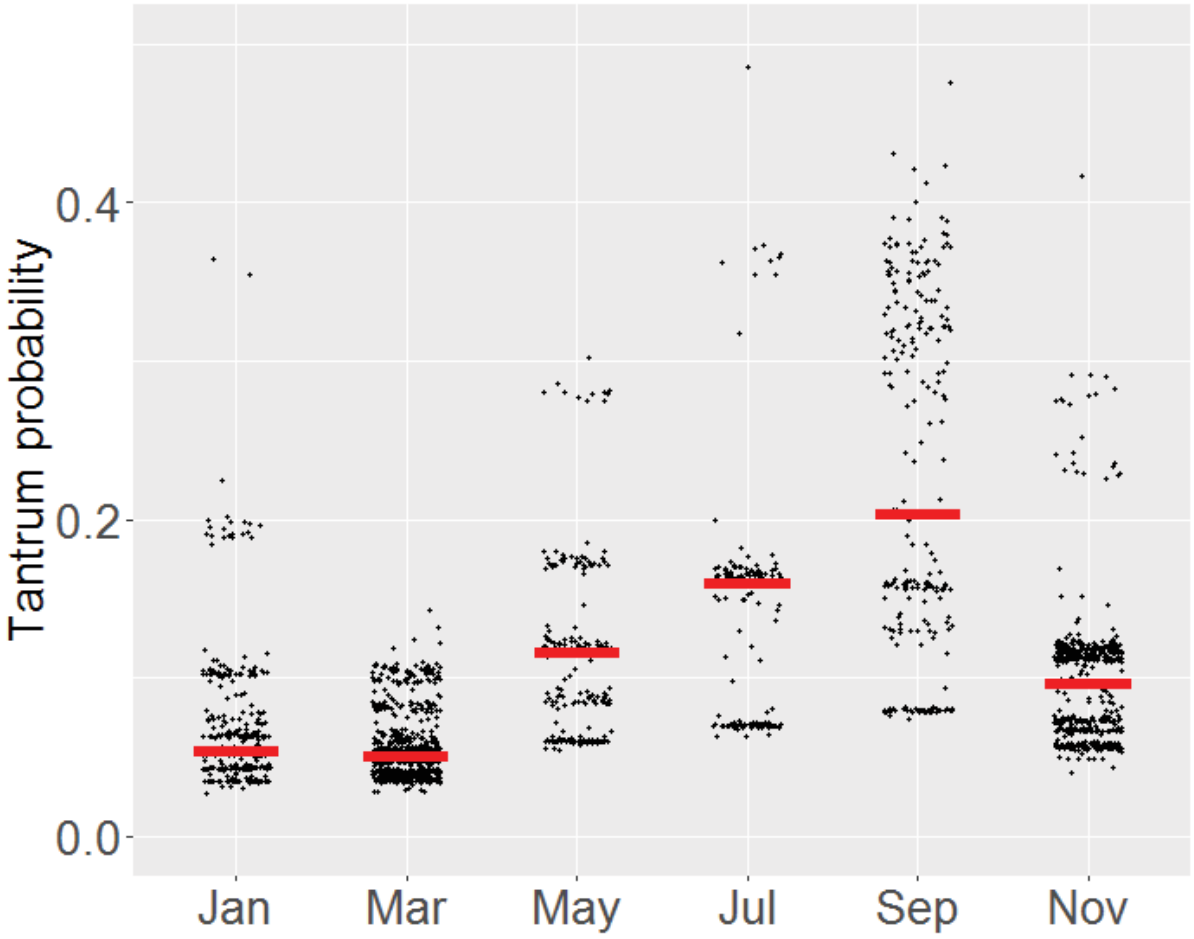


Figure 3: Influence of birth timing on tantrum probability.

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



SUPPLEMENTAL INFORMATION

APPENDICES

Appendix 1. Seasonal effects on maternal care and tantrum probability

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

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

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

Appendix 2. Correlations between rainfall and NDVI at Tsaobis

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

Appendix 3. Estimations of the dates of conceptions, births and cycle resumptions

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

1. ***Births.*** The dates of births, conceptions, and cycle resumptions were directly observed where possible, but otherwise estimated for those periods when no observers were present. We observed a total of 84 births. Of those, 62 were seen by observers on the exact day, and 22 were witnessed after a short absence (leading to a small uncertainty in the actual date: median=17 days, range=1-30). When the conception only was observed (n=52 births), we estimated birth dates by adding the mean gestation length (n=190 days, range: 181-200 days, SD=5, n=13 pregnancies where both conception and birth were observed) to the conception date. Conception was considered to occur on the day of deturgescence (D-day) of the swelling during a conceptive cycle. This generated a total of 136 birth dates known with high accuracy. When neither conception nor birth were observed (n=56 births), the birth date was estimated using infant coloration (based on the progressive loss of natal coat and skin coloration) following a method recently described and validated in our population [1], with further refinement provided by the reproductive history of the mother (e.g., if the mother was pregnant during the last three months of a field season, then the infant was necessarily born in the three months following the end of this season given that a pregnancy lasts 190 days). Finally, when neither birth nor conception was observed, and infant colour when first seen was unknown or uninformative (i.e., the transition from natal to adult coat had already occurred) (n=23 births), we used the reproductive state of females in the preceding field season to minimize uncertainty over birth timing. For example, if a female was cycling the last day of the preceding season, the infant was necessarily born at least 190 days after this day. In total, our sample comprised 215 births between 2005 and 2019, with a median uncertainty of 10 days (range: 0-153 days) (Table S5).

2. ***Conceptions.*** We observed 81 conceptions: 68 conceptions were witnessed (observers were present during the conceptive cycle), and 13 occurred during a short absence of observers (leading to a small uncertainty in the actual date: median=10 days, range=3-30). The exact date of conceptions

was the day of swelling detumescence of the conceptive cycle (when witnessed) [2]. When the birth was observed but not the conception, the latter was estimated to occur 190 days prior to birth (n=65 conceptions). When neither conception nor birth were observed but birth occurred (i.e. no miscarriage), we estimated birth date as explained above, and inferred conception from the birth date using the mean gestation period (n=79). Finally, when pregnancy signs were seen (i.e. red paracallosal skin and an absence of cycles) but conception was not observed and there was no birth due to a miscarriage or early death (occurring before an infant was recorded by observers), we estimated the date of conception using female reproductive states (n=16 conceptions). For example, if a female was seen pregnant on the first day of a field season, we knew that the conception occurred from 0-190 days prior to this date (as gestation lasts 190 days in this population). All in all, we generated a sample of 241 conceptions, with a median uncertainty of 10 days (range: 0-164 days).

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

Appendix 4. Characterization of developmental stages: weaning and lactation peak

In order to understand which stage of the reproductive cycle might be timed with the seasonal food peak, we characterized the sequential behavioural stages of weaning, which is the infant's gradual transition to nutritional independence [3], along with the peak of lactation for mothers in our population. First, the onset of weaning can be defined as the period when solid foods start to account for an important part of an infant's energy intake, and is characterized by an increase in maternal refusals to accede to the

offspring's demands. The onset of behavioural conflict between a mother and her offspring has therefore often been used as a proximate measure of the early-weaning period [3]. In our population, tantrum probabilities peak between 6 and 9 months of age (Figure S2), and we therefore used this age window to characterize 'early-weaning'. The peak of lactation typically occurs around the beginning of weaning [3,4], when offspring have grown larger but are still fully dependent. So we can considered that lactation peak occurs around 6 months after birth in our population. Similar ages for early-weaning and lactation peak have been found in other baboon populations [5–7], albeit weaning age and lactation durations can vary substantially between populations [8].

The end of weaning can be defined as the complete cessation of nursing, i.e. when offspring feed exclusively on solid foods. Looking at behavioural data, suckling frequencies decrease gradually from 2 to 18 months old, before stabilizing to ca. 2% of time from 18 to 24 months old (Figure S2). In addition, the maximum length of post-partum amenorrhea (PPA), often used as a proxy for the end of weaning [3], was 550 days (i.e. 18.1 months) in this population (based on n = 33 cases for which both birth and cycle resumption were known with accuracy). We considered this age of 18.1 months of weaning as upper threshold for our models on infant mortality and IBI (see man text), as we are certain that infants aged of 18.1 months are fully weaned in our population. However, the end of weaning is likely to be highly variable between individuals, which is confirmed by the wide range of PPA durations: from 8 to 18 months, with a mean of 12 months. To take this variation into account, we defined the 'end of weaning' as the age window of 12-18 months after birth for Figure 1B (meaning that some individuals can be weaned before 18 months old).

All in all, for Figure 1B, in order to better understand the relationship between reproductive phenology and environmental seasonality, we considered the lactation peak to occur around 6 months after birth, early-weaning between 6 and 9 months of age, and the end of weaning between 12 and 18 months of age. These windows are coarse-grained and essentially based on behavioural and life-history data, and proposed here to guide interpretations of reproductive phenology in relation to environmental seasonality. Nevertheless, the use of behavioural data shows some limitations in the evaluation of the

stages of lactation [9,10] and further studies based on more objective measures, such as isotopic comparisons of mother-offspring hair or faecal samples [11–14], may help to refine our estimations.

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

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

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

In our multivariate mixed models investigating the effect of seasonal birth timing on offspring mortality before weaning (Model 1) and maternal interbirth intervals (Model 2), we controlled for the uncertainties in dates of birth which could affect both our response variables and our main fixed effect of interest (seasonal birth timing). For Model 1, we generated 1000 simulations with random birth dates

drawn, for each birth, between minimal and maximal birth date estimations for this particular birth, and subsequently ran 1000 mixed models, one for each simulated value of the offspring's birth date and for each survival outcome (as birth date affects an offspring's age, and therefore its estimated age at death). For Model 2, we similarly generated 1000 simulations with random birth dates drawn between minimum and maximum birth date estimations for the two births defining the IBI. We subsequently ran 1000 models with randomized values for both IBI (the response variable, i.e. number of days between the first and second birth) and the birth date fixed effect. For both models, we then extracted the 1000 p-values of our fixed effect 'seasonal birth timing' and computed the confidence intervals of these p-values (see the footnote of Table S1).

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

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

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TABLES

Table S1: Predictors of offspring mortality before weaning and maternal interbirth interval (IBI) duration.

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

Fixed Effect		Estimate	IC		X^2	P-value
			Lower	Upper		
Model 1: Offspring mortality						
Infant birth date		**-1.12**	**-1.84**	**-0.4**	**9.36**	**0.002**[a]
Infant sex	(Male)	0.14	-0.82	1.09	0.08	0.780
Female parity	(Primiparous)	-0.84	-2.33	0.66	1.19	0.270
Female rank		-0.45	-0.96	0.07	2.91	0.088
Group	(L)	-1.28	-2.38	-0.18	5.22	0.074
	(M)	-0.12	-4.12	3.89		
Model 2: Maternal IBI						
Infant birth date		**37.06**	**7.93**	**66.20**	**6.22**	**0.013**[b]
Infant sex	**(Male)**	**39.79**	**2.88**	**76.70**	**4.46**	**0.035**
Female parity	(Primiparous)	43.93	-3.64	91.49	3.28	0.070
Female rank		**-25.68**	**-50.53**	**-0.83**	**4.10**	**0.043**
Group	(L)	**-49.78**	-104.39	4.83	3.24	0.198
	(M)	-29.52	-148.18	89.14		

[a] 95% CI: [0.01001 – 0.01118]

[b] 95% CI: [0.02264 – 0.02514]

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

In order to identify the best birth timing effect on our various indicators of fitness and maternal care, we ran 12 different models, with 12 different phases φ for the sine wave term of the birth date (as a fixed effect), for each full model (Models 1-2 & 5-7). If the estimate of the sine term fixed effect is positive, then the birth date maximised is indicated in the 'Date maximised' column and the one minimised is indicated in the 'Date minimised' column. On the contrary, if the estimate of the sine term fixed effect is negative, then the birth date maximised is indicated in the 'Date minimised' column. ΔAIC of each model equals the AIC value of the considered model minus the AIC value of the best model (ΔAIC=0 for the best model, indicated in bold writing). We selected the best phase as the one minimizing the AIC, i.e. for which ΔAIC=0. For example, for Model 2, the best phase is $\varphi = 2 * \pi/12$, and the estimate of the sine term fixed effect is positive (Table S1), indicating that IBIs are maximised in March 1st, and minimized in September 1st. Wherever the fixed effect 'birth date' was significant (Model 1, 2 and 7), we considered all phases φ for which ΔAIC<2 to define the optimal time window presented in the main text (see greyer background), for instance between August 1st and September 15th for Model 2.

Phase φ	Date maximised	Date minimised	Δ AIC				
			Mortality (Model 1)	IBI (Model 2)	Suckling (Model 5)	Infant carrying (Model 6)	Tantrum (Model 7)
0	1st April	1st October	8.26	2.16	0.67	**0**	1.15
π/12	15th March	15th September	9.42	0.72	1.13	0.17	0.34
2*π/12	1st March	1st September	9.45	**0**	1.62	0.65	**0**
3*π/12	14th February	15th August	8.12	0.33	1.96	1.29	0.39
4*π/12	1st February	1st August	5.66	1.61	1.92	1.85	1.49
5*π/12	15th January	15th July	2.91	3.36	1.46	2.16	2.94
6*π/12	1st January	1st July	0.84	5.02	0.86	2.18	4.20
7*π/12	15th December	15th June	**0**	6.16	0.37	1.93	4.84
8*π/12	1st December	1th June	0.47	6.59	0.09	1.53	4.80
9*π/12	15th November	15th May	1.99	6.29	**0**	1.05	4.20
10*π/12	1st November	1st May	4.10	5.31	0.08	0.56	3.27

11*π/12	15th October	15th April	6.34	3.84	0.32	0.17	2.19

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

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

Fixed Effect		Estimate	IC		X^2	P-value
			Lower	Upper		
Model 5: Suckling						
Infant birth date		-0.32	-0.76	0.13	1.96	0.16
Infant sex	(Male)	-0.01	-0.72	0.70	0.00	0.99
Female parity	(Primiparous)	-0.89	-2.21	0.43	1.76	0.18
Female rank		-0.09	-0.42	0.23	0.31	0.57
Infant age		**-1.66**	**-1.97**	**-1.35**	**112**	**$<10^{-4}$**
Group	**(L)**	**0.18**	**-0.54**	**0.90**	**7.84**	**0.02**
	(M)	**1.51**	**0.36**	**2.65**		
Observation year	**(2017)**	**0.21**	**-1.21**	**1.63**	**41.7**	**$<10^{-4}$**
	(2018)	**1.73**	**0.85**	**2.61**		
	(2019)	**0.03**	**-0.82**	**0.87**		
Model 6: Infant carrying						
Infant birth date		0.53	-0.18	1.24	2.13	0.14
Infant sex	**(Male)**	**-0.94**	**-1.60**	**-0.28**	**7.78**	**0.005**
Female parity	**(Primiparous)**	**-1.08**	**-2.11**	**-0.05**	**4.21**	**0.040**

Female rank		**-0.51**	**-0.82**	**-0.19**	**10.0**	**0.002**
Infant age		**-1.94**	**-2.69**	**-1.20**	**26.2**	$<10^{-4}$
Group	(L)	0.01	-0.53	0.55	0.67	0.71
	(M)	-0.35	-1.34	0.64		
Observation year	(2017)	-11.5	-262	239	3.69	0.30
	(2018)	1.36	-0.36	3.09		
	(2019)	0.86	-1.19	2.91		
Model 7: Tantrum						
Infant birth date		**-0.32**	**-0.62**	**-0.02**	**4.38**	**0.036**[a]
Infant sex	(Male)	-0.03	-0.37	0.31	0.03	0.85
Female parity	(Primiparous)	0.37	-0.30	1.04	1.17	0.28
Female rank		0.04	-0.12	0.20	0.23	0.63
Infant age	**Age**	**-40.8**	**-53.8**	**-27.8**	**52.2**	**$<10^{-4}$**
	Age^2	**-19.1**	**-28.3**	**-9.91**		
Group	(L)	-0.33	-0.66	0.01	3.78	0.15
	(M)	-0.18	-0.79	0.42		
Observation year	**(2017)**	**0.12**	**-1.39**	**1.63**	**13.10**	**0.004**
	(2018)	**0.32**	**-0.78**	**1.43**		
	(2019)	**-0.43**	**-1.56**	**0.69**		
Offset		**0.40**	**0.10**	**0.70**	**6.80**	**0.009**

[a] 95% CI: [0.04979 – 0.05614]

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

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

Fixed Effect		Estimate	IC		X^2	P-value
			Lower	Upper		
Model 5bis: Suckling						
Observation date		**-1.66**	**-2.91**	**-0.40**	**6.69**	**0.0097**
Infant sex	(Male)	0.00	-0.74	0.74	0.00	0.99
Female parity	(Primiparous)	-0.88	-2.24	0.49	1.59	0.21
Female rank		-0.11	-0.44	0.23	0.38	0.54
Infant age		**-1.62**	**-1.93**	**-1.30**	**98.8**	**<10-4**
Group	(L)	0.31	-0.46	1.07	6.81	0.033
	(M)	1.53	0.34	2.73		
Observation year	**(2017)**	**-2.35**	**-4.89**	**0.19**	**30.5**	**<10-4**
	(2018)	**1.75**	**0.84**	**2.66**		
	(2019)	**-2.63**	**-4.94**	**-0.33**		
Model 6bis: Infant carrying						
Observation date		**-1.14**	**-1.98**	**-0.30**	**7.12**	**0.0076**
Infant sex	**(Male)**	**-0.90**	**-1.56**	**-0.24**	**7.20**	**0.0073**
Female parity	(Primiparous)	-0.78	-1.77	0.22	2.33	0.13
Female rank		**-0.45**	**-0.76**	**-0.15**	**8.31**	**0.0039**
Infant age		**-2.40**	**-2.83**	**-1.97**	**120**	**<10-4**
Group	(L)	-0.003	-0.53	0.54	2.04	0.36
	(M)	-0.63	-1.62	0.37		
Observation year	**(2017)**	**-13.10**	**-2410**	**2384**	**12.2**	**0.007**
	(2018)	**0.66**	**-1.19**	**2.52**		
	(2019)	**-0.73**	**-2.77**	**1.31**		
Model 7bis: Tantrum						
Observation date		0.62	-0.15	1.15	2.24	0.13
Infant sex	(Male)	-0.02	-0.37	0.33	0.01	0.91
Female parity	(Primiparous)	0.10	-0.54	0.74	0.09	0.76
Female rank		0.05	-0.11	0.22	0.40	0.53
Infant age	**Age**	**-32.9**	**-42.8**	**-22.2**	**49.9**	**<10-4**
	Age^2	**-20.9**	**-30.00**	**-11.9**		
Group	(L)	-0.30	-0.62	0.06	3.15	0.21
	(M)	-0.03	-0.60	0.56		

	(2017)	0.57	-1.28	1.83		
Observation year	(2018)	0.23	-0.90	1.32	0.21	0.98
	(2019)	0.45	-1.25	1.51		
Offset		**0.40**	**0.10**	**0.71**	**6.72**	**0.0095**

Table S5: Different methods used to estimate the dates of births of the 215 baboon infants born at Tsaobis between 2005 and 2019.

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

Table S6: Summary of the structure of all models included in the study.

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

FIGURES

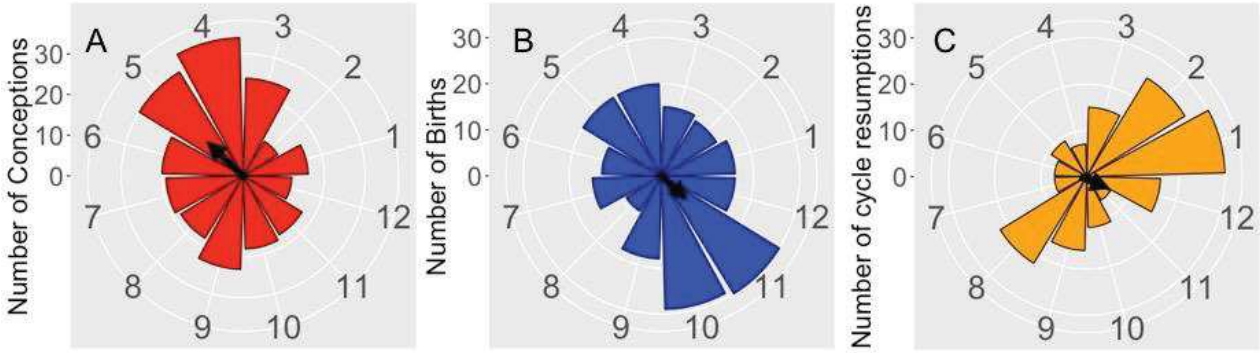

Figure S1: Chacma baboons breed all year round.

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

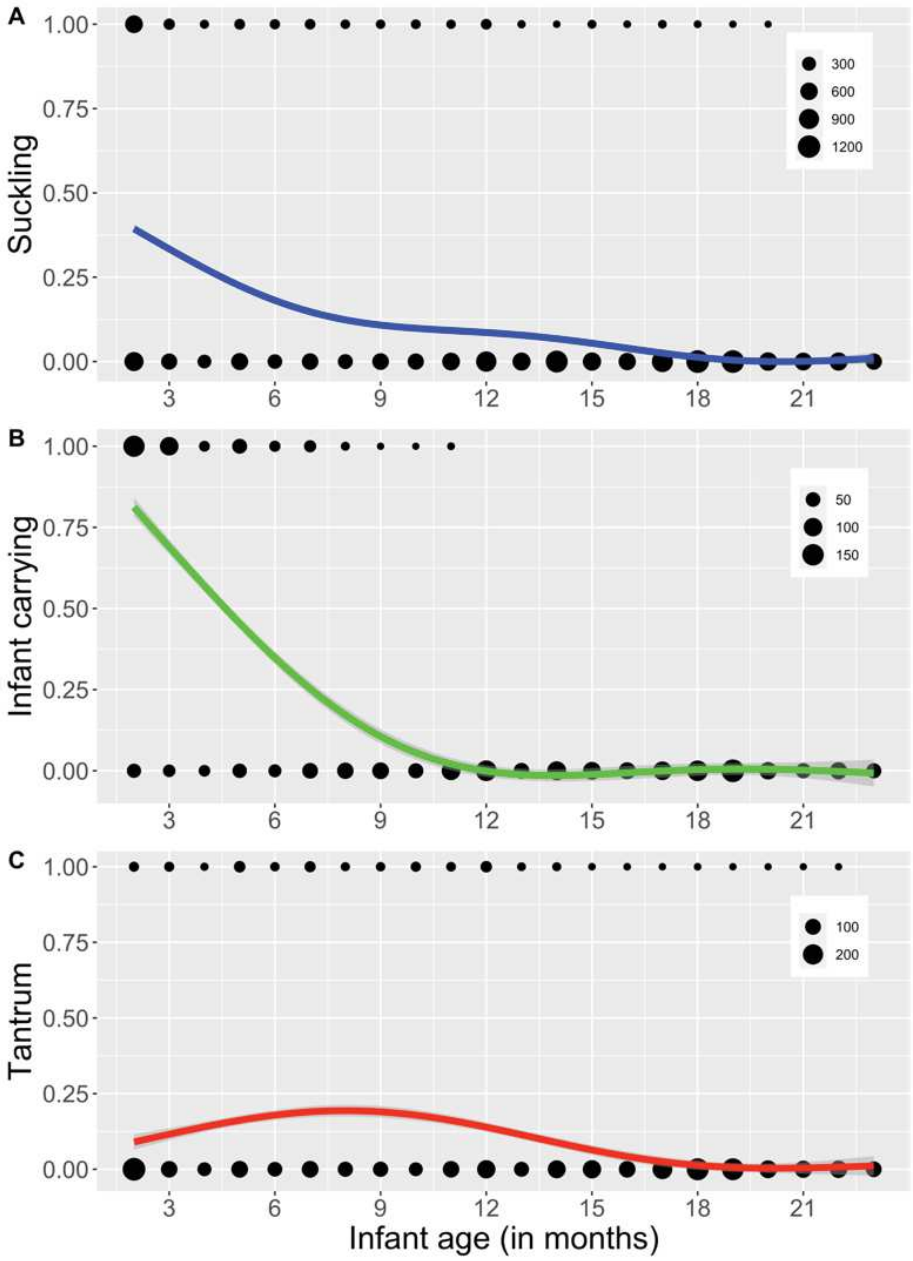

Figure S2: Variation in the probabilities of suckling, infant carrying, and tantrums, according to infant age.

We plotted (A) the probability of suckling during a scan, (B) the probability of infant carrying during a travelling scan, and (C) the probability of tantrum during a focal observation according to infant age (in months). For all panels, the size of black dots is proportional to the number of observations (see plot legends). The coloured curves show the predicted fit using a general additive function (method 'gam' of geom_smooth function in 'ggplot2' R package). The darker area around each curve represents the confidence interval of the fitted curve.

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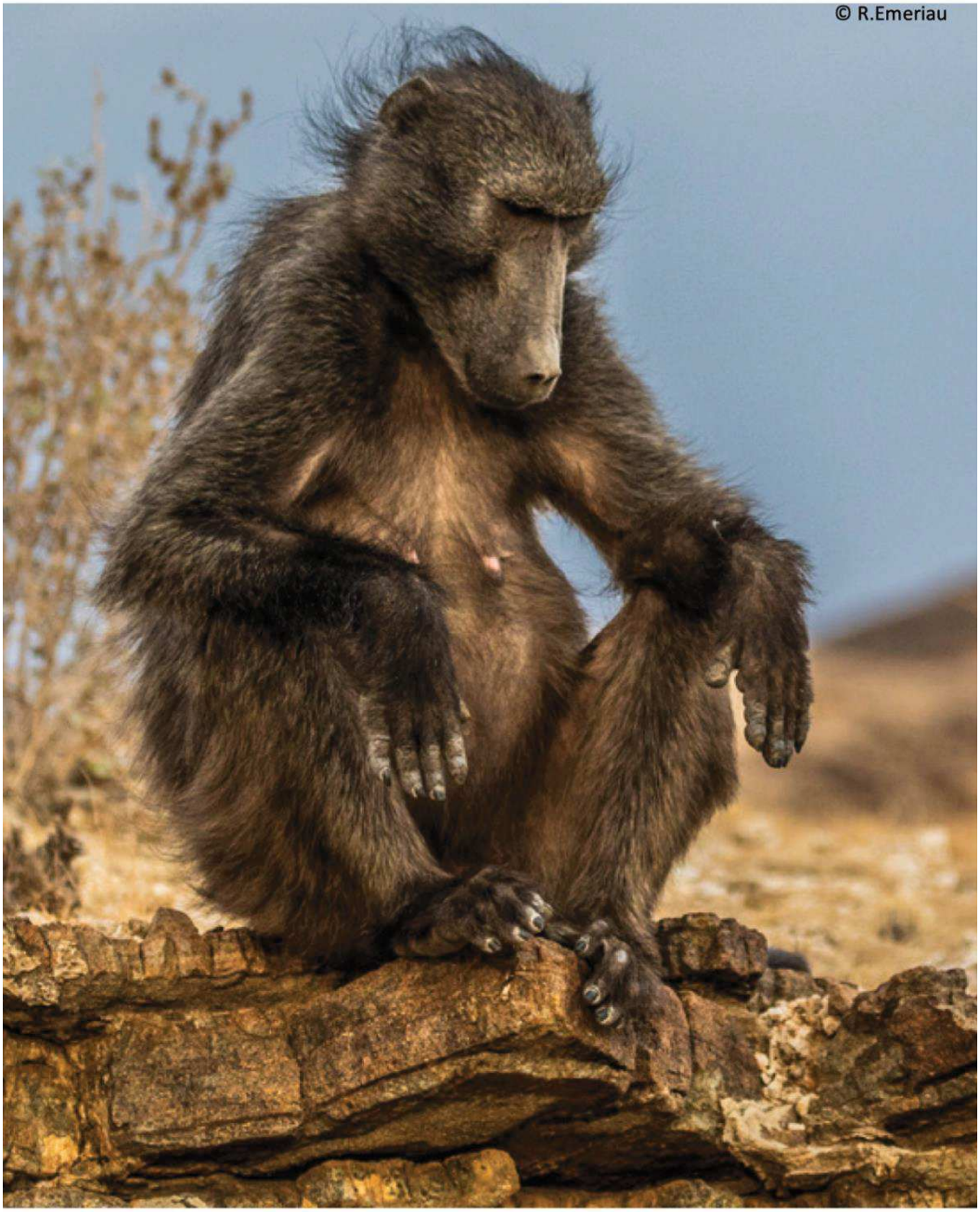

Chapter 4

Evolutionary determinants of non-seasonal breeding in wild chacma baboons

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ABSTRACT

Animal reproductive phenology varies from strongly seasonal to non-seasonal, sometimes among closely related or sympatric species. While the extent of reproductive seasonality is often attributed to environmental seasonality, this fails to explain many cases of non-seasonal breeding in seasonal environments. We investigated the evolutionary determinants of non-seasonal breeding in a wild primate, the chacma baboon (*Papio ursinus*), living in a seasonal tropical environment characterized by high climatic unpredictability. We tested three hypotheses, respectively proposing that non-seasonal breeding has evolved in response to (1) climatic unpredictability, (2) reproductive competition between females favouring birth asynchrony, and (3) individual, rank-dependent variations in optimal birth timing. We only found support for the reproductive asynchrony hypothesis: (i) birth synchrony is costly to subordinate females, lengthening their interbirth intervals, and (ii) females flexibly adjust their reproductive phenologies (fertility periods and conceptions) to other females in the group, in order to stagger conceptions. These results indicate that reproductive competition generates reproductive asynchrony and contributes to weaken the intensity of reproductive seasonality at the population level. This study emphasizes the importance of sociality in mediating the evolution and modalities of reproductive phenology in gregarious organisms, a result of broad significance to understand key demographic parameters driving population responses to increasing climatic fluctuations.

INTRODUCTION

Reproduction is energetically costly, and many species therefore adjust the timing of their reproduction, referred to as reproductive phenology, to seasonal fluctuations in food availability (Boyce 1979). Reproductive seasonality, the temporal cluster of reproductive events in one period of the annual cycle (Lindburg 1987), is widespread taxonomically and geographically (Brockman and van Schaik 2005; Bronson 2009), and usually characterized by the timing and width of the birth peak. Although non-seasonal breeders reproduce throughout the annual cycle (unlike seasonal breeders, who experience a period without any birth), they may still exhibit a seasonal peak in the annual distribution of births (Janson and Verdolin 2005).

The intensity of reproductive seasonality varies widely, from the African elephant that breeds year round (Moss 2001) to the banded mongoose where each female is usually sexually receptive for only one night a year (Hodge et al. 2011). Ultimate explanations for seasonal reproduction have largely assumed that variation in the intensity of reproductive seasonality reflects variation in the intensity of environmental seasonality (Rutberg 1987; Conover 1992; Di Bitetti and Janson 2000). However, numerous sympatric species exhibit a range of reproductive schedules despite sharing the same climate. For example, in the Serengeti National Park (Tanzania), the korrigum *Damascilus korrigum* is a highly seasonal breeder while the phylogenetically related hartebeest *Alcelaphus buselaphus* is not, and seasonal breeders vary widely in the timing and length of their breeding season (Sinclair et al. 2000). More generally, numerous species living in highly seasonal environments breed year round (Burthe et al. 2011; Swedell 2011; Campos et al. 2017). Overall, the intensity of environmental seasonality is not always a reliable predictor of a species' reproductive seasonality.

Several additional predictors might be considered. First, if the height and/or the timing of the annual food peak vary between years, individuals may benefit from maintaining a flexible

reproductive schedule (Colwell 1974; van Schaik and van Noordwijk 1985; Loe et al. 2005). It has recently been shown in 38 ungulate species that the intensity of seasonal breeding decreases with seasonal unpredictability, i.e., inter-annual variation in the timing and strength of environmental seasonality (English et al. 2012). In environments where within-year (seasonal) variations are negligible compared to between-year (non-seasonal) variations, individuals adjusting their reproductive events with relative flexibility might be favoured (van Schaik and van Noordwijk 1985), in order to exploit the unpredictable food peak opportunistically; and this flexibility may cause the absence of reproductive seasonality. In the context of the income-capital breeder continuum, a common framework for the study of alternative strategies to finance offspring production, capital breeders (which are able to store energy for later use) are often better adapted to such between-year variable environments than income breeders (which rely on current energy available to breed) (Drent and Daan 1980; Brockman and van Schaik 2005; Stephens et al. 2014). Yet, few studies have asked whether seasonal predictability could represent an evolutionary driver of reproductive seasonality.

Second, social factors might further affect reproductive seasonality by modulating reproductive synchrony, the 'phenomenon caused by biological interactions to produce a tighter clustering of reproductive events than environmental seasonality alone' (Ims 1990). Synchronizing births in order to satiate predators is a common anti-predator adaptation producing extreme reproductive synchrony for numerous species, including some ungulates (Rutberg 1987; Ims 1990; Sinclair et al. 2000; Canu et al. 2015) and squirrel monkeys (Boinski 1987). Sociality could also lead to the reverse pattern where staggering reproductive events may aim at decreasing reproductive competition over access to mates, paternal care or food (Wiebe et al. 1995). For instance, oestrus asynchrony has been reported in both seasonal breeding ring-tailed lemurs (*Lemur catta)* (Pereira 1990) and non-seasonal breeding

chimpanzees (*Pan troglodytes)* (Matsumoto-Oda et al. 2007), apparently allowing females to choose their mate by decreasing female mating competition.

Third, individual variation in reproductive seasonality might also occur, leading to non-seasonal breeding across the population as a whole. This is especially true in hierarchical societies, where dominant females often have privileged access to resources and may subsequently exhibit earlier age at first reproduction, shorter interbirth intervals, higher offspring survival and increased longevity (Clutton-Brock and Huchard 2013; Stockley and Bro-Jørgensen 2011). The consequences of rank-related variation in foraging success and life history traits on reproductive seasonality have not been studied, but may mediate both the effects of environmental variation and group reproductive synchrony described above. In the first case, a high rank may buffer seasonal fluctuations of food resources while a low rank may incur increased competition during the lean season (Barton and Whiten 1993; Clutton-Brock et al. 2001), leading to lower-ranking females reproducing more seasonally than higher-ranking females. In the second case, higher-ranking females might reproduce at the optimal time and actively supress the reproduction of lower-ranking ones to minimize reproduction synchrony, leading to subordinate females reproducing less seasonally than dominant.

Here we investigate the evolutionary determinants of non-seasonal breeding in a wild social primate, the chacma baboon (*Papio ursinus*), by testing three non-exclusive hypotheses. (H1) The 'non-seasonal environment hypothesis' proposes that the absence of reproductive seasonality stems from a population-level factor, namely the non-seasonal environmental fluctuations. (H2) The 'group asynchrony hypothesis' proposes that the absence of reproductive seasonality results from a group-level factor, where females within a group stagger their reproductive events to minimize reproductive synchrony in response to reproductive competition. (H3) The 'social rank hypothesis' proposes that an individual-level factor, namely social rank, leads to the absence of reproductive seasonality at the population level because

there are dominance-related differences in how females are affected by seasonal and non-seasonal environmental variation (H3a), and/or reproductive synchrony (H3b).

Focusing on a long-lived, tropical, social mammal will bring a fresh perspective on the breeding seasonality literature, which is biased towards short-lived passerines in temperate climates (Verhulst and Nilsson 2008; Bronson 2009; Varpe et al. 2009). In addition, the selective pressures affecting breeding seasonality in tropical latitudes, where environment is characterized by more unpredictable rainfall (Feng et al. 2013), have been less studied. Extensive variations in patterns of reproductive synchrony occur across primate populations (Ostner et al. 2008; Gogarten and Koenig 2013), and may reflect female reproductive competition (Beehner and Lu 2013). Finally, social primates such as baboons, which live in large multimale-multifemale groups where female dominance hierarchy is linear and affects foraging success and reproductive performances (Pusey 2012), may provide a valuable model for understanding rank differences in sensitivity to environmental and social factors likely to lead to individual variations in seasonal breeding strategies. In our study population, a recent study revealed fitness variations associated with seasonal birth timing (Chapter 3), and hence raised the question of the nature of the benefits of non-seasonal breeding.

We tested these three hypotheses according to their predicted effects on females' fitness, assayed by female interbirth interval (IBIs) and offspring survival until weaning; and on reproductive timings, assayed by the monthly probabilities of cycle resumption and conception. Under the non-seasonal environment hypothesis (H1), female reproduction should be responsive to current environmental conditions, such that a scarcity of food (after controlling for patterns of seasonal variation) should lead to longer IBIs, higher infant mortality, and lower probabilities of cycling resumption and conception. Under the reproductive synchrony hypothesis (H2), female reproduction should be responsive to the degree of reproductive synchrony in the group, such that higher group synchrony should lead to longer IBIs, higher

infant mortality, and lower probabilities of cycling resumption and conception. Under the social rank hypothesis, lower-ranking females should be more restricted in their access to food resources (H3a), or experience greater costs of reproductive synchrony (H3b), such that the respective negative effects of food scarcity and group synchrony on IBI, infant mortality, cycle resumption, and conception would be greater for subordinate females. A summary of these hypotheses and their associated predictions is provided in Table 1.

METHODS

a) Field site and population

Data were collected between 2005 and 2019 from three habituated groups of wild chacma baboons (J and L since 2005, and M, a fission group from J, since 2016) living in a desert edge at Tsaobis Nature Park (22°23S, 15°44'50E) in central Namibia. Tsaobis environment is characterized by steep rocky hills descending towards alluvial plains, and crossed by the ephemeral Swakop riverbed (Cowlishaw and Davies 1997). It is a strongly seasonal environment: the desert vegetation responds quickly to the austral summer rains, which usually fall between December and April, and then dies back during the dry winter months. The annual rainfall is sparse and highly variable between years. Each year, a field season of variable length (mean=137 days, range: 57-240 days) was conducted, mainly during the dry winter season (between May and October). The groups were followed on foot from dawn to dusk on a daily basis, allowing us to collect demographic and behavioural data, as well as GPS locations.

b) Individual data

A female was considered adult when she reached menarche. The reproductive state of each adult female was monitored on a daily basis. A female could be assigned as: (i) pregnant, with pregnancy being determined *post hoc* following infant birth, and encompassing the six months between the conceptive cycle and the birth; (ii) lactating, as long as the female did not resume cycling after an infant birth; (iii) cycling, including both swollen females in oestrus (i.e., sexually receptive with a perineal swelling) and non-swollen females (i.e. at other stages of their cycle). Conceptive cycles were established based on the beginning of a pregnancy, noticeable with both the paracallosal skin turning red and the absence of other cycles in the following months, and were usually confirmed by a birth. The first post-partum cycle (i.e. cycle resumption) is the first cycle following an infant's birth, when the female resumes cycling after lactation. The exact date of the cycle resumption corresponds to the first day of oestrus of the first post-partum cycle, i.e. the first day when a sexual swelling is recorded. The dates of these reproductive events were known with accuracy when they were recorded by field observers, and were estimated in their absence using the methods detailed below.

For females born after 2005, their dates of births were either witnessed in the field or estimated with relative precisions (see Table S1, electronic supplementary material). For females born before 2005, age was estimated through dentition, using both tooth eruption schedules and the eruption of the molars (Huchard et al. 2009; Kahumbu and Eley 1991).

Female's parity was determined using long-term life history data and defined as: nulliparous (before the birth of her first infant), primiparous (between the birth of her first and second infant) and multiparous (after the birth of her second infant).

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

control for group size. Each female was thus assigned one rank per year, ranging from 0 (lowest ranking) to 1 (highest ranking).

Each year, we also computed the number of adult females in each group. A female was considered in the group this year if she was present more than half of the annual field season.

c) Individual reproductive data

To test our hypotheses, we considered two measures of female fitness, namely the interbirth interval duration and offspring mortality before weaning, and two measures of the timing of female reproduction, namely the monthly probabilities of conception and of cycle resumption.

As baboons are not followed all year long at Tsaobis, we had to estimate dates of conceptions, births and cycle resumptions in a number of cases. The dates of those unobserved events - as well as the number of days of uncertainty around those events - were established using a combination of photographs and field observations of infant fur and skin color (ears, eye contours, hands and feet, muzzle, muzzle tip, and ischial callosities), following a protocol described in details in a recent study (Dezeure et al. 2020). All in all, we generated a sample of 241 conceptions, with a median uncertainty of 10 days (range: 0-164 days) (Table S1, electronic supplementary material); 215 births, with a median uncertainty of 10 days (range: 0-153 days); and 155 cycle resumptions, with a median uncertainty of 93 days (range= 0-272 days), between 2005 and 2019. The uncertainty of each reproductive event date has been considered in all analyses (see below and more details in Appendix A).

We defined interbirth intervals (IBIs) as the number of days between two consecutive live births of a same female. We only considered IBIs for which the first infant reached weaning (i.e. survived until 550 days old) (Gesquiere et al. 2017), because females resumed cycling rapidly after their infant's death (median=21 days, range=9-51, n=9 observed death), and their

IBIs would have been shortened regardless of environmental or social factors. This age threshold (550 days) was estimated to be the maximum length of post-partum anoestrus in our population (Chapter 3), and presumably reflected the upper threshold of weaning age, assuming that females who resumed cycling had weaned their offspring (Lee et al. 1991; Saltzman et al. 2011; Borries et al. 2014). We further remove one IBI where the infant closing the IBI was born dead (because it might have been due to premature delivery). We computed a total of 120 interbirth intervals from 43 adult females, ranging from 397-1132 days with a mean of 678 days (SD=128).

For each infant born between 01/01/2005 and 01/08/2018, we investigated whether it died (yes/no) before weaning, i.e. before reaching 550 days of age. Death was recorded when a corpse was observed or when the infant had been missing in the group for five consecutive days. Infants born later than August 2018 were not considered as their survival outcome at 550 days was unknown. Four infants that disappeared between two consecutive field seasons (in absence of observers) were omitted because we could not establish whether the age of death was before or after 550 days. In our final dataset, a total of 39 infants of 195 died before reaching 550 days of age, with mortality occurring at a median age of 74 days (range 1-284 days, n=17 known dates of death).

d) Characterization of environmental variation

We first considered four aspects of environmental variation at Tsaobis: the temperature, rainfall, vegetation cover (food availability) and photoperiod (daytime length) (see Appendix B, electronic supplementary material). However, we found that our indicator of food availability (vegetation cover, NDVI) was always selected as the best environmental variable affecting reproductive success and timings (see Appendices B, C and D of the electronic

supplementary material for further details on the selection of this variable). Therefore, we only present in the main text methods and results associated with food availability.

We used the Normalized Difference Vegetation Index (NDVI) as a measure of vegetation cover and therefore food availability. NDVI is computed using the near-infrared and red light reflected by the surface of an area and measured with satellite sensors; it produces a quantitative index of primary productivity with higher values corresponding to a higher degree of greenness (Didan et al. 2015). It has previously been used as an indicator of habitat quality for the Tsaobis baboons (Baniel et al. 2018*a*; Dezeure et al. 2020; Baniel et al., in prep.) and other baboon populations (Zinner et al. 2001). See Chapter 3 first manuscript for more details about NDVI data extraction per studied group.

In subsequent analyses, in order to test the influence of environment unpredictability on baboon reproductive seasonality, we disentangled seasonal from non-seasonal variations of NDVI. Indeed, we found that between-year NDVI and rainfall variations were important (Figure S1), whereas between-year variations were negligible in the case of temperatures and photoperiod (see Appendix B, electronic supplementary information). For NDVI decomposition, we first computed the mean monthly values across all 15 years of study, and labelled this variable 'NDVI_S'. We then computed the difference between each actual monthly value in a given year and this averaged monthly value across years, and labelled this variable 'NDVI_NS'. Here, seasonal variables reflect within-year variation only (predictable variations, consistent between years), while non-seasonal variables reflect between-year variation only (unpredictable, inconsistent between years).

e) Statistical analyses

We tested our three hypotheses about the causes of non-seasonal breeding (H1, non-seasonal environment hypothesis; H2, group asynchrony hypothesis; H3, individual rank hypothesis) in a series of four models. Models 1 and 2 tested our hypotheses in relation to their effects on female fitness, using two measures: interbirth interval and infant mortality, respectively. Models 3 and 4 tested our hypotheses in relation to their effects on female reproductive timings, again using two measures: the timing of cycle resumption and probability of conception, respectively.

For Model 1, exploring the length of the interbirth interval (IBI) following the birth on an infant (in days), we ran a linear mixed model (LMM), while for Model 2, exploring the probability of infant mortality before weaning (i.e. before 550 days), we ran a generalized linear mixed model (GLMM) with a binomial error structure (Appendix C, electronic supplementary material for more details). The identity of the female/mother was put as a random effect to control for the non-independence of observations on the same female/mother. Both models comprised the following fixed effects. First, to test our hypotheses:

- *Non-seasonal environmental variation (NDVI_NS)*. Under the non-seasonal environment hypothesis (H1), female reproductive performance should be highly sensitive to non-seasonal environmental variations in an environment with important between-year fluctuations of rainfall and food availability. Therefore, we expected females to have longer IBIs and higher offspring mortality before weaning when monthly food availability was lower than on average for those months (i.e. accounting for seasonal variation). We estimated the non-seasonal environmental variation using the NDVI_NS variable described above. We averaged NDVI_NS across the whole period spanning the IBI for Model 1, and from conception to 550 days of age (for live infants) or to death (for dead infants) for Model 2.

- *Reproductive synchrony*. Under the asynchrony hypothesis (H2), we expected that when reproductive synchrony increased, IBI would be longer and infant survival would be lower. In both models, we considered as a proxy of reproductive synchrony the number of infants born in the same group, in a given time window of variable length around the birth of the focal infant. We computed the number of infants born *x* months before, *x* months after, and *x* months before and after the birth of the focal infant, where *x*=1 month, 3 months, or 6 months. We identified the best of these nine variables as the one minimizing the AIC of a model including only this fixed effect (but controlling for all random effects) for each of our two response variables. We then incorporated this best synchrony variable, which was the number of infants born the past 3 months for IBI, and the 6 following months for infant mortality, into the full model (Appendix C, electronic supplementary materials for more details).
- *Interactions between female rank and both seasonal (see metric below) and non-seasonal (NDVI_NS) environmental variations*. Under the social rank hypothesis (H3a), we expected lower-ranking females to suffer higher fitness costs during environmental harshness.
- *Interaction between female rank and reproductive synchrony*. Under the social rank hypothesis (H3b), we expected lower ranking females to suffer higher fitness costs when reproductive synchrony in the group is higher.

Second, as control variables:

- *Seasonal environmental variation*, to control for those seasonal variations which are known to affect individual fitness, even for this non-seasonal breeder (Chapter 3). We captured seasonal environmental variation by using a sine term of the birth date of the focal infant to describe the timing of an infant's birth in the annual cycle (in radians). We used only one harmonic and changed the phase value φ (to 0, π/6, π/3, π/2, 2*π/3 or

5*π/6), to account for potential phase shifts across the year (see Appendixes C and D). For these models, we could not average NDVI_S to capture seasonal environmental variations as the mean duration between two births (for IBI) and between conceptions and weaning (for mortality) equals two years on average (and thus an average of two years would be constant for every individual). Nonetheless, the sine wave with the best phase was highly correlated with seasonal fluctuations of NDVI (phase = 5* π/6, for J group, Pearson correlation test: R=-0.92, t=-31.5, p<10-4) so we only used this fixed effect to capture seasonal environmental variation.

- *The number of adult females in the group* the birth year of the focal infant, which is an indicator of within-group competition. It has been shown that a reduction in group size is often associated with an increase of primate (including baboon) female fertility, especially with shorter IBI (Altmann and Alberts 2003; Borries et al. 2008)
- *Group identity*, to control for possible differences between social groups.
- *Maternal social rank* during the birth year. Lower-ranking females were expected to have longer interbirth intervals and lower infant survival (Bulger and Hamilton 1987; Packer et al. 1995; Chapter 3).
- *Maternal parity.* Primiparous females have not yet achieved full body size and may lack the relevant experience to provide optimal offspring care in comparison to multiparous females. Consequently, they could have longer interbirth intervals, and their offspring could face a higher mortality probability (Altmann and Alberts 2005; Gesquiere et al. 2017).
- *Infant sex.* We expected mothers of males to have longer interbirth intervals than mothers of female infants, and possibly lower survival, in this sexually dimorphic species (Bercovitch and Berard 1993) (but see Cheney et al. 2004; Gesquiere et al. 2017).

For the IBI model, we also included the quadratic effect of female age (years). Following Gesquiere et al. (2017), we expected both younger and older females to have longer IBIs. We kept parity as fixed effect in the IBI model for homogeneity, and after checking for the absence of collinearity between our fixed effects (parity and female age) in our model (vif<2).

In the case of Models 3 and 4, because seasonal reproduction is usually characterized by a mating season (determined by the seasonality of female fertility or sexual receptivity) and/or a birth season (determined by the seasonality of conceptions), we tested our hypotheses in relation to both the monthly timing of cycle resumptions, i.e., the beginning of the mating period for each female (Model 3), and the monthly timing of conceptions (Model 4). We did not analyse births because conceptions and births were highly dependent in our dataset (most conceptions had been estimated based on the dates of birth), and because females should have more flexibility to adjust the timings of conceptions than births. There were several differences in our approach between Models 1 and 2 versus Models 3 and 4.

First, we used different proxies of reproductive synchrony because reproductive timings were likely to be affected by the current and past reproductive states of other females in the group. We used two distinct metrics of reproductive synchrony in each model: the 'monthly number of conceptions' and 'monthly number of cycling females' in the same group as the focal event. For the first variable, we observed 155 cycle resumptions and 241 conceptions. For the latter variable, we restricted our dataset to those months for which observations were available (to avoid accumulating uncertainties in the date estimates of reproductive state changes), resulting in a dataset comprising n=61 cycle resumptions and n=103 conceptions. We did not include in the same model our two metrics of reproductive synchrony, as the numbers of conceptions and of cycling females in a given month are correlated (Pearson correlation test: $R=0.23$, $t=6.21$, $p<10^{-4}$).

Second, the effects of environmental variation (NDVI_S and NDVI_NS) and group reproductive synchrony (number of cycling females or of conceptions per month) on the timing of cycle resumptions and conceptions may operate over various time periods. We thus used a moving window approach to consider possible time period effects (van de Pol et al. 2016). For environmental variables, we identified the best time window testing periods covering 0 to over 12 month(s) prior to the focal event using an AIC-based selection procedure, in a univariate mixed model containing only the fixed effect of interest. We then added the best variable as a fixed effect in our final multivariate model. For the reproductive synchrony variable 'monthly number of conceptions', we similarly identified the best time window but for different durations, from 0 to 6 months. For the second reproductive synchrony variable 'monthly number of cycling females', we could not explore its effects over the same time periods due to the limitations of our dataset, and we only tested its past and current effect from 0 to 2 month time periods. All in all, we thus investigated the effects of the number of conception the same month, the mean number of conceptions over the past 1-6 months, the number of cycling females the same month, and the mean number of cycling females over the past 1-2 months, resulting in 10 different models for each response variable. Details on these procedures are given in the Appendix D and Figure S2, electronic supplementary materials.

To calculate the 'cycle resumption' response variable, we assessed the monthly probability that a female would resume cycling during those time windows in which cycle resumption was possible, i.e., following the post-partum anoestrus period, which lasts between 223 to 550 days in our population (7-18 months). During the 14 years of study and for each female, we only considered those months that were included within this window of possibility (7-18 months after each birth) and coded 0 if she did not recycle in a given month, and 1 if she did. Similarly, to calculate the 'conception' response variable, we considered if a female was cycling during each month of the 14 years of study, and for each cycling month coded 0 if she did not conceive

and 1 if she did. We ran a GLMM with a binomial error structure. The identity of the female was set as a random effect. To test our hypothesis, fixed effects in both models comprised:

- *Non-seasonal environmental variations* (NDVI_NS). Under the non-seasonal environment hypothesis (H1), we expected the probabilities of cycling resumption and conception to increase when the food availability was higher than average for this particular time of the year.
- *Reproductive synchrony*. Under the asynchrony hypothesis (H2), we expected the probabilities of cycling resumption and conception to increase when the group synchrony decreased.
- *Interactions between female rank and environmental variations (both seasonal and non-seasonal)*. Under the social rank hypothesis (H3a), we expected that higher-ranking females would be less sensitive to environmental variation than lower-ranking ones.
- *Interaction between reproductive synchrony and female rank*. Under the social rank hypothesis (H3b), we expected lower-ranking females only to adjust their reproductive timings depending on group reproductive synchrony.

As control variables we also included:

- *Seasonal environmental variations* (NDVI_S). Even for non-seasonal breeders, the intensity of the seasonal environment (regardless of its non-seasonal variation) could affect both the probability to resume cycling and to conceive for adult females (Cheney et al. 2004). We already showed in this population that the annual conceptive peak occurs at the end of the rainy season (Chapter 3) and we therefore expect seasonal environmental variations to affect conception probabilities.
- *The number of adult females in the group*, the year of the reproductive event. We expected to find a negative effect of this indicator of within-group competition on the

probability of conception (Bulger and Hamilton 1987; Beehner et al. 2006; Roberts and Cords 2013), and possibly on cycle resumption timings.

- *Group identity*, to control for possible differences between social groups.
- *Female rank*. Higher-ranking females could exhibit a higher probability of conception, even if this has not been found in previous baboon studies (Wasser et al. 1998; Beehner et al. 2006; Gesquiere et al. 2017).
- *Female parity*. Nulliparous and primiparous females often have lower reproductive performances than multiparous females, in particular a lower probability of conception (Gesquiere et al. 2017).

We did not include interaction terms between rank and environmental variations in our model looking at the effect of the number of cycling females on probability to resume cycling and conceive, in order to avoid overfitting and facilitate model convergence in this restricted dataset.

All statistical analysis had been conducted in R version 3.5.0 (R Core Team, 2018). To test our hypothesis with our four mixed models, we used 'lmer' (for LMM, i.e. Model 1) or 'glmer' (for binomial GLMMs, i.e Models 2, 3 and 4) function on the lme4 package (Bates et al. 2015). The distribution of residuals were checked using 'qqPlot' function of the car package for LMMs (Fox et al. 2019) and using 'simulateResiduals' from DHARMa package for binomial GLMMs (Hartig 2020). All quantitative variables were z-transformed to have a mean of zero and a standard deviation of one in order to facilitate model convergence. When the fits obtained were singular, we double checked the results by running the exact same models with a Bayesian approach, using the 'bglmer' function from the blme package (Dorie 2015). To diagnose the presence of multicollinearity, we calculated the variance inflation factor (VIF) for each of the predictors in each full model using the vif function of the R car package (Fox et al. 2019). These VIFs were <2.5 across all our final 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 95% Wald confidence intervals to assess the strength of the fixed effects. Only those fixed effects whose confidence intervals did not cross zero and whose P-values < 0.05 were treated as having support. Uncertainty in the dates of conceptions, births, and cycle resumptions were taken into account in all models (Appendix A, electronic supplementary materials). We also removed from the models presented in main text the non-significant interactions, in order to interpret the estimates of simple effects (and when an interaction was significant, we also tested the significance of simple effects, and presented the results if necessary).

RESULTS

We tested our three non-exclusive hypotheses to explain the evolution of non-seasonal breeding, focusing on two fitness parameters (IBI and infant mortality before weaning, Models 1 and 2) and two timings of reproductive events (cycle resumption and conception, Models 3 and 4). See Table 1 for a summary of predictions and results.

1/ Minimal support for the non-seasonal environment hypothesis (H1)

While non-seasonal NDVI variation (NDVI_NS) was consistently identified as providing the better model fit (over non-seasonal rainfall variation, Rain_NS), it had no effect on our first indicator of reproductive performances: IBI (Table 2). However, infants were more likely to die before being weaned when they grew up in relatively bad periods in terms of food availability (Table 3, Figure 1), in support of H1. Non-seasonal variations of NDVI did not affect timing of cycle resumption (Table 4), or probability of conception (Table 5), and thus

failed to support H1 in these models. In contrast, we found various effects of seasonal environmental variation, either expressed by the sine term derived from the infant date of birth (for IBI and infant mortality) or by seasonal NDVI variation (for conception). While the effects of environmental seasonality on IBI and infant mortality were reported in a previous study (Baniel et al. in prep., Dezeure et al., in prep.) we further found a positive effect of seasonal environmental variation (indexed by vegetation greenness over the past 2 months) on conception probability (Table 5, Figure S3). However, we did not detect any effect of seasonal environment variation on cycle resumption timings (Table 4). All in all, we found more effects of seasonal than non-seasonal environmental variation on baboon reproduction.

2/ Support for the reproductive asynchrony hypothesis (H2)

We did not find any effect of the number of cycling females (Table S2 of the supplementary electronic material) or of the number of conceptions on cycle resumption timings (Table 4), and we also failed to detect any effect of group reproductive synchrony on the IBI (Table 2) and infant mortality (Table 3). In support of H2, we found a negative effect of the number of cycling females, one of our indicator of group reproductive synchrony, on the likelihood to conceive in a given month (Table 6, Figure 2). However, contrary to H2 expectations, we found that greater reproductive synchrony, indexed by the number of conceptions per month, led to a higher rate of conceptions in the group. More precisely, we detected a positive effect of the mean number of monthly conceptions over the past 4 months on the probability to conceive (model presented in Table 5, without the interaction between rank and reproductive synchrony fixed effect was: Estimate=0.28, X^2=11.64, p-value=$9.76*10^{-4}$, CI p-value = [0.00075 – 0.00085]). The same effect of reproductive synchrony was detected in relation to the mean number of monthly conceptions occurring over the past 2, 3, 5 and 6 months, but not of the number of conception the same month or over the last month (Table S3, electronic supplementary material). It would

indicates that female conceptive probability reacts more to past than current number of conception in the group. Thus, we did find evidence for a lagged effect of reproductive synchrony, where greater reproductive synchrony, i.e. higher number of cycling females and higher number of conceptions in the group, suppresses current conceptions in others who are then more likely to conceive once that suppressive effect has been released in later months.

3/ Social rank hypothesis: strong support for rank-related variation in response to reproductive synchrony (H3b), but not in response to environmental fluctuations (H3a)

We did not detect any support for rank-related variation of reproductive seasonality in response to non-seasonal environmental fluctuations (H3a), tested by our interactions between rank and environmental variation for each of our four measures of reproduction: IBI (Table 2), infant survival (Table 3), the timing of cycle resumption (Table 4), and the probability of conceptions (Table 5). However, three of our four models did show rank-related variation in reproductive seasonality in response to reproductive synchrony, tested by interactions between rank and synchrony, in support of H3b. Firstly, subordinate females experienced longer IBIs when more infants were born in the group in the three months before they gave birth; this effect was not detectable for high-ranking females (Table 2, Figure 3). Secondly, low-ranking females were less likely to resume cycling when there had been more conceptions over the past 6 months, whereas high-ranking females were unaffected (Table 4, Figure 4A). This interaction was not significant for other time windows (number of conceptions occurring in the past 0-5 months before the focal birth) (Table S4, electronic supplementary material). Thirdly, subordinate females were more likely to conceive when there had been more conceptions in the group over the past four months but this pattern was not seen in dominant females (Table 5, Figure 4B). The same effect was also detected over the past 1, 3 and 5 months, but not 2 and 6 months nor the same month (Table S3, electronic supplementary material). Therefore, subordinate females

were more likely to delay their conceptions in the group, waiting for other females to conceive, and generating breeding asynchrony in the group. In contrast to the effects on IBI and the probability of cycling resumption and conception, we did not detect any rank-dependent effects of reproductive synchrony on infant mortality before weaning (Table 3).

DISCUSSION

Our study emphasizes the importance of social environment, and more precisely of group reproductive synchrony, on reproductive phenology in a wild social primate. Females stagger their reproductive events to avoid breeding synchronously, regardless of the season. Below we speculate over the potential drivers of the intrasexual reproductive competition driving breeding asynchrony, with limited access to paternal care as a primary candidate. We further shed light on individual variations of strategies over reproductive phenology, depending on female rank. Finally, and surprisingly, despite living in a highly unpredictable environment (with important between-year variation of rainfall and food availability), the reproductive performances of the Tsaobis baboons respond more to predictable (seasonal) variations than unpredictable ones.

The asynchrony hypothesis explains non-seasonal breeding (H2 and H3b)

Several results converged to indicate that non-seasonal breeding was an emergent consequence of individual strategies aimed at limiting breeding synchrony. **First**, our results showed a fitness cost of birth synchrony, for subordinate females only, who experienced a longer interval to the next conception when more infants were born in the same group in the 3 months preceding the birth of their own infant. Such an effect will contribute to reduce the intensity of reproductive seasonality by de-synchronizing the reproductive phenology among females of different ranks.

Second, the more conceptions that occurred during the past 6 months in the group, the less likely a lower-ranking female would resume cycling. Such an effect could potentially result in the total loss of a birth season at the population level by mechanistically staggering conceptions. In line with this, there was no effect of seasonal or non-seasonal environmental variation on the probability of cycling resumption, indicating that reproductive competition may be the most important factor causing the extension of the mating season in chacma baboons, and thus decreasing the strength of reproductive seasonality. **Third,** our results further show that the chances of conception decrease when the number of cycling females in the group increase, irrespective of dominance rank, and generating an additional force to extend periods of sexual receptivity – and thus the mating season - that affects all females. **Fourth**, the likelihood to conceive increased after conceptions had peaked in their group in the previous months, but was unaffected by the number of conceptions occurring the same month. Subordinate females were more strongly affected by this positive effect. Although a positive effect of others' conceptions on a female's conceptive probability was unexpected, it may reflect reproductive asynchrony rather than synchrony, where females, in particular lower-ranking ones, conceive after others have conceived. Because conceptions, unlike cycle resumptions, are influenced by the season, with a moderate peak between April and May, such delays in conceptions likely contribute to flatten and extend this peak at the group level. All in all, subordinate females experienced greater costs and are more sensitive to reproductive asynchrony and consequently, their reproductive phenology is more sensitive to the current and past reproductive states of other females within a group. However, reproductive synchrony does also affect dominant females' reproductive timing: the number of cycling females and the number of adult females both negatively affect the likelihood to conceive, regardless of female social rank.

At the proximate level, such reproductive suppression can be explained by female-female competition at different stages of the reproductive cycles. Previous evidence in this

population shows that females face intense aggression when they are cycling at the same time as other females (Huchard and Cowlishaw 2011; Baniel et al. 2018*a*), and this study further shows that they struggle to conceive in such circumstances. Another recent study suggests that the stress induced by female-female aggression may contribute to down-regulate female reproductive physiology by showing that cycling females who mated with a male were harassed by the pregnant or lactating females who had already conceived with this male; such harassment further decreased the likelihood of conception for the victim, in a form of reproductive suppression (Baniel et al. 2018*b*). Subordinate females suffer more strongly from reproductive synchrony, as they face more aggression from other females. However, studies in different social mammals show that strategies used to suppress subordinates' reproduction can also be costly to dominants in various societies (Sapolsky 2005; Clutton-Brock et al. 2010), and may contribute to explain why dominant females also suffer from reproductive synchrony, though to a lower extent than subordinate females.

At the ultimate level, females likely adopt such competitive tactics to minimise the number of other females with whom they will have to share paternal care in a polygynous mating system, where the alpha male sires nearly 70% of offspring born in the group (Tsaobis: Huchard et al. 2010; other baboons: Alberts 2012). Such an interpretation is strengthened by recent evidence that female aggression selectively targets females who mate with the father of the aggressor's offspring, in an attempt presumably to delay the birth of a paternal half-sibling (Baniel et al. 2018b). Paternal care in baboon societies increases offspring survival and growth (Charpentier et al. 2008) through several mechanisms, including protection against infanticide (Huchard et al. 2010; Palombit 2012; Palombit 2003; Palombit et al. 1997) and aggression from conspecifics (Lemasson et al. 2008; Nguyen et al. 2009), and increased access to food during weaning (Huchard et al. 2012). Another ultimate explanation may be that females compete over access to food. In mammals, lactation and pregnancy are associated with an increase of energy

intake for females (Lee et al. 1991; Emery Thompson 2013) and females could therefore benefit from staggered reproduction, in order to reduce the number of females that are simultaneously lactating in their group. However, predictions generated by these hypotheses, such as the fact that we should expect more aggression among pregnant and lactating females than among females in other reproductive states, or more aggression at times of food scarcity, have received weak support in our study population (Huchard and Cowlishaw 2011; Baniel et al. 2018*a*). A third ultimate explanation is that staggering birth would decrease competition over food between offspring during and after weaning (rather than between mothers). However, no empirical studies confirmed yet the existence of such competition.

More generally, although fitness costs of synchronous births have been reported in several species, including social primates like yellow baboons (Wasser and Starling 1988) and bonnet macaques (Silk 1989), cooperative breeders such as meerkats and banded mongooses (Clutton-Brock et al. 2001; Nichols et al. 2012), and polygynous birds where females compete over paternal care (Yasukawa et al. 1990, 1993; Slagsvold and Lifjeldt 1994), their consequences for patterns of seasonal reproduction have never been established at the population level. Our study provides the first empirical evidence that reproductive competition at the individual level may generate reproductive asynchrony at the population level.

No support for the non-seasonal environment hypothesis (H1) or for a rank-mediated response to seasonal and non-seasonal environmental variations (H3a)

Non-seasonal variation in food availability, and in particular periods of unusual food scarcity (beyond the seasonal norm), increased offspring mortality before weaning. Periods of food scarcity are known to negatively impact offspring survival before weaning in various baboon or primate populations (Altmann et al. 1977; Cheney et al. 2004; Kleindorfer and Wasser 2004;

Gogarten et al. 2012; Campos et al. 2020). Nonetheless, these studies did not disentangle predictable/seasonal environmental variations from unpredictable/non-seasonal ones, and therefore, our results show here than when infants face harsher periods in early life than usual (i.e. lower than the yearly average), they are more likely to die. Extreme climatic conditions, including severe droughts, become more and more frequent with climate change (Easterling et al. 2000; Dai 2013), and such results confirm, in addition to other studies (Wiederholt and Post 2011; Korstjens and Hillyer 2016; Campos et al. 2020), that it would have dramatic effect on the demography of wild primates – and probably many other taxa.

We failed to detect any additional evidence in support of the non-seasonal environment hypothesis. First, females did not adjust their fertility periods and conceptions in response to between-year variations of rainfall or food availability (Tables 3 and 4). It suggests that females may adjust their reproductive timings in prevision of future seasonal/predictable environmental fluctuations, in a probable attempt to time lactation peak, or late-weaning with future annual food peaks. Indeed, a previous study in this population showed that females who time births in order to synchronize the annual food peak with early-weaning and/or lactation peak display shorter interbirth intervals, while matching it with late-weaning leads to lower offspring mortality (Chapter 3). Therefore, they do not rely on the energetic stores built based on recent food availability to onset their reproduction or conceive. Such observation goes against a mechanistic hypothesis provided by the income-capital breeder framework, which assumes that capital breeders match conception with the annual food peak because conception is condition-dependent. Females therefore wait for their energetic stores to be replenished to start a new reproductive cycle (Jönsson 1997; Brockman and van Schaik 2005). Despite important year-to-year variations in cumulative rainfall and food availability in Southern Africa, rainfall nearly always occurs during the rainy season (Alberts et al. 2005; Baniel et al., in prep.). In other words, the timing of rain, and the associated food peak, remains relatively predictable, which

may explain why female reproductive phenology is more responsive to seasonal than non-seasonal environmental variations. Lastly, and more surprisingly, we did not detect any effect of non-seasonal environmental variation on IBI duration, in contrast to seasonal variation (Table 2). This result may reflect the fact that interbirth interval are affected by overall environmental variation, and that the effects of seasonal variations, i.e. giving birth in the rainy season, are more important than the effects of giving birth in worst years than others. In addition, given that interbirth intervals are long in the Tsaobis baboons, it is likely that they often integrate both better-than-average and worst-than-average periods, which may cancel each other out, possibly limiting the impact of year-to-year environmental variation on such long-lived species.

Females show similar reproductive responses to variation in food availability irrespective of their social rank. Although low-ranking females would be expected to be disadvantaged by their inability to access monopolisable food resources, especially when food is scarce, it is possible that such females use more non-monopolisable and/or fallback foods during food scarcity, or negotiate the tolerance of dominant females to access food patches (Sick et al. 2014; Marshall et al. 2015). This ability of subordinates to develop counter-strategies to limit the costs of contest feeding competition has been found in a wide range of animal species (Bugnyar and Kotrschal 2004; Hewitson et al. 2007; Held et al. 2010). Nevertheless, although subordinate females might have been able to minimise competition for food, it appears they were less able to minimise competition over access to mates, given the observed rank-dependent effects of reproductive synchrony on female reproduction.

Other perspectives to explain the evolution of non-seasonal breeding

On top of reproductive asynchrony, several additional ecological or evolutionary mechanisms can contribute to explain non-seasonal breeding in social primates, and probably beyond. First, a previous study in this population shows the existence of two optimal birth timings in the annual cycle, as the timing that minimizes mother's interbirth interval occurs four months apart from the timing that minimizes offspring mortality (Chapter 3). Maternal trade-offs over birth timing may commonly occur, and contribute to explain extended birth seasons between these optima, due to individual variation in strategies of conflict resolution. Second, offspring mortality occurs year-round for a variety of reasons including disease, predation, and infanticide, with the latter cause that can affect up to 30% of offspring in some baboon populations (Palombit 2012). Females typically resume reproduction quickly after losing an infant in social primates (Palombit et al. 2000; Palombit 2003, 2012, 2015) and this may occur even outside the reproductive season. For example, in geladas (*Theropithecus gelada*), females who lose an infant during a seasonal burst of infanticides can conceive outside the main mating season, resulting in a second annual peak of births (Tinsley Johnson et al. 2018). Such ability to conceive/onset reproduction year-round, which may have evolved as a counter-strategy to infanticide, or more broadly in response to high level of extrinsic infant mortality (which spans from 13 to 26% in our population: Baniel et al. in prep.), may contribute to explain the absence of seasonal breeding at the population level. Future studies can usefully explore the interplay between ecology, life-history and sociality that may contribute to explain variations in the intensity of reproductive seasonality across mammals, a field that has been largely understudied so far.

Conclusion

We detected fitness costs associated to birth synchrony, and showed that females, in particular subordinates, adjust their reproductive phenology to the phenology of other females in the

group in order to mitigate the costs of synchronous births, which are likely linked to intrasexual competition over access to paternal care. The unpredictability of the environment failed to explain the absence of reproductive seasonality in this population, suggesting that females plan their reproductive investment based on future, predictable food peaks, rather than relying on the energetic stores built thanks to past food availability as proposed by the capital breeding theoretical framework. This study highlights the importance of female reproductive competition as a main driver of the evolution of mammalian reproductive seasonality, opening new avenues for future research in this area. It further points to the necessity of understanding the causes and mechanisms of competition at the behavioural level to gain insights on key demographic parameters of a population, including its responses to environmental change.

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TABLES

Table 1: Models and predictions of each fixed effect depending on the hypothesis tested.

We indicated with a (+) the predictions supported by our results.

		Fitness effects		**Timing effects**	
		Model 1	**Model 2**	**Model 3**	**Model 4**
		IBI	**Infant survival**	**Cycling resumption**	**Conception**
H1	**Non-seasonal environmental variation:** Unpredictable environmental variation leads females to retain a flexible reproductive schedule that responds opportunistically to better environmental conditions	Longer when food is scarce	Lower when food is scarce (+)	Less likely when food is scarce	Less likely when food is scarce
H2	**Reproductive synchrony:** Females avoid simultaneous reproduction to reduce competition for mates, paternal care or ecological resources	Longer when female synchrony is higher	Lower when female synchrony is higher	Less likely when synchrony is higher	Less likely when synchrony is higher (+)
H3a	**Rank*environment effects:** Subordinate females experience more restricted resource access during the lean season	Negative effects of food scarcity on IBI greater for subordinate females	Negative effects of food scarcity on infant survival greater for subordinate females	Negative effects of food scarcity on cycling resumption greater for subordinate females	Negative effects of food scarcity on conception greater for subordinate females
H3b	**Rank*synchrony effects:** Costs of reproductive synchrony fall more heavily on subordinate females	Negative effects of synchrony on IBI greater for subordinate females (+)	Negative effects of synchrony on infant survival greater for subordinate females	Negative effects of synchrony on cycling resumption greater for subordinate females (+)	Negative effects of synchrony on conception greater for subordinate females (+)

Table 2: Environmental and social determinants of interbirth interval (IBI) duration (Model 1).

We ran 1000 models with simulated birth date, in order to consider the uncertainty of birth dates. The table shows the mean estimates, mean confidence intervals, mean X^2 statistics and mean p-values of the predictors provided by these 1000 linear mixed models including female identity as random effect, based on 120 observations from 43 females. Significant effects are indicated in bold. For relevant significant effect (i.e. discussed in this study), we also indicated in the footnote the Wilcoxon confidence interval of the p-values. The best fit for seasonal environmental variation is the sine term of the infant date of birth with a phase of $\pi/6$. The best fit for non-seasonal environmental variation is the mean 'NDVI_NS' between the two births. The best fit for reproductive synchrony is the number of infants born in the group over the past three months. For categorical predictors, the tested category is indicated in parentheses.

Hypothesis tested	Fixed Effect		Estimate	IC		X^2	P-value
				Lower	Upper		
H1	Non-seasonal environmental variation		-5.71	-28.69	17.27	0.25	0.628
H2	Reproductive synchrony		16.47	-4.32	37.26	2.42	0.122
H3b	**Reproductive synchrony : Rank**		**-28.68**	**-50.01**	**-7.34**	**6.95**	**0.009**[a]
Control	**Seasonal environmental variation**		**53.08**	**21.88**	**84.28**	**11.29**	**0.002**
	Number of adult females		-2.33	-27.05	22.39	0.05	0.845
	Group	(L)	-60.68	-121.6	0.29	3.85	0.149
		(M)	-19.45	-169.3	130.4		
	Rank		**-32.78**	**-60.51**	**-5.06**	**5.38**	**0.021**
	Parity	(primiparous)	-14.47	-84.64	59.70	2.61	0.736
	Sex	(male)	33.60	-7.25	74.46	0.12	0.109
	Age		**-202.8**	**-349.7**	**-55.94**	**7.35**	**0.007**
	Age²		**179.00**	**39.20**	**318.80**	**6.31**	**0.012**

[a] CI: [0.0085 – 0.0088]

Table 3: Environmental and social determinants of infant mortality before weaning (0/1: survived until weaning / died before weaning, Model 2).

We ran 1000 models with simulated birth date, in order to consider the uncertainty of birth dates. The table shows the mean estimates, mean confidence intervals, mean X^2 statistics and mean p-values of the predictors of these 1000 binomial generalized mixed models including female identity as a random effect, based on 19 dead infants out of 195 from 57 females. Significant effects are indicated in bold. For relevant significant effect, we also indicated in the footnote the Wilcoxon confidence interval of the p-values. The best fit for seasonal environmental variation is the sine term of the infant date of birth with a phase of $\pi/2$. The best fit for non-seasonal environmental variation is the mean 'NDVI_NS' from infant conception to weaning or death. The best fit for reproductive synchrony is the number of infants born in the group the following six months. For categorical predictors, the tested category is indicated in parentheses.

Hypothesis tested	Fixed Effect		Estimate	IC		X^2	P-value
				Lower	Upper		
H1	**Non-seasonal environmental variation**		**-0.66**	**-1.24**	**-0.08**	**5.01**	**0.025**[a]
H2	Reproductive synchrony		0.16	-0.31	0.63	0.44	0.507
Control	**Seasonal environmental variation**		**-1.18**	**-1.89**	**-0.48**	**10.86**	**0.002**
	Number of adult females		-0.09	-0.66	0.48	0.10	0.760
	Group	(L)	-1.18	-2.24	-0.11	5.09	0.079
		(M)	0.59	-2.88	4.07		
	Rank		**-0.52**	**-1.02**	**-0.02**	**4.10**	**0.043**
	Parity	(primiparous)	-0.43	-1.89	1.03	0.34	0.563
	Sex	(male)	0.13	-0.78	1.05	0.09	0.776

[a] CI: [0.0251 – 0.0255]

Table 4: Environmental and social determinants on the timing of cycle resumption in a given month (Model 3).

We ran 1000 models with simulated cycle resumption date in order to take into account their uncertainty. The table shows the mean estimates, mean confidence intervals, mean X^2 statistics and mean p-values of the predictors of these 1000 binomial generalized linear mixed model including female identity as a random effect, based on 155 cycle resumptions out of 1768 observations from 56 females. Significant effects are indicated in bold. For relevant significant effect, we also indicated in the footnote the Wilcoxon confidence interval of the p-values. The best fit for seasonal environmental variation is the 'NDVI_S' over the past four months. The best fit for non-seasonal environmental variation is the 'NDVI_NS' over the past three months. The best fit reproductive synchrony is the mean number of conceptions in the group over the past six months. For categorical predictors, the tested category is indicated in parentheses.

Hypothesis tested	Fixed effects		Estimate	IC		X^2	P-value
				Lower	Upper		
H1	Non-seasonal environmental variation		0.13	-0.03	0.32	2.74	0.132
H2	Reproductive synchrony		-0.20	-0.37	0.01	2.16	0.192
H3b	**Reproductive synchrony : Rank**		**0.22**	**0.03**	**0.41**	**5.23**	**0.036**[a]
Control	Seasonal environmental variation		-0.13	-0.31	0.05	2.46	0.202
	Number of adult females		-0.03	-0.31	0.26	0.18	0.749
	Group	(L)	0.14	-0.22	0.49	1.66	0.453
		(M)	-0.61	-1.95	0.73		
	Rank		0.04	-0.13	0.21	0.93	0.795
	Parity	(primiparous)	-0.23	-0.68	0.23	0.97	0.330

[a] CI: [0.02719 – 0.0308]

Table 5: Environmental and social determinants on the probability of conception in a given month (Model 4).

We ran 1000 models with simulated conception date in order to take into account their uncertainty. The table show the mean estimates, mean confidence intervals, mean X^2 statistics and mean p-values of the predictors of these 1000 binomial generalized linear mixed model including female identity as a random effect, based on 241 conceptions out of 1484 observations from 68 females. Significant effects are indicated in bold. For relevant significant effect, we also indicated in the footnote the Wilcoxon confidence interval of the p-values. The best fit for seasonal environmental variation is the 'NDVI_S' over the past two months. The best fit for non-seasonal environmental variation is the 'NDVI_NS' over the past 12 months. The best fit reproductive synchrony is the mean number of conceptions in the group over the past four months. For categorical predictors, the tested category is indicated in parentheses.

Hypothesis tested	Fixed effects		Estimate	IC		X^2	P-value
				Lower	Upper		
H1	Non-seasonal environmental variation		-0.12	-0.28	0.04	2.22	0.145
H2	**Reproductive synchrony**		**0.30**	**0.14**	**0.46**	**11.49**	**0.001**
H3b	**Reproductive synchrony : Rank**		**-0.18**	**-0.34**	**-0.03**	**5.86**	**0.019**[a]
Control	**Seasonal environmental variation**		**0.19**	**0.04**	**0.35**	**5.92**	**0.019**
	Number of adult females		**-0.49**	**-0.77**	**-0.21**	**11.74**	**0.001**
	Group	(L)	-0.10	-0.45	0.25	3.54	0.173
		(M)	-1.14	-2.11	0.09		
	Rank		0.11	-0.06	0.28	0.60	0.447
	Parity	**(nulliparous)**	**-1.01**	**-1.42**	**-0.59**	**26.50**	**$<10^{-4}$**
		(primiparous)	0.16	-0.30	0.62		

[a] CI: [0.0167 – 0.0181]

Table 6: Negative effect of the number of cycling females on the probability of conception, based on 103 conceptions out of 759 observations from 50 females.

We ran 1000 models with simulated conception date in order to take into account their uncertainty. The table show the mean estimates, mean confidence intervals, mean X^2 statistics and mean p-values of the predictors of these 1000 binomial generalized linear mixed model investigating the effect of the number of cycling females in the group on the probability of conception, along with other fixed effects. Significant effects are indicated in bold. For relevant significant effect, we also indicated in the footnote the Wilcoxon confidence interval of the p-values. The seasonal environmental variation is the 'NDVI_S' over the past two months. The non-seasonal environmental variation is the 'NDVI_NS' over the past 12 months. The reproductive synchrony here is characterized by the number of cycling females in the group in the focal month. For categorical predictors, the tested category is indicated between brackets.

Hypothesis tested	Fixed effects		Estimate	IC		X^2	P-value
				Lower	Upper		
H1	Non-seasonal environmental variation		-0.21	-0.43	0.01	3.64	0.128
H2	**Reproductive synchrony**		**-0.25**	**-0.48**	**-0.01**	**4.43**	**0.050**[a]
Control	Seasonal environmental variation		0.17	-0.04	0.37	2.72	0.128
	Number of adult females		0.12	-0.23	0.47	0.50	0.514
	Group	(L)	-0.15	-0.63	0.34	0.97	0.654
		(M)	0.09	-62.8	63.97		
	Rank		0.04	-0.19	0.27	0.19	0.720
	Parity	(nulliparous)	-0.64	-1.17	-0.11	6.24	0.053
		(primiparous)	0.50	-0.62	0.72		

[a] CI: [0.0413 – 0.0460]

FIGURES

Figure 1: Effects of non-seasonal variations of NDVI on infant mortality before weaning.

The black points represent the fitted value of our full model (Table 3) focusing on infant survival before weaning according to the mean value of the non-seasonal NDVI (NDVI_NS) between infant conception and infant death or end of weaning (550 days). The blue curve represents the linear fit, and the shaded area displays 95% confidence interval around it.

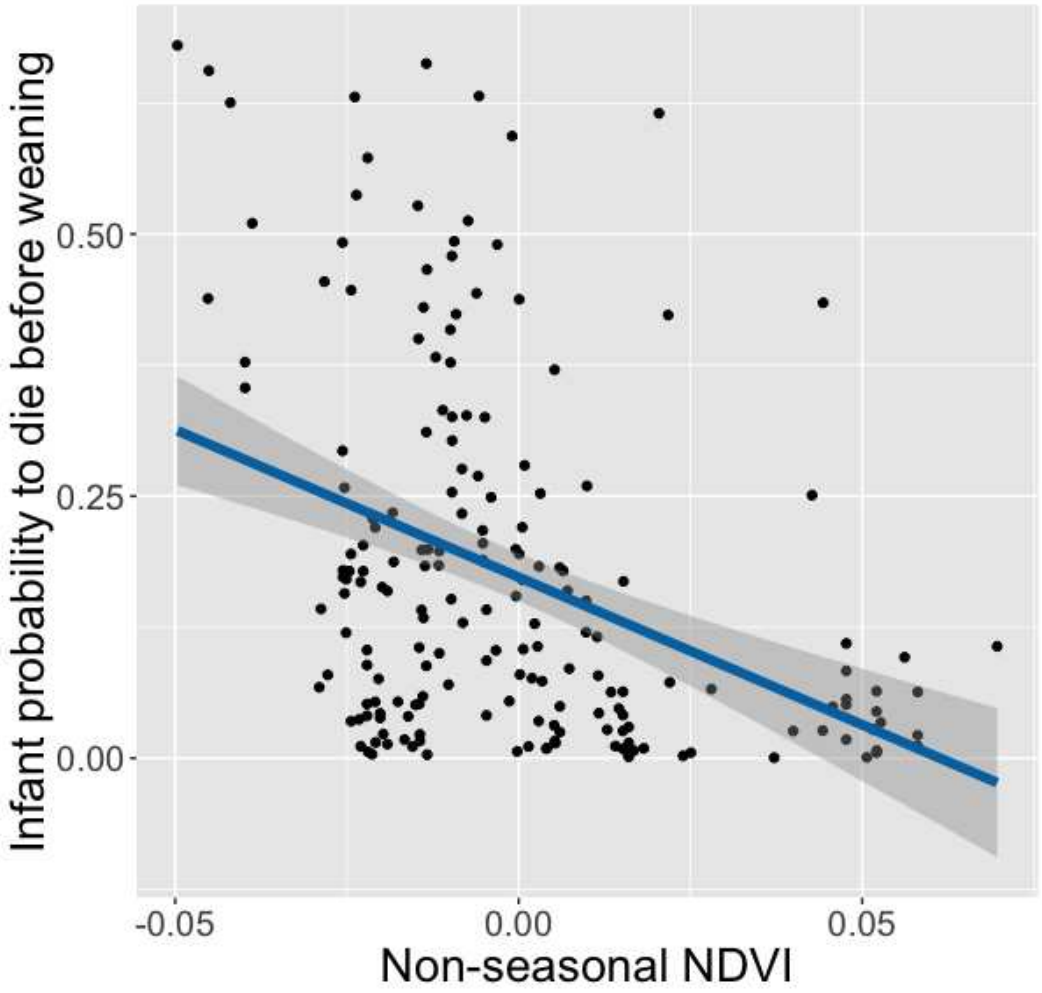


Figure 2: Negative effects of the number of cycling females in the group on the likelihood to conceive in a given month.

The black points represent the fitted value of our full model focusing on the effects of one indicator of group reproductive synchrony, i.e. the number of cycling females in the group, on the conception likelihood. The orange curve represents the linear fit, and the shaded area displays 95% confidence interval around it.

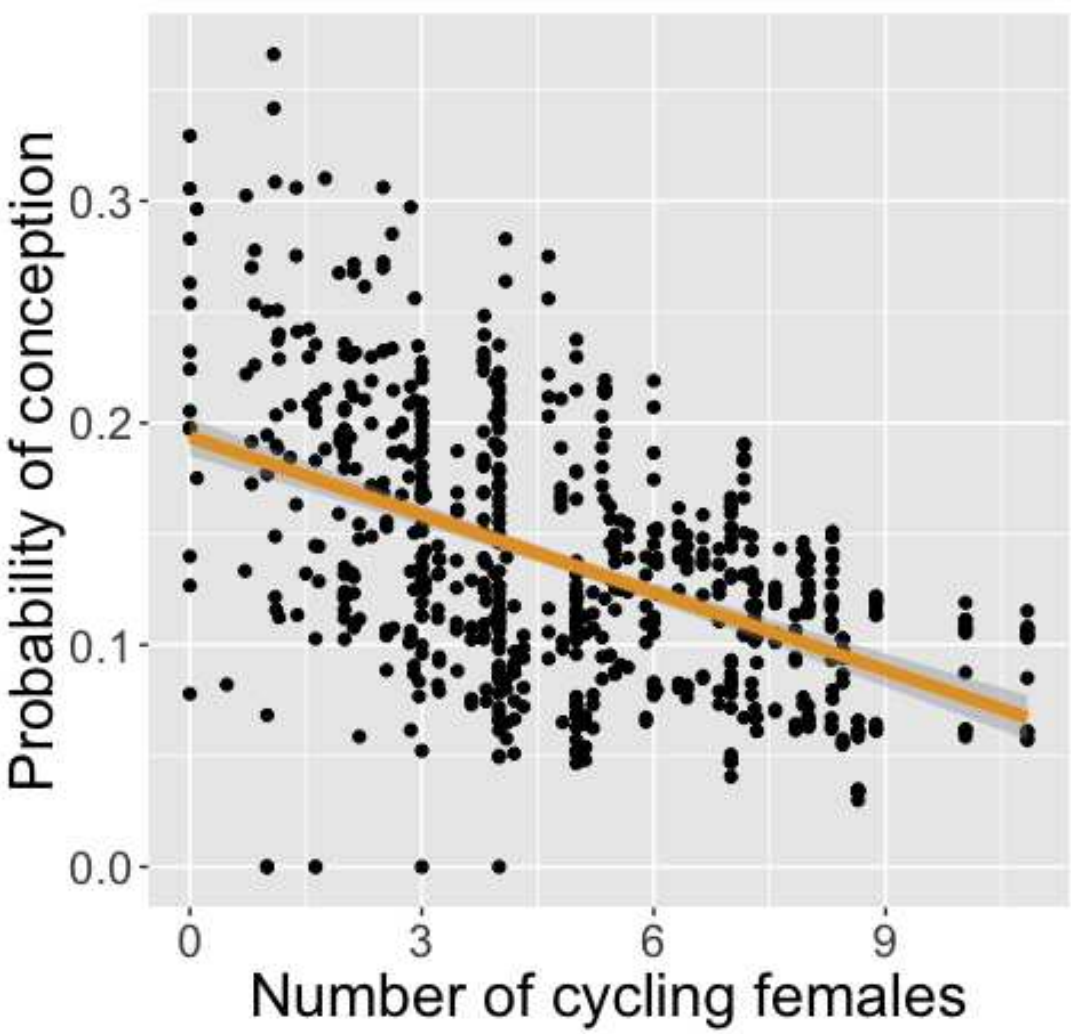


Figure 3: Low and mid-ranking females, but not high-ranking ones, show longer interbirth intervals (IBI) when reproductive synchrony in their group is higher.

Each dot represents a fitted value of the full model (Table 2) focusing on IBI according to the number of infants born in the focal female's group in the three months preceding the birth of her infant. For illustrative purposes, female social rank has been converted into a categorical variable, with females being low-ranking when their rank value is below 0.34 (blue points), high-ranking when it is above 0.67 (black points), and mid-ranking otherwise (orange points). The three curves represent the linear fit for each social rank.

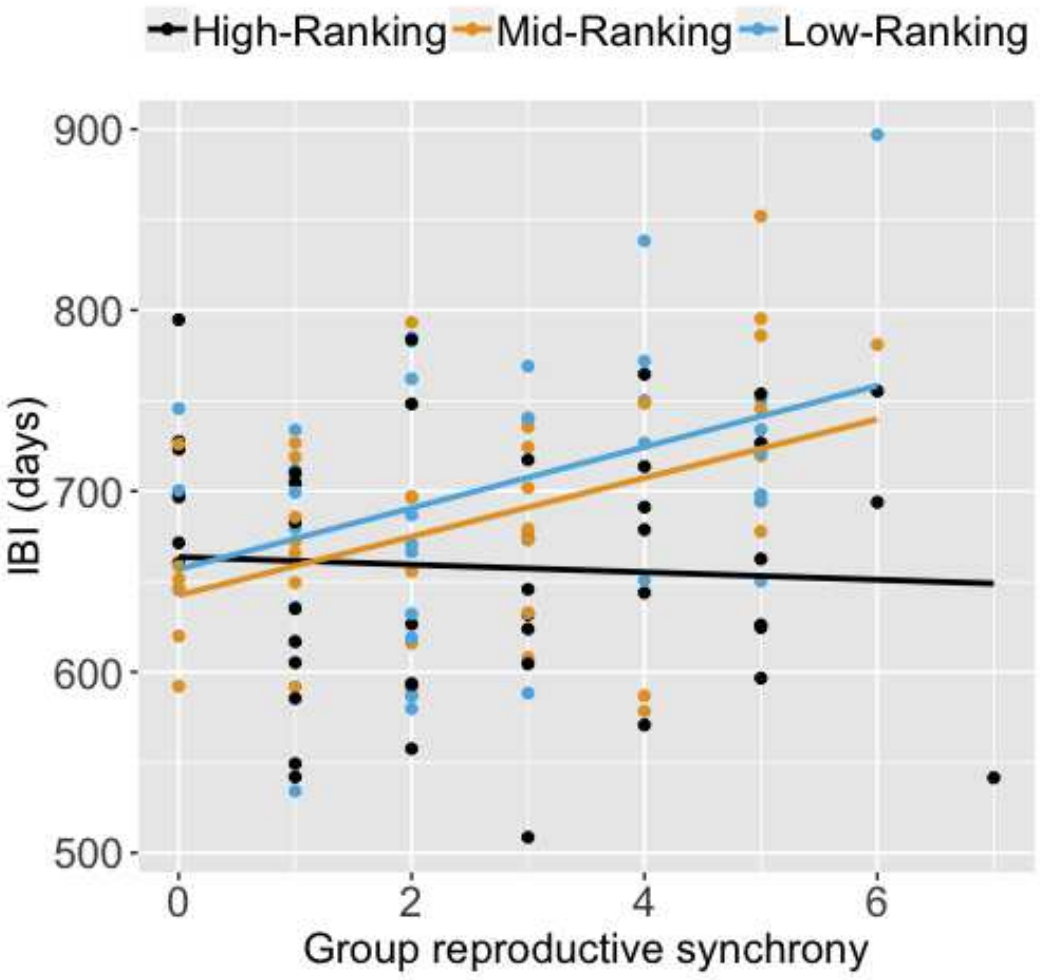
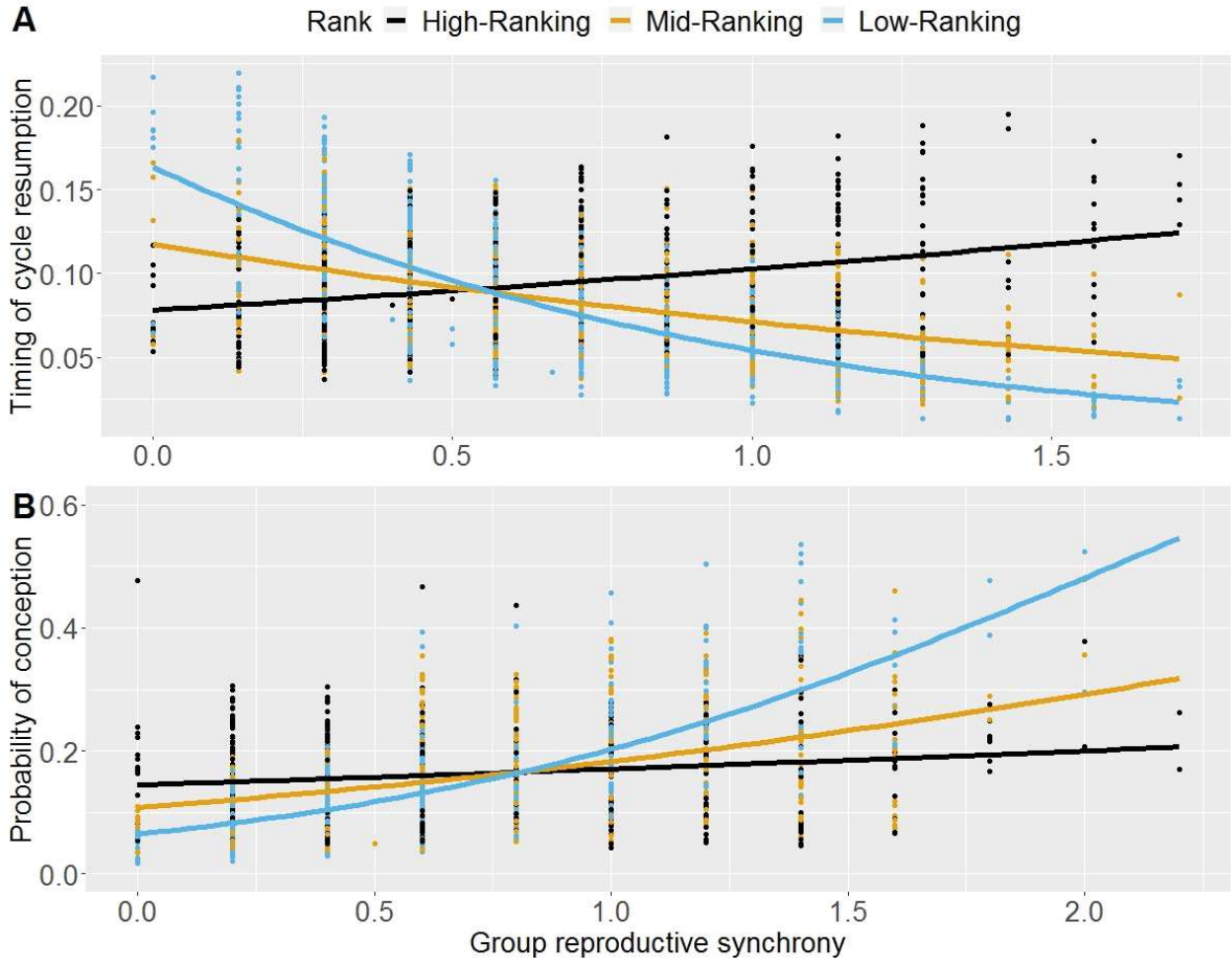


Figure 4: (A) Timings of cycle resumption and (B) monthly probability of conception of lower-ranking females are affected by group reproductive synchrony.

The group reproductive synchrony is either the mean number of conceptions over the past 6 months for the timing of cycle resumption (Panel A), or the mean number of conceptions over the past 4 months for the probability of conception (Panel B). For illustrative purposes, female social rank has been converted into a categorical variable, with females being low-ranking when their rank value is below 0.34 (blue points), high-ranking when it is above 0.67 (black points), and mid-ranking otherwise (orange points). Each dot represents a fitted value of the full model focusing on timing of cycle resumption (Table 4) or probability of conception (Table 5). The coloured curves show the logistic fit for different categories of social ranks, using the glm method of stat_smooth function of ggplot2 package.



ELECTRONIC SUPPLEMENTARY MATERIAL

APPENDICES

Appendix A. Uncertainty of the dates of conceptions, births and cycle resumptions in our models

Dates of conceptions, births and cycle resumptions were estimated in many cases, because the Tsaobis baboons were not followed all year long. Uncertainty in these estimations varied with the time of year, as we generally followed baboons during the cold and dry months, which introduced a systematic bias in our dataset that was important to account for in these analyses. We ran a set of randomizations to evaluate the robustness of the significant effects (see also Dezeure et al., in prep., following the same procedure). For each estimated value of our variables (date of cycle resumptions, conceptions and births), we created an artificial set of 1000 simulated dates covering the full range of potential dates for a given reproductive event. A random date was drawn between the minimal and maximal estimate for each value of a given reproductive parameter, and this procedure was repeated 1000 times. For example, for a birth estimated to occur between the 13th of January and the 2nd of February, we randomly chose a date between Jan 13th and Feb 2nd in one given iteration of our 1000 simulations.

For the (i) costs and benefits of reproductive seasonality on IBI and offspring mortality, the randomizations affected the sine component, introduced as a fixed effect in the full model, as the dates of births of the focal infant could be uncertain. We ran 1000 models, and computed the mean estimates, confidence intervals, X^2 tests and p-values associated based on these simulations. For the (ii) influence of social and ecological factors on reproductive seasonality, the randomization affected the response variables (probability to resume cycling and to conceive). We similarly ran 1000 models using each of the 1000 simulated dataset, and extracted the mean estimates, confidence intervals, X^2 test and p-values associated. All tables of model results (Table 2-6) presented in main text indicate the mean values of the parameters obtained through these randomization process in order to control for uncertainties in the estimates of reproductive events. We further computed a 95% confidence interval for the relevant p-values of each model, i.e. significant or borderline effects in support of our hypotheses, using a

Wilcoxon test. These p-values confidence intervals are shown in the footnotes of the Tables presented in the main text.

Appendix B. Characterization of Tsaobis environmental variations

We considered four environmental aspects to characterize environmental variation at Tsaobis: the photoperiod (daytime length), temperature, rainfall and vegetation cover (food availability). First, we extracted these four environmental factors as follow.

(i) Daily daytime length at Karibib (situated 60km north of Tsaobis) was computed using sunset and sunrise time in this city from a website ('https://dateandtime.info'), then converted into minutes and averaged per month. (ii) Mean daily daytime land surface temperatures over an 8-day period per pixel of 1km*1km resolution were obtained using MODIS data (product MOD11A2) provided by NASA (Wan, Hook, & Hulley, 2015). These data were extracted from a rectangular geographic area encompassing the global ranging area of the Tsaobis baboons, computed using GPS locations collected by observers every 30 minutes when following the study groups. We used the minimal and maximal latitude and longitude recorded between 2005 and 2019. Monthly means of the daily temperatures were then calculated across 2004-2019. (iii) Daily rainfall in a 0.25*0.25 degree resolution (corresponding to 28*28km at this latitude) using the same geographical area as for temperatures was extracted from satellite data sensors with the Giovanni NASA website (product TRMM 3B42) (Savtchenko, 2016). Monthly accumulated rainfalls (summed across daily values) were subsequently averaged between 2004 and 2019. (iv) The method of extraction of NDVI, our proxy of food availability, reflecting vegetation cover, is provided in the main text.

Once extracted, we were interested to disentangle seasonal from non-seasonal variations of our four environmental variables, allowing us to test in subsequent analyses the influence of environmental unpredictability on baboon reproduction. These environmental conditions might show either strong seasonality, varying in a consistent predictable pattern across years, or weak seasonality, varying in less predictable way between years. We identified which of these four conditions showed strong versus weak

seasonality by assessing how well they were predicted by a sine wave. Sine waves provide an ideal representation of seasonal variation (English, Bateman, & Clutton-Brock, 2012; Rickard et al., 2012). At Tsaobis where environmental variation is unimodal, with one rainy season followed by one food peak per year, these variations are by definition periodic (with a period of one year). Importantly, sine waves allow the introduction of a circular variable into a multivariate model: the possible effects of the month or date of birth are circular with a period of one year, and not linear, as the 31st of December is the day before the 1st of January, and should be considered as close as the 31st of October and the 1st of November are, for example. In addition, a sinusoidal term can be used to detect any seasonal effects, i.e. any effect of month or date of birth on reproductive parameters, which may not be captured by our other environmental variables. For example, the phenology of some baboon foods may depend on particular combinations of climatic and photoperiodic cues that very between plant species. To assess the strength of seasonal variations of each of our environmental factor, we ran four linear models in which each of our four environmental variables was the response variable and a sinusoidal term was the only fixed effect. This sinusoidal term was as follows (as all our environmental variables were monthly values):

$$sin(Month + \varphi)$$

The month of the year in the formula above was converted in a radian measure, so that the period, i.e. one year, equalled to 2*π, ranging from π/6 for January to 2*π for December. We tested different phase values φ (0, π/6, π/3, π/2, 2*π/3 or 5*π/6), to account for potential phase shifts across the year. For example, a phase of 0 could maximise the months of March or September, a phase of π/6 could maximise the months of February or August (depending on the sign of the fitted coefficient), etc. We then selected the best phase as the one minimizing the AIC in our model. We found that the sine term of phase π/2, maximising December (the solstice), explains 88% of temperature variation and 99% of photoperiod variation between 2004 and 2019. Thus, in the following analyses, temperature and photoperiod are represented with the sine term only, as we show that between-year variations of temperatures and photoperiod are negligible compared to within-year variations. On the contrary, and as expected (see Figure S1, with substantial between-year variations of rainfall and NDVI), the sinusoidal term with the

best phase only explained 18% of NDVI variation and 20% of rainfall variation. For NDVI and rainfall, we thus decomposed their seasonal and non-seasonal variation. We first computed the mean monthly values across all 15 years, and labelled these variables as 'NDVI_S' and 'Rain_S'. We then computed the difference between each actual monthly value in a given year and this averaged monthly value across years. We labelled these differences as 'NDVI_NS' and 'Rain_NS'. Here, seasonal variables reflect within-year variation only (predictable variations, consistent between years), while non-seasonal variables reflect between-year variation only (unpredictable, inconsistent between years).

Appendix C. Models focusing on interbirth intervals and infant mortality

In those models, we investigated the costs of environmental variations, group synchrony and rank-related variations of these costs on the fitness of both mothers and offspring, looking at two response variables: interbirth intervals (IBI) and infant mortality before weaning. We test our three non-exclusive hypotheses, and expect to find fitness costs associated with non-seasonal environmental variations under the non-seasonal environment hypothesis (H1), with reproductive synchrony under the asynchrony hypothesis (H2), and with rank-related fitness costs, possibly linked with environmental fluctuations or synchrony, under the social rank hypothesis (H3). The different fixed effects considered are listed in the main text: non-seasonal environmental variation ('NDVI_NS'), reproductive synchrony ('Number_of_Infants' born around the focal birth), interaction term between female rank and environmental variation (both seasonal and non-seasonal: 'sin(Date of Birth $+\varphi$): $Rank'$ and 'NDVI_NS:Rank'), interaction term between female rank and reproductive synchrony, seasonal environmental variation (sine term of juvenile birth date), number of adult females in the group ('Number_Adult_Females'), group identity ('Group'), female rank ('Rank'), female parity ('Parity'), and infant sex ('Sex'). We also included female identity ('Identity_female') as random effect. The two final global models we ran to test our hypothesis are shown in the equations (1) and (2) below:

(1) $IBI \sim NDVI_NS + Number_of_Infants(Window_IBI) + (\sin(Date\ of\ Birth + \varphi): Rank) + (NDVI_NS: Rank) + (Number_of_Infants(Window_IBI): Rank) +$

$\sin(Date\ of\ Birth + \varphi) + Number_Adult_Females\ + Group + Rank + Parity + Sex,\ random = Identity_female,\ family = 'gaussian'$

(2) $Infant\ mortality\ before\ weaning \sim NDVI_NS + Number_of_Infants(Window_Mortality) + (\sin(Date\ of\ Birth + \varphi) : Rank) + (NDVI_NS : Rank) + (Number_of_Infants(Window_IBI) : Rank) + \sin(Date\ of\ Birth + \varphi) + Number_Adult_Females\ + Group + Rank + Parity + Sex,\ random = Identity_female,\ family = 'binomial'$

First, we ran the six following univariate models (3), (4), (5), (6), (7) and (8), considering only the seasonal environmental variations, i.e. the offspring dates of births with a sine term:

(3) $IBI \sim \sin(Date\ of\ Birth), random = Identity_female, family = 'gaussian'$

(4) $IBI \sim \sin(Date\ of\ Birth + \pi/6), random = Identity_female, family = 'gaussian'$

(5) $IBI \sim \sin(Date\ of\ Birth + \pi/3), random = Identity_female, family = 'gaussian'$

(6) $IBI \sim \sin(Date\ of\ Birth + \pi/2), random = Identity_female, family = 'gaussian'$

(7) $IBI \sim \sin(Date\ of\ Birth + 2 * \pi/3), random = Identity_female, family = 'gaussian'$

(8) $IBI \sim \sin(Date\ of\ Birth + 5 * \pi/6), random = Identity_female, family = 'gaussian'$

The only differences between these three models are the value of the phase φ.The best phase was identified as the phase included in the model minimizing the AIC. We followed the same steps for the infant mortality models. For the IBI model, the best phase equaled to π/6 while for infant mortality model, it equalled π/2. By doing so, we characterized the best seasonal environment fluctuations likely to affect our two response variables.

Secondly, we estimated the non-seasonal environmental variation using the NDVI_NS and Rainfall _NS variables described above. We averaged NDVI_NS and Rainfall_NS across the whole period spanning the IBI for Model 1, and from conception to 550 days of age (for live infants) or to

death (for dead infants) for Model 2. The two non-seasonal fixed effects: (i) NDVI_NS and (ii) Rain_NS were introduced in separate models given that they reflect the same effect and are well correlated (Pearson correlation test: R=0.51, t=8.10, p<10-4). We ran the following models, (9) and (10), to determine which non-seasonal environmental variation was the best in each model:

(9) $IBI \sim \sin\left(Date\ of\ Birth + \frac{\pi}{6}\right) + NDVI_NS, random = Identity_female, family = 'gaussian'$

(10) $IBI \sim \sin\left(Date\ of\ Birth + \frac{\pi}{6}\right) + Rainfall_NS, random = Identity_female, family = 'gaussian'$

For both IBI and infant mortality, the models containing NDVI_NS had lower AIC values, and were thus used subsequently this metric to represent non-seasonal environmental variation.

Thirdly, we selected the best time window for our reproductive synchrony variable, i.e. the number of infants born around the focal infant (written 'Number_of_Infants' in models (1) and (2)). We used a set of univariate models relying on a strictly similar sample of observations. 'Window_IBI' and 'Window_Mortality' could thus be: before 1 month, after 1 month, both before and after 1 month, before 3 month, after 3 month, both before and after 3 month, before 6 month, after 6 month, or both before and after 6 month. Therefore, we ran nine univariate models for each response variable, with these different time windows, with the structure of the following models (11) and (12):

(11) $IBI \sim Number_of_Infants(Window_IBI), random = Identity_female, family = 'gaussian'$

(12) $Infant\ mortality\ before\ weaning \sim Number_of_Infants(Window_Mortality), random = Identity_female, family = 'binomial'$

We identified the best time window, 'Window_IBI' and 'Window_Mortality', as the one minimizing the AIC across models. 'Window_IBI' was the number of infants born over the past three months in the same group, while 'Window_Mortality' was the number of infants born six months after in the same

group. We finally incorporated these best synchrony time windows and best phase of seasonal variation, along with all other predictors, in our global models (1) and (2).

Appendix D. Models focusing on timing of cycle resumption and probability of conception

In those models, we investigated if females adjusted their reproductive timings, focusing on their onset of cycle resumption and conception, in order to limit the fitness costs associated with (H1) non-seasonal environmental fluctuations under the non-seasonal environment hypothesis, or (H2) reproductive synchrony under the asynchrony hypothesis. In (H3), we tested whether female reproductive timings showed rank-related adjustments in response to environmental variations or group synchrony. The different fixed effects considered are listed in the main text: non-seasonal environmental variation ('NDVI_NS'), reproductive synchrony ('Mean_Number_of_Conception' before the reproductive event focal), interaction term between female rank and environmental variation (both seasonal and non-seasonal: 'NDVI_S:Rank' and 'NDVI_NS:Rank'), interaction term between female rank and reproductive synchrony ('Mean_Number_of_Conception:Rank'), seasonal environmental variation ('NDVI_S'), number of adult females in the group ('Number_Adult_Females'), group identity ('Group'), female rank ('Rank') and female parity ('Parity'). We also included female identity ('Identity_female') as random effect. The two final global models we ran to test our hypothesis are shown in the equations (1) and (2) below:

$$
\begin{aligned}
(1)\ & Conception \sim NDVI_NS(Window_NS_Conception) + \\
& Mean_Number_of_Conceptions(Window_Conception) + \\
& +(NDVI_S(Window_S_Conception): Rank) + \\
& (NDVI_NS(Window_NS_Conception) : Rank) + \\
& (Mean_Number_of_Conceptions(Window_Conception): Rank) + \\
& NDVI_S(Window_S_Conception) + Number_Adult_Females + Group + Parity + \\
& Rank,\ random = Identity_female, family = binomial
\end{aligned}
$$

(2) $Cycle\ resumption \sim NDVI_NS(Window_NS_Cycle_resumption) +$
$Mean_Number_of_Conceptions(Window_Cycle_resumption) +$
$+(NDVI_S(Window_S_Cycle_resumption): Rank) +$
$(NDVI_NS(Window_NS_Cycle_resumption) : Rank) +$
$(Mean_Number_of_Conceptions(Window_Cycle_resumption): Rank) +$
$NDVI_S(Window_S_Cycle_resumption) + Number_Adult_Females + Group +$
$Parity + Rank,\ random = Identity_female, family = binomial$

Before running these models, we first investigated which was the best ecological factors to consider between sinusoidal parameters (seasonal environmental fluctuations only, reflecting temperatures, day time length, or any other seasonal parameter), rainfall and the normalized difference vegetation index (NDVI). The three seasonal effects: (i) the sine wave, (ii) NDVI_S, and (iii) Rain_S were introduced in separate models given that they reflect seasonal environmental variations and were highly correlated (Pearson correlation test: R>0.84 and p<10-4 for each pair). Similarly, the two non-seasonal fixed effects: (i) NDVI_NS and (ii) Rain_NS were introduced in separate models given that they reflect the same effect and are well correlated (Pearson correlation test: R=0.51, t=8.10, p<10-4). We therefore introduced each of our seasonal environmental parameters (sine wave of the month, Rain_S, NDVI_S), and likewise each of our non-seasonal parameters (Rain_NS, NDVI_NS), in separate models. Although we could have simply tested one representative of each, the timing of cycle resumptions and conceptions could be affected by different environmental factors, so we considered the best of all possible environmental predictors for each model.

First of all, we estimated the best phase of the sine fixed effects (with the months in radian), by running the six following models (3), (4), (5), (6), (7), (8):

(3) $Conception \sim \sin(Month),\ random = Identity_female, family = binomial$

(4) $Conception \sim \sin(Month + \pi/6),\ random = Identity_female, family = binomial$

(5) $Conception \sim \sin(Month + \pi/3),\ random = Identity_female, family = binomial$

(6) $Conception \sim \sin(Month + \pi/2),\ random = Identity_female, family = binomial$

(7) $Conception \sim \sin(Month + 2 * \pi/3),\ random = Identity_female, family = binomial$

(8) $Conception \sim \sin(Month + 5 * \pi/6),\ random = Identity_female, family = binomial$

The only differences between these three models are the value of the phase φ. We selected the best phase as the model with the minimized AIC. It was the phase π/6 which was selected. We followed the same method for the timings of cycle resumption as response variables, and we selected π/3 as the best phase.

For rainfall and NDVI fixed effects, we investigated a time window of 0-12 months because (i) other studies found lagged effects of similar length when studying the effect of weather variability on the demography and reproduction of primates (Campos et al., 2017; Wiederholt & Post, 2011), and (ii) a lag of more than 12 months (i.e. one annual cycle) would presumably not influence reproductive seasonality. See also Figure S1 for a graphical representation of the 12 time windows tested (taking the example of NDVI_S). We ran sets of univariate models to select the best time window for each rainfall and NDVI predictors (see models (9), (10), (11), (12)). A time window of N months meant that we averaged the value of the fixed effect over the past N months. Therefore, each time window indicated below ('Rainfall_Window_S_Conception', 'Rainfall_Window_NS_Conception', 'NDVI_Window_S_Conception', 'NDVI_Window_NS_Conception') reflects the average value of the environmental effect considered over the past N months, N going from 0 to 12.

(9) $Conception \sim Rain_S(Rainfall_Window_S_Conception),\ random = Identity_Female, family = binomial$

(10) $Conception \sim Rain_NS(Rainfall_Window_NS_Conception),\ random = Identity_Female, family = binomial$

(11) $Conception \sim NDVI_S(NDVI_Window_S_Conception),\ random = Identity_Female, family = binomial$

(12) $Conception \sim NDVI_NS(NDVI_Window_NSConception),\ random = Identity_Female, family = binomial$

We selected each best time window as the one minimizing the AIC of the models. We thus selected Rain_S over the past 4 months, Rain_NS over the past 12 months, NDVI_S over the past 2 months, and NDVI_NS over the past 12 months. We similarly ran the same models ((9), (10), (11), (12)) with the timings of cycle resumption as the response variable. We selected for the cycle resumption Rain_S over the past 10 months, Rain_NS over the past 4 months, NDVI_S over the past 4 months and NDVI_NS over the past 3 months.

After this first step of best time window and best phase selection, we ran other models in order to estimate which ecological factors, between the sine term, rainfall (Rain_S and Rain_NS), and NDVI (NDVI_S and NDVI_NS) effects, were the best to predict our response variables. To do so, we ran the three following models ((13), (14), and (15)):

(13) $Conception \sim \sin(Month + pi/3) + (1|ID)$

(14) $Conception \sim Rain_S(4) + Rain_NS(12) + (1|ID)$

(15) $Conception \sim NDVI_S(2) + NDVI_NS(12) + (1|ID)$

The best model was the one minimizing the AIC, and we similarly ran models (13), (14) and (15) for cycle resumptions as response variable. For both our response variables, the NDVI model was the best one, and we consequently only kept the NDVI fixed effects in our global model looking at reproductive synchrony effects too (and only presented the models with NDVI fixed effects in the main text of this study).

After selecting the best time windows for ecological factors, and selecting the best ecological factors, we wanted to run a global model considering reproductive synchrony as a fixed effect. The first variable we considered as an indicator of reproductive synchrony was the number of conceptions occurring in the same group. We arbitrarily restricted our exploration to a possible lag of 6 months prior to the focal event, on the basis that females were unlikely to react to reproductive events occurring more than 6 months before. In addition, females in this species were expected to compete over paternal care,

which is especially important in the first 6 months of life, the age window where vulnerability to infanticide was maximum (Palombit, 2003), meaning that female reproductive competition may decrease when the age gap between their offspring is greater than 6 months. We therefore investigated the effects of past and present reproductive synchrony by considering (1) a time window of increasing length (from 0 to 6 months) before the observation (model (16) below): here, our fixed effect is the mean number of conception in the group occurring in the past X months (X referring to 'Window_Conception' in the model (16) below, and ranging from 0 to 6). See also Figure S1 for a graphical representation of the various past and present reproductive synchrony tested.

$$
\begin{aligned}
(16)\quad & Conception \sim NDVI_NS(Window_NS_Conception) + \\
& Mean_Number_of_Conceptions(Window_Conception) + \\
& +(NDVI_S(Window_S_Conception) : Rank) + \\
& (NDVI_NS(Window_NS_Conception) : Rank) + \\
& (Mean_Number_of_Conceptions(Window_Conception) : Rank) + \\
& NDVI_S(Window_S_Conception) + Number_Adult_Females + Group + Parity + \\
& Rank,\ random = Identity_Female, family = binomial
\end{aligned}
$$

We therefore ran 7 models for each response variable (see Table S2). We ran the exact same models, with different best time windows for the NDVI effects, for the cycle resumption response variable. The results showed in the tables of the main text were the ones of the models minimizing AIC, i.e. with the mean number of conceptions over the past four months for the probability of conception, and with the mean number of conceptions over the past six months for the timing of cycling resumption.

The second variable we considered as an indicator of reproductive synchrony was the number of cycling females in the same group. In contrast to the number of conceptions, it was not possible to estimate with precision this number of cycling females during the months when we were not in the field. That is why we restricted our dataset to the months where we were present in the field only to investigate the potential effects of the number of cycling females in the group along with our other predictors. Following the same rationale as our other indicator of reproductive synchrony (i.e. the number of conceptions in the group), we investigated the combined effect of current and past synchrony.

Nonetheless, due to the limitations of our dataset, we could only explore the effect of reproductive synchrony in the two months prior to a reproductive event. As before, we explored the effect of the mean number of cycling females over the past X months (X referring to 'Window_Cycling_Females' in the model (18), and ranging from 1 to 2), and the effect of the number of cycling females the same month of the observation ('Number_Cycling_Females_Same_Month' in the model (19)).

(17) $$Conception \sim NDVI_NS(Window_NS_Conception) + Mean_Number_of_Cycling_Females(Window_Cycling_Females) + (Mean_Number_of_Cycling_Females(Window_Cycling_Females): Rank) + NDVI_S(Window_S_Conception) + Number_Adult_Females + Group + Parity + Rank,\ random = Identity_female, family = binomial$$

(18) $$Conception \sim NDVI_NS(Window_NS_Conception) + Number_of_Cycling_Females_Same_Month + (Number_of_Cycling_Females_Same_Month: Rank) + NDVI_S(Window_S_Conception) + Number_Adult_Females + Group + Parity + Rank,\ random = Identity_female, family = binomial$$

We similarly ran the exact same models, with different best time windows for the NDVI effects, for the cycle resumption response variable.

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TABLES

Table S1: Different methods used to estimate the dates of 241 conceptions of baboons in Tsaobis between 2005 and 2019.

Criteria used for estimation	Number of conception estimated	Median of the number of days of uncertainty	Range of the number of days of uncertainty
Conceptions observed in the field	68	0	0
Conceptions occurred during a field break	13	10	3 - 30
Birth date observed (in the field or during a field break)	65	10	10 - 40
Infant coloration & mother reproductive state (Dezeure et al AJPA)	56	61	0 - 151
Mother reproductive state only (with birth observed)	23	65	21 - 153
Mother reproductive state only (with no birth observed)	16	90	24 - 164
Total	241	10	0 - 164

Table S2: Absence of effect of the number of cycling females on the timing of cycle resumption, based on 61 cycle resumptions from 32 females.

We ran 1000 models with simulated conception date in order to take into account their uncertainty. The table show the mean estimates, mean confidence intervals, mean X^2 statistics and mean p-values of the predictors of these 1000 binomial generalized linear mixed model investigating the effect of the number of cycling females in the group on the timing of cycle resumption, along with other fixed effects. Significant effects are indicated in bold. The seasonal environmental variation is the 'NDVI_S' over the past four months. The non-seasonal environmental variation is the 'NDVI_NS' over the past three months. The reproductive synchrony here is characterized by the number of cycling females in the group in the focal month. For categorical predictors, the tested category is indicated between brackets.

Hypothesis tested	Fixed effects		Estimate	IC		X^2	P-value
				Lower	Upper		
H1	Non-seasonal environmental variation		0.25	0.01	0.49	4.50	0.064
H2	Reproductive synchrony		0.05	-0.23	0.32	0.29	0.685
Control	**Seasonal environmental variation**		**-0.30**	**0.56**	**-0.05**	**5.49**	**0.031**
	Number of adult females		-0.10	-0.45	0.25	0.41	0.576
	Group	(L)	0.11	-0.44	0.66	0.59	0.763
		(M)	-6.71	-949.95	936.52		
	Rank		-0.09	-0.35	0.17	0.58	0.517
	Parity	(primiparous)	-0.12	-0.82	0.58	0.25	0.693

Table S3: Effect of the number of conceptions over various time-windows on the probability to conceive on a given month.

For each modality of reproductive synchrony time window (mean number of conception over the past 0-6 months), we ran (i) 1000 models without any rank interactions, and extracted the mean AIC of these models, along with estimate and P-value of the reproductive synchrony fixed effect ('Term alone' rows) ; and (ii) 1000 full models with rank interactions (see Table 5), and extracted the mean AIC of these models, along with estimate and P-value of the interaction between female rank and reproductive synchrony fixed effect ('Interaction rank' rows).

Group reproductive synchrony	AIC	Fixed effects	Estimates	P-values
Number of conception the same month	1145.1	Term alone	0.09	0.270
	1148.1	Interaction Rank	-0.01	0.160
Mean number of conception over last month	1142.6	Term alone	0.16	0.053
	1143.6	Interaction Rank	-0.16	**0.043**
Mean number of conception over the last 2 months	1140.1	Term alone	0.20	**0.010**
	1142.1	Interaction Rank	-0.14	0.059
Mean number of conception over the last 3 months	1140.6	Term alone	0.21	**0.013**
	1142.3	Interaction Rank	-0.16	**0.046**
Mean number of conception over the last 4 months	**1136.7**	**Term alone**	**0.26**	**0.002**
	1137.0	**Interaction Rank**	**-0.18**	**0.021**
Mean number of conception over the last 5 months	1138.5	Term alone	0.24	**0.004**
	1139.9	Interaction Rank	-0.17	**0.036**
Mean number of conception over the last 6 months	1138.9	Term alone	0.25	**0.005**
	1141.0	Interaction Rank	-0.16	0.057

Table S4: Effect of the number of conceptions over various time-windows on the timing of cycle resumption on a given month.

For each modality of reproductive synchrony time window (mean number of conception over the past 0-6 months), we ran (i) 1000 models without any rank interactions, and extracted the mean AIC of these models, along with estimate and P-value of the reproductive synchrony fixed effect ('Term alone' rows) ; and (ii) 1000 full models with rank interactions (see Table 4), and extracted the mean AIC of these models, along with estimate and P-value of the interaction between female rank and reproductive synchrony fixed effect ('Interaction rank' rows).

Group reproductive synchrony	AIC	Fixed effects	Estimates	P-values
Number of conception the same month	1008.3	Term alone	0.01	0.597
	1011.8	Interaction Rank	0.07	0.473
Mean number of conception over last month	1008.5	Term alone	-0.06	0.529
	1011.9	Interaction Rank	0.09	0.402
Mean number of conception over the last 2 months	1007.0	Term alone	-0.15	0.177
	1010.1	Interaction Rank	0.10	0.332
Mean number of conception over the last 3 months	1005.7	Term alone	-0.19	0.084
	1008.7	Interaction Rank	0.12	0.275
Mean number of conception over the last 4 months	1007.9	Term alone	-0.13	0.236
	1010.4	Interaction Rank	0.13	0.204
Mean number of conception over the last 5 months	1008.3	Term alone	-0.12	0.253
	1009.7	Interaction Rank	0.17	0.109
Mean number of conception over the last 6 months	1007.2	Term alone	-0.17	0.123
	1006.8	**Interaction Rank**	**0.22**	**0.035**

FIGURES

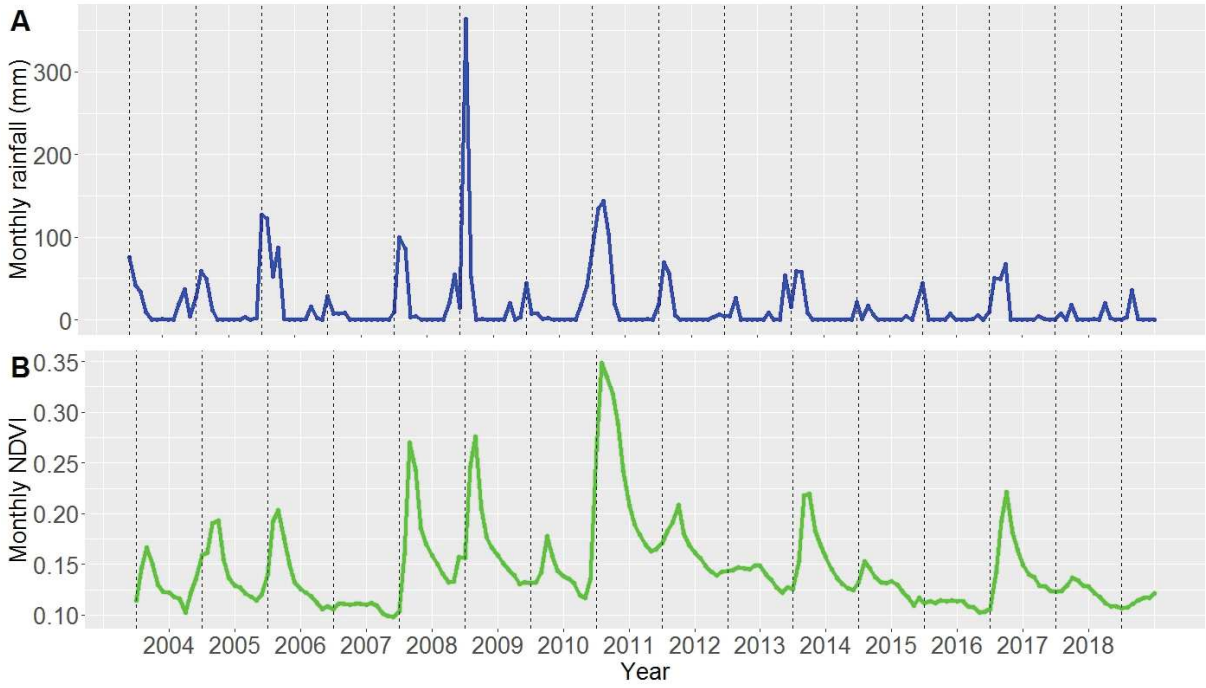

Figure S1: Tsaobis rainfall and food availability variations over the study period (2004-2019).

We represented the monthly cumulative rainfall in mm (Panel B) and monthly NDVI value on J group homerange (Panel B) according to time (between January 2004 and July 2019). We indicated with vertical dashed black line the month of January for each year.

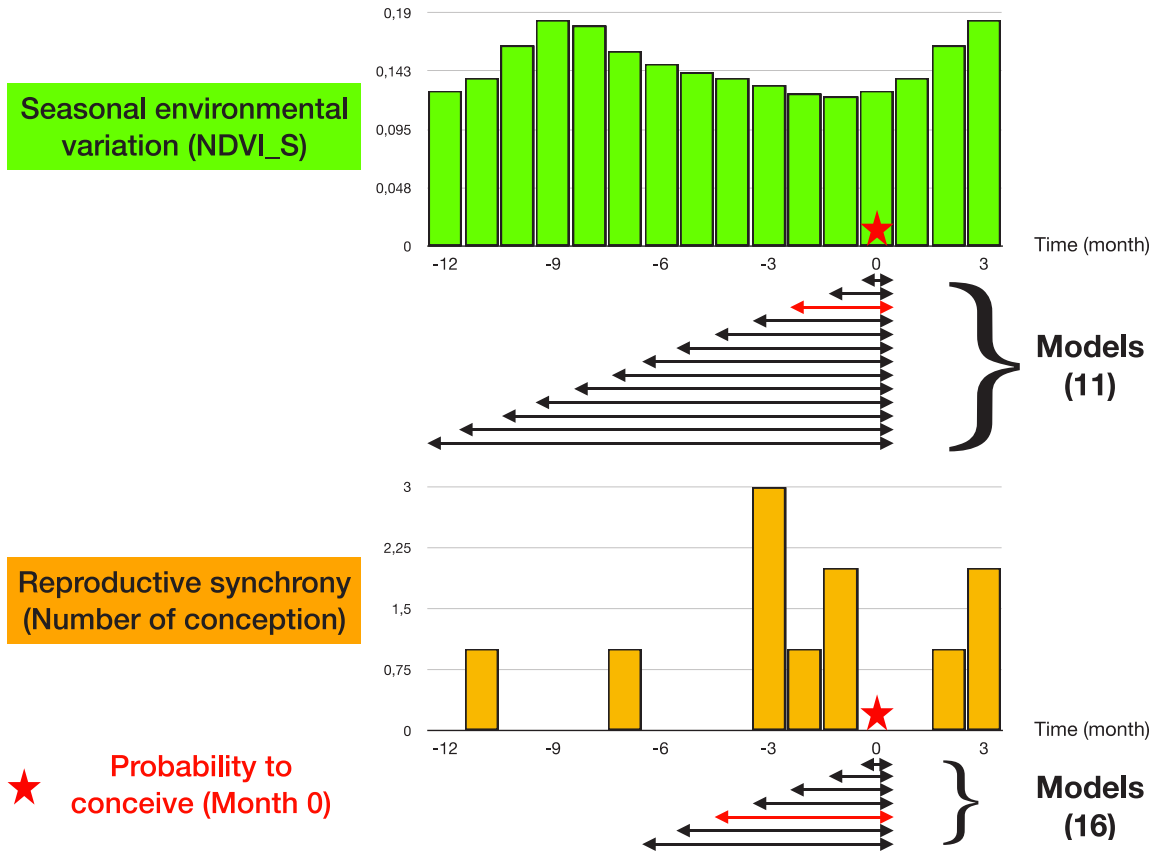

Figure S2: Examples of the different time windows considered when investigating the effects of current and past environmental variation and reproductive synchrony on female conception probability.

The model numbers indicated correspond to the ones listed in Appendix B. We plotted the seasonal NDVI ('NDVI_S') per month in green and the number of conceptions in J group per month in yellow, considering December 2018 as time 0 (and so, for example, December 2017 is indicated with -12). Models (11) tested the effect of the mean NDVI_S over the X past months, X going from 0 to 12. Models (16) tested the effect of the mean number of conceptions over the past X months, X going from 0 to 6. The arrows in red indicate the best time window effect selected for each model sets, with conception probability as response variable.

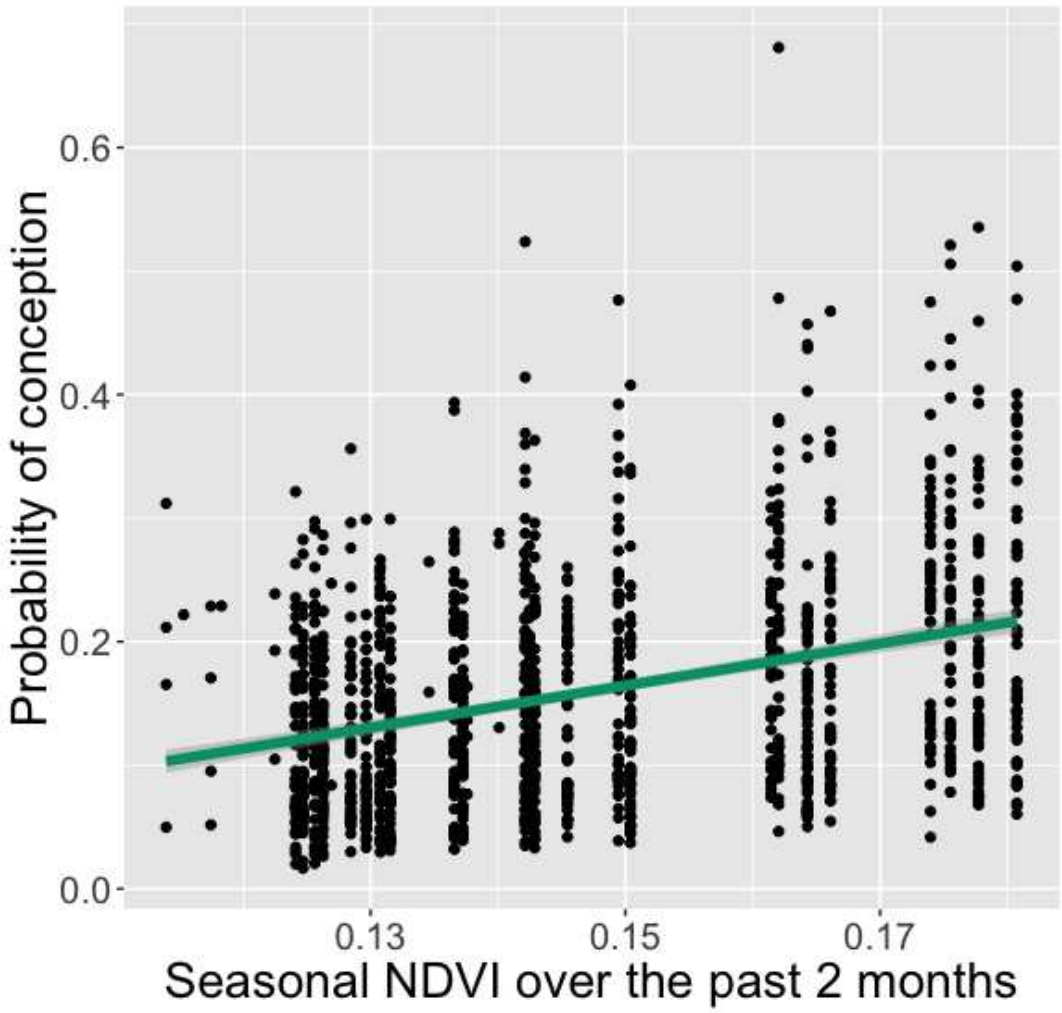

Figure S3: The probability of conception increases with higher seasonal variations of NDVI over the past two months.

Each black dots represents a fitted value of the full model (Table 5) focusing on the probability of conception according to the mean seasonal NDVI over the past 2 months. The green curve shows the logistic fit (using the glm method of stat_smooth function), and the shaded area displays 95% confidence intervals around it

Accra



Chapter 5

Evolutionary determinants of reproductive seasonality in a long-lived social primate living in the equatorial forest

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(Article in preparation)

ABSTRACT

Reproductive seasonality is the norm in mammals from temperate regions where environmental seasonality is marked, but is less common, and often less pronounced, in species living at lower latitudes. Our understanding of the evolutionary determinants shaping patterns of reproductive seasonality in tropical species is, at best, fragmentary. In addition, in long-lived species whose full reproductive cycle cannot fit within one season, it remains unclear which stage(s) of the reproduction, from offspring' conception to independence, reproductive females match with the seasonal food peak, and with which fitness consequences. Here we investigate the reproductive consequences of variations in birth timing in a long-lived and seasonally-breeding social primate endemic to the Congo basin (*Mandrillus sphinx*), using life history and behavioural data from a natural population. We first characterize patterns of environmental and reproductive seasonality, showing that mandrills' reproduction is seasonal, and that their resource availability is affected by seasonal variations in rainfall. Second, we show that the tight birth peak maximises future (shorter interbirth intervals) reproduction for females by matching the lactation peak with the seasonal peak of food availability. Yet, in contrast to most seasonal breeders, females can conceive year-round without suffering detectable costs on post-natal offspring survival, which explains the absence of a strict birth season, as observed for most species living in productive habitats. Finally, we show potential socially-mediated variations in reproductive phenology: infanticide that could cause seasonal spontaneous miscarriages, may also promote a tighter birth peak, whereas social rank weakens reproductive seasonality as dominant females are less seasonal than subordinate ones. Taken together, these results reveal the flexibility of patterns of reproductive phenology in long-lived species inhabiting rich tropical environments, shedding new light on the evolution of vertebrate reproductive seasonality.

INTRODUCTION

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 (Hodge, Bell, & Cant, 2011) to births occurring year-round in African elephants (Moss, 2001). Along this continuum, species are either classified as strict seasonal breeders, when there are births occurring only during a restricted period of the year, or as non-seasonal breeders, when births occur year-round. Non-seasonal breeders, however, may largely vary in the intensity of their reproductive seasonality (Lancaster & Lee, 1965; Lindburg, 1987). Ultimate explanations for seasonal reproduction have largely assumed that variation in the intensity of reproductive seasonality mirrors variation in the intensity of environmental seasonality (Conover, 1992; Di Bitetti & Janson, 2000; Rutberg, 1987). For example, the intensity of birth seasonality increases with latitude across 27 ruminant species (Rutberg, 1987). Nevertheless, reproductive seasonality is common, and sometimes acute, in tropical species, such as in Malagasy mammals (Heldstab et al., 2020; Wright, 1999). While seasonal variation in temperature and photoperiod are low in tropical areas, seasonal variation in rainfall is usually intense (Feng, Porporato, & Rodriguez-Iturbe, 2013), and likely shapes the annual distribution of resource availability for most tropical organisms, even though food might not be as limiting as in higher latitudes during the harsh dry season (Hau, 2001; Van Schaik, Terborgh, & Wright, 1993). Much less is thus known about the evolutionary determinants of reproductive phenology in tropical ecosystems, which host most of the biomass (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000) including the largest terrestrial mammals, and where patterns of reproductive phenology vary widely (Heldstab et al., 2020; Sinclair, Mduma, & Arcese, 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; F. H. Bronson, 2009). However, in long-lived species, development from conception to weaning often extends over multiple seasons or years, so that the seasonal food peak(s) can be synchronized with some, but not all, reproductive and developmental stages. For example, in long-lived mammals with slow reproductive paces, females can either minimize their own reproductive costs by matching periods of high energetic demands such as early or mid-lactation (Emery Thompson, 2013; Lee, 1996) with the annual food peak, or alternatively minimize offspring mortality by matching periods of offspring vulnerability, presumably late weaning, with the food peak (Brockman & van Schaik, 2005; C. H. Janson & Verdolin, 2005; van Schaik & van Noordwijk, 1985). In such cases, mothers consequently face a trade-off between current and future reproduction over birth timing (Chapter 3), which may ultimately weaken the intensity of reproductive seasonality. Most studies focusing on the fitness consequences of reproductive phenology were conducted on fast-lived organisms, such as rodents and passerines, from temperate regions (F. H. Bronson, 2009; Franklin H. Bronson & Heideman, 1994; Williams et al., 2017). In addition, these studies have usually considered only one fitness component, typically measuring offspring number, survival or growth (Ellison, Valeggia, & Sherry, 2005; Varpe, Jørgensen, Tarling, & Fiksen, 2009), but omitting potential effects on mother's future reproduction (but see for a bird species, *Fulica atra*: Brinkhof et al., 2002). When studying long-lived species, it appears essential to investigate the consequences of reproductive phenology across multiple fitness components because trade-offs between current and future reproduction may affect the selective pressures shaping reproductive seasonality.

In addition, few studies have attempted to identify if 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 causing individual variation in condition, such as female age, parity and previous reproductive history are also likely to affect a female reproductive phenology (Garel et al., 2009; Paul & Thommen, 1984; Plard et al., 2014). In addition, in gregarious species with social hierarchies, female social rank is another important parameter to consider, as dominant females often 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 and Huchard 2013; Stockley and Bro-Jørgensen 2011). However, the consequences of rank-related variation in life history traits on reproductive phenology have rarely been examined.

In this study, we investigate the causes and consequences of reproductive phenology across multiple measures of female reproductive success in a natural population of an equatorial, long-lived and social primate, the mandrill (*Mandrillus sphinx*) from Gabon. Mandrills live in the equatorial forests of central Africa, which are typically characterized by intense intra-annual rainfall variation (Feng et al., 2013). Such variations affect mandrill dietary composition across seasons (Nsi Akoue et al., 2017), though it remains unknown whether such qualitative seasonal changes significantly impact mandrill resource availability. Most of our knowledge about mandrill reproductive parameters come from a semi-free ranging population (Setchell, Lee, Jean Wickings, & Dixson, 2001; Setchell, Lee, Wickings, & Dixson, 2002; Setchell & Wickings, 2004) because mandrills have been poorly studied in the wild. However, a preliminary study on a wild unhabituated population showed that mandrill reproduction is seasonal: matings occur almost exclusively during the long dry season, while births are concentrated in the middle of the rainy season (Hongo, Nakashima, Akomo-Okoue, & Mindonga-Nguelet, 2016). Female mandrills can live more than 18 years in captivity (Setchell et al., 2001) and give birth to a single offspring every 1-3 years (Setchell et al., 2002) that they

breastfeed during an extensive and highly variable period of time (8 months on average: Setchell & Wickings, 2004). As in many other cercopithecines species, females are philopatric and formed a strict social hierarchy, which is matrilineal and affects their reproductive performances (Setchell et al., 2002).

Here, we use long-term 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 characterize both environmental and reproductive seasonalities in this population and specifically ask whether mandrill food availability is affected by environmental seasonality, and which reproductive stage is synchronized with the annual food peak.

(2) What are the consequences of variation in reproductive phenology for female reproductive success? We use three measures of female current and future reproductive success, respectively offspring pre- and post-natal mortality, and the length of maternal interbirth interval (IBI).

(3) Do females vary in their birth timings, and which individual traits may drive such variation? We specifically investigate the effects of female age, recent reproductive history and social rank.

METHODS

1) Study site and population

A natural population of habituated mandrills is monitored daily since 2012 within the framework of the Mandrillus Project, a long-term field site 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), who were released in the park in two waves, in 2002 and 2006 (Peignot et al., 2008). During the first months post-release, mandrills were provisioned with bananas and monkey chow in low quantities to supplement their natural diet. This food supplementation decreased rapidly (from 2008 to 2012) and completely ceased in April 2012. The study mandrills live in a private park (Lékédi Park) and its vicinity, situated 7 km northwest away from the closest village, Bakoumba, in Southern Gabon. The park and surroundings are composed of a mosaic of evergreen forests, grasslands and savannahs (Brockmeyer et al., 2015). The environment is usually characterized by four distinct ecological seasons, driven by variations in rainfall, with a long-rainy season (February-May), a long-dry season (June-September), a short-rainy season (October-November) and a short-dry season (December-January) (Charpentier et al., 2018; Nsi Akoue et al., 2017). In early 2020, the study group was composed of approx. 250 individuals, including ca. 180 recognizable ones. During daily monitoring, we record data on individual life history, developmental trajectory, behaviour, as well as group demography and GPS locations. Data used in this study were collected from March 2012 to March 2020.

2) Reproductive parameters

A female is considered adult when she reaches menarche when her peri-anal area is turgescent for the first time. Female parity is determined using long-term life history data 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).

For adult females, age is either known thanks to long-term demographic records of CIRMF for the captive-born individuals (N=15 females), thanks to direct field observations for those born after 2012 (N=26 females), or estimated using general condition and patterns of

tooth eruption and wear for others (N=30 females) (see also: Dibakou, Basset, Souza, Charpentier, & Huchard, 2019).

The reproductive state of each adult female is monitored on a daily basis. However, given the number of individuals in the group, and the dense vegetation where they are ranging, all individuals are not seen every single day of field observation, leading to small uncertainties in the date of reproductive events in certain cases. A female is assigned as either being: (i) 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 using the presence of a noticeable and distinctive pink and swollen tumescence present about two months following impregnation (the main clue confirming pregnancy in case of female's miscarriage); or (ii) lactating, when a live offspring is less than six months old or until the death of the offspring before 6 months of age; or (iii) cycling, including both swollen females in oestrus (i.e., sexually active with a perineal swelling) and non-swollen females at other stages of their menstrual cycle.

We considered a total of 215 conceptive cycles that either result in 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. These 215 conceptions occurred between 2012 and 2020 (median uncertainty of 2 days; range=0-30 days). In 60 cases, observers were present on the D-day while in 114 other cases, conceptions occurred during a gap in the reproductive recordings, leading to a small 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 dataset 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 between 2012 and 2020 (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 new-born a few days after birth (uncertainty in the actual date: median=4 days, range=1-30).

Finally, the first post-partum 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 post-partum 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 between 2012 and 2020, either following an infant that survived (N=133) or died (N=17) during its first 6 months of life. We chose to include cycle resumption following the death of an unweaned infant, as such event may disrupt female reproductive seasonality and must thus be taken into account when investigating the timing and intensity of reproductive seasonality.

3) Fitness estimates

For each infant born, we investigated whether it died or not before reaching 6 months of age. We use this age threshold because older infants are often harder to recognize, generating uncertainty on their survival after this age. Death is recorded when a corpse is observed, often carried by the mother for a few days, or when the mother is seen without her infant for a few days. We discarded four infants whose survival outcomes were uncertain. In our dataset, a total of 20 infants out of 208 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 (yes), typically when a female is observed with a pregnancy swelling (as described above) but does not subsequently give birth. If an infant is born following a conception, we considered that no miscarriage occurred (no). We discarded the few conceptions for which the pregnancy outcome was unknown and probably resulted from an early miscarriage (N=4). 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. We only considered IBIs for which the first infant survived at least its first 6 months of life (Gesquiere, Altmann, Archie, & Alberts, 2017) because females resume cycling rapidly after their infant's death (median number of days between an infant's death and a mother's cycle resumption: 15, range=7-111 days, N=15 cases where the infant's date of death is known with less than 30 days of uncertainty, and for which the mother resume cycling afterwards). We computed a total of 122 IBIs collected from 47 adult females, ranging from 323-1024 days with a median of 566 days.

4) Environmental data

We extracted rainfall using satellite data from a point close to the centre of the Lékédi Park where mandrills are ranging (1°47'51.85'' S, 13°01'12.92'' E). More precisely, daily rainfall in a 0.25*0.25 degree resolution (corresponding to 28*28km at this equatorial latitude) was extracted from this geographical point using satellite data sensors from the Giovanni NASA website (product TRMM 3B42) (Savtchenko, 2016). Monthly cumulated rainfalls (summed across daily values) were computed between January 2012 and December 2019.

5) Behavioural data

Five-minute focal observation samplings (Altmann, 1974) are performed daily on all adult females (since August 2012) and known juveniles (since October 2012), who are chosen randomly. During focals, we record 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 time adult females spent foraging and adult females' social rank.

Seasonal variation in time budgets. We used seasonal variations in the proportion of time adult females spent foraging to characterize the environmental seasonality of food availability. Indeed, mandrills are omnivorous with a frugivorous tendency, and eat a wide range of vegetal items from more than 150 plant species (Nsi Akoue et al., 2017). Therefore, assessments of food availability based on phenology data targeting plant species exploited by mandrills is at best complex, and probably impossible. Several studies on various wild primate populations have shown that time spent foraging is negatively correlated with the amount of food available in the environment (Alberts et al., 2005; Byrne, Whiten, Henzi, & Mcculloch, 1993; Doran, 1997; Dunbar & Dunbar, 1988; Muruthi, Altmann, & Altmann, 1991; Overdorff, Strait, & Telo, 1997; Swedell, 2011). Therefore, seasonal variations of the proportion of time spent foraging can be used as a good indicator of food availability. We considered females aged more than four years for this analysis as we were interested to quantify variation in food availability for mothers (four years roughly correspond to the youngest age at which females may conceive). We further restricted our dataset to focal observations longer than one minute. We gathered a total of 29774 focal observations corresponding to 2116 hours of observation obtained from 80 females. For each focal observation, we computed the time the female spent foraging and the total time of observation.

Female rank. Females' social rank is yearly established 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). The correlations of ranks per female across the years were significant (example between the two extreme years of the study, i.e. 2012-2013 and 2019 years: R=0.81, t=5.92, $p<10^{-4}$). Therefore, each adult female was assigned one rank encompassing all years of the present study (2012-2020), ranging from 0 (lowest ranking) to 1 (highest ranking).

6) Statistical methods

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

A) Characterization of reproductive and environmental seasonalities

In order 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 milestones (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 single day), along with the Rayleigh test to investigate its significance (Batschelet, 1981). We used the 'r.test' function from 'CircStats' package to run the Rayleigh test (Agostinelli & Lund, 2018).

In addition to the graphical representation of monthly rainfall variation, we assessed environmental variations in food availability using the time spent foraging in females aged four years and more. More precisely, we used a Generalized Linear Mixed Model (GLMM) with a

negative binomial error structure investigating seasonal variation on 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 spent foraging per focal observation, in seconds, as a response variable, and the log-transformed time of observation (in seconds too) as an offset term. We included the female's identity and the year of observation as random effects to control respectively for the non-independence of multiple observations on the same female and for between-year environmental variations. To test the effect of seasonality, we used a sine term as a fixed effect. Such a sinusoidal term allows the introduction of circular variables into a multivariate model (Dezeure et al., 2020; S. English, Bateman, & Clutton-Brock, 2012; Rickard et al., 2012), to account for the circularity of seasonality, as January is just as close to December than to February, and where the cyclic period is one year. This term was as follow: sine(date of observation + φ), and assumed only one maximum (food peak) and one minimum (lean season) per year, located six months apart. Such a 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 (Figure 1). The date of observation in this formula was converted in a radian measure, so that the period of one year equalled to 2*π, ranging from 2*π/365 for the 1st of January to 2*π for the 31st of December. We tested twelve different phase values φ (0, π/12, 2*π/12, 3*π/12, 4*π/12, 5*π/12, 6*π/12, 7*π/12, 8*π/12, 9*π/12, 10*π/12, 11*π/12), to account for potential phase shifts across the year. For example, a phase of 0 maximizes March 1st and minimizes October 1st if the estimate is positive, and the reverse if the estimate is negative (see Dezeure et al., 2020 for more details on this procedure). We ran sequentially twelve multivariate models, which contained random effects and the offset term, and all were strictly similar, except for the value of the phase φ. We selected the best phase as the one minimizing the Akaike Information Criterion (AIC) in this model set, which happened to retain a value of 3*π/12 for the phase φ.

B) Consequences of reproductive phenology on female reproductive success

We investigated the effect of reproductive timings on three indicators of female reproductive success: offspring mortality probability (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 before 6 months of age 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 if it occurred within (yes) or outside (no) the annual birth peak. We first assigned a birth 'cohort' for each birth (N=212). We considered July 1st as the transition date from one cohort to the next (as the mean population birth date, January 1st, occurs 6 months apart). As a result, two births occurring on the 22nd of November 2014 and the 2nd of February 2015 belonged to the same cohort (the 2014-2015 one), while they did not occur the same year (2014 *versus* 2015). We discarded all births occurring away from 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 have disproportionately influenced the mean annual birth date. We recorded on average 24 births per cohort (SD=8, range=15-39 over 8 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 December 6th (for 2017-2018 cohort) to January 31st (for 2012-2013 cohort), and the birth distributions between these two extreme years were significantly different (Watson-Williams test for homogeneity of means: F=56.2, P-value<10^{-4}). This indicates substantial between-year

variations in the timing of the annual birth peak, which may reflect either between-year variations of environmental seasonality, or stochastic variations due e.g. to low sample sizes. 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 (for N=212 births), and outside the birth peak (no) otherwise (given the raw monthly distribution of births in the population; see Figure S1). For Model 3 focusing on miscarriages, we used the same method as described above to compute the mean annual conception date for each 'conceptive cohort', considering January 14th as the transition date from one cohort to the next (as the mean population conception date, i.e. July 14th, occurs 6 months apart). We similarly discarded all conceptions that occurred between October 14th and April 14th (N=24 conceptions). For each conception (N=215), we considered that it occurred within (yes) the annual conception peak if distributed two months around the annual mean 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. A negative value represented a birth that occurred before the actual mean birth date of a given cohort, while a positive value indicated a birth that occurred after. 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 a same model as they addressed different questions and were not statistically independent (though not collinear). Indeed, by construction, births occurring outside the annual birth season were either very early or very late in the birth season. Models with the fixed effect "within or outside" the annual peak were named 'A' (Models 2-4A), while models with the fixed effect deviation from the mean date were named '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).

C) Female determinants of variations in birth timing

We finally investigated different determinants of variation in female strategies of reproductive seasonality, i.e. 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 annual mean birth date (in days) for the LMM (Model 6).

Both models comprised as fixed effects female rank, age (in years) and past reproduction outcome because these effects are likely to affect birth timings (Holand et al., 2004; Paul & Thommen, 1984). Past reproduction outcome referred to the previous conception and was a categorical variable with the following classes: (1) previous infant survived to 6 months (N=130), (2) miscarriage (N=16), (3) previous infant died before 6 months (N=16), or (4) primiparous female (no previous conception; N=41). 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.

Information about the structure (type of models, fixed and random effects) and sample sizes of each model performed in this study are summarized in the Supplemental Information (Table S1). 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 'bglmer' 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 VIFs 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 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 'past reproduction'.

RESULTS

1) How is reproductive phenology adjusted to environmental seasonality?

Conceptions, births and cycle resumptions all showed one pronounced seasonal peak (Figure 1 and Figure S1, Supplemental Information): 64% of conceptions, 66% of births and 54% of post-lactation cycle resumptions occurred during a three months-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, μ=14th of July, R=0.63, p<10^{-4}; births: N=212, μ=1st of January, R=0.68, p<10^{-4}; cycle resumptions: N=150, μ=19th of June, R=0.52, p<10^{-4}), although births appeared more seasonal than both conceptions and cycle resumptions.

Environmental seasonality was also pronounced in the study area (Figure 1). Mean annual cumulative rainfall was high, with moderate inter-annual variability (N=8 years, from 2012 to 2019, mean ± SD=1871 ± 175mm). Rainfall was highly seasonal, with a long rainy season observed between October and May characterized by two peaks, one in October-November, and the other in April, followed by a long dry season occurring from June to September (Figure 1). Our proxy for food availability, the proportion of time females spent foraging, also varied seasonally (Figure 1): females spent significantly more time foraging around August 15th (long dry season) than around February 14th (long rainy season), as indicated by the negative effect of the sine term with a phase 3*pi/12 of the month of observation (Model 1: Estimate=-0.20, 95% confidence intervals= [-0.22, -0.19], X^2=681, P-value<10^{-4}). The birth peak happened midway through the long rainy season, just before the peak of food availability (Figure 1).

2) What are the consequences of variation in reproductive phenology for female reproductive success?

First, we quantified the consequences of birth and conception timings on current reproduction, focusing on respectively post- (Model 2) and pre- (Model 3) natal offspring survival. Birth timing did not affect offspring survival probability to 6 months old: offspring born outside the annual birth peak were as likely to survive as those born inside (Table 1). Similarly, whether offspring were born early or late in the birth season did not affect their survival probability (Table 1). However, conception timing affected prenatal survival (Table 1): conceptions that

occurred outside the annual conceptive peak (Figure 2A), especially later in the mating season (Figure 2B), were more likely to lead to miscarriages than other conceptions (Table 1).

Birth timing also affected mothers' future reproduction (Model 4): females that gave birth within the annual birth peak had shorter IBIs (Table 2, Figure 2C). In addition, females that gave birth early in the birth season tended to have shorter IBIs (Table 2, Figure 2D).

We finally found pronounced rank-related variation in female reproductive success, with dominant females having lower likelihood to abort (Table 1) and shorter IBIs (Table 2; high-ranking females: median IBI=15.0 months, mid-ranking females: 20.5 months, low-ranking females: 22.0 months; see also Figure S2). These variations of reproductive phenology depending on female rank are further represented with two actual cases in Figure S3, Supplemental Information.

3) Do females vary in their reproductive phenologies, and which individual traits may drive such variation?

Given such large rank-related differences in reproductive success, we investigated whether individual traits (female social rank, age, and past reproductive success) may influence reproductive phenology. First, we did not detect any effect of female's 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, higher-ranking females were more likely to give birth outside the birth season, although neither earlier nor later than lower-ranking females (Table 3, Figure 3A and C). In addition, females that lost an infant or that miscarried were more likely to subsequently give birth early in the birth season, although neither within nor outside the season (Table 3, Figure 3B and D). Finally, female age did not affect birth timing (Table 4).

DISCUSSION

In this study, we show that mandrills' reproduction is seasonal: 53% of births occurred in a two months-time window (December-January). Such results confirm previous studies on semi-free ranging (Setchell et al., 2002; Setchell & Wickings, 2004) or non-habituated wild (Hongo et al., 2016) mandrill populations, that classified this primate as a strong seasonal breeder. We now discuss how our results help to understand the surprisingly strong reproductive seasonality of a long-lived and large equatorial species.

Mandrills breed seasonally in an equatorial, yet seasonal forest

Several reasons may explain why a species breed seasonally in an equatorial environment. First, Gabonese forests show important seasonal variation in rainfall (Feng et al., 2013; Van Schaik et al., 1993; this study) and such seasonality is reflected in the food available for mandrills, who spend more time looking for food during the long dry season. Food availability likely mirrors seasonal variations in plant phenology (Takenoshita, Ando, Iwata, & Yamagiwa, 2008), as shown by clear qualitative seasonal shifts in mandrills' diet (Nsi Akoue et al., 2017). The equatorial environment may therefore be characterized by important within-year variation in food resources, which may affect reproductive timing and performances, even in long-lived omnivorous species.

In addition to the intensity of seasonal fluctuations, their predictability (i.e. low inter-annual variation) is also important to understand variations in the intensity of reproductive seasonality across species. For example, a higher predictability of seasonal cycles favours increases in reproductive seasonality in vertebrates (Jönsson, 1997), as shown in ungulates (A.

K. English, Chauvenet, Safi, & Pettorelli, 2012). Between-year variations of rainfall are relatively low in Gabon compared to other African sites (Alberts et al., 2005; Campos et al., 2017; A. K. English et al., 2012), and may have contributed to the emergence of mandrill's reproductive seasonality, with little year-to-year variations observed in the mean annual birth date (1st of January ± 1 month, in 8 years of study). A comparative study investigating the possible effect of environmental predictability on primate reproductive seasonality across a wide panel of populations living in different environments would now be necessary to confirm such interpretation.

Reproductive seasonality maximises both current and future reproduction

Timing early-lactation with the food peak accelerates female future reproduction

Births mainly precede the seasonal food peak by around two months, whereas cycle resumptions and conceptions mainly occur during the long-dry and food-deprived season. This birth peak may have evolved to match the food peak with early lactation. Such birth timings are the norm among fast-lived and temperate or arctic species (F. H. Bronson, 2009; Franklin H. Bronson & Heideman, 1994), and similar patterns of phenology have also been observed in other tropical primates (Brockman & van Schaik, 2005; Carnegie, Fedigan, & Melin, 2011; Heesen, Rogahn, Ostner, & Schülke, 2013; C. Janson & Verdolin, 2005) and ungulates (Sinclair et al., 2000). Indeed, early-to mid-lactation often corresponds to the peak of lactation during which mothers cover the full nutritional needs of their infants, in contrast with later stages of lactation where infants start feeding in autonomy (Langer, 2008; Lee, 1996). Such a reproductive stage is therefore particularly costly for mammalian females (Emery Thompson, 2013; Lee, 1987). This phenology strategy brings reproductive benefits for mandrill females. Indeed, females that give birth within the birth peak accelerates their future reproduction

(shorter IBIs). Our study therefore emphasizes that reproductive seasonality in tropical species can emerge in response to seasonal variation in food availability to enhance maternal reproductive pace, regardless of the absolute annual amount of food available.

Mammals, and especially primates, also often synchronize weaning with the seasonal peak of food (Brockman & van Schaik, 2005; C. Janson & Verdolin, 2005; Wright, 1999). Indeed, in various populations, including large primates like baboons, weaning corresponds to the period of highest infants' vulnerability because they must ensure their own provisioning. Consequently, matching weaning with the most productive season should enhance offspring survival (Altmann, 1980; Lycett, Henzi, & Barrett, 1998; van Schaik & van Noordwijk, 1985; Wright, 1999). However, in this study, we showed that female mandrills can give birth year-round without any costs on post-natal offspring survival until six months old, an age at which infant mandrills are in the process of weaning (median post-partum amenorrhea –PPA- duration lasts eight months in this population: median=8.1, range=2.6-18.0, N=123 PPAs for which infants survived their first six months of life). There might be several reasons why we did not find offspring mortality costs associated with birth timing occurring outside the birth peak. First, the statistical power of our analyses might be limited, given the low numbers of infants born outside the birth season (only 6 births, i.e. 3%, between May and August). Second, we looked at infant mortality before 6 months (due to data and identification limitations), while the end of weaning may often occur a few month later this threshold and might be the most vulnerable period of infant's life. Third, during the weaning period, female mandrills may mitigate the costs of giving birth outside the birth peak by extending lactation, as reflected by their longer IBIs, to improve the survival of their current offspring. Such flexibility may be possible because of the high productivity of their environment, suggested by the shorter IBIs exhibited by females from this population compared to baboons and geladas, primates of comparable size and ecology (Swedell, 2011). In addition, the moderate infant mortality

observed in our population (only 20, i.e. 9% of infants) and the fact that mandrill females are able to lactate and gestate simultaneously (see the case of the dominant female in Figure S3) may both indicate that seasonal food shortage is rarely a cause of poor condition and death in offspring and their mothers. Similarly, in white-faced capuchins (*Cebus capucinus*), a seasonal breeder living in a rich tropical habitat, deviance from the birth season does not translate into increased offspring mortality (Carnegie et al., 2011). Given the lack of costs on offspring survival to match weaning with the seasonal food peak, mandrill females may preferentially adjust early lactation with the seasonal food peak.

Our findings on the fitness consequences of reproductive timing on female reproductive success highlights the female ability to trade future over current reproduction in birth timing away from the birth season, promoted in highly productive environments (although other factors may also be taken into account, such as the ability to store energy or allo-parental care for instance: Heldstab, van Schaik, & Isler, 2017), where the selective pressures favouring a strict breeding season may be weakened. In contrast, in higher latitude where food availability is a limiting factor during the harsh season, females may not similarly mitigate the costs of suboptimal birth timing on offspring survival by extending their period of care, resulting in a strict breeding seasonality generally observed in temperate and arctic long-lived species (F. H. Bronson, 2009; Rutberg, 1987). This trade-off between current and future reproduction over reproductive timing may therefore account for the lower reproductive seasonality often encountered in species living in more productive environments, e.g. closer to the equator (ruminants: Rutberg, 1987; Zerbe et al., 2012, carnivores: Heldstab et al., 2018, primates: Di Bitetti & Janson, 2000; Heldstab et al., 2020).

Seasonal miscarriages as a possible counter-strategy to infanticide

We further show that the risk of miscarriage increases when females conceive too late in the mating season. It is unlikely that such pregnancy failures are caused by food scarcity during pregnancy, as observed in e.g. yellow baboons (*Papio cynocephalus*) (Beehner, Onderdonk, Alberts, & Altmann, 2006). Indeed, pre-natal mortality is relatively low (9% of conceptions) and conceptions occur during the dry season, suggesting that they are not limited by food availability in this system. Our results may suggest an alternative scenario, linked with social rather than ecological factors. We propose that infants born late in the birth season are more likely to be killed by immigrating males who enter the group at the onset of the mating season, generally around April (Abernethy, White, & Wickings, 2002; Hongo et al., 2016; pers. obs.). If a birth occurs late in the birth season, the resulting offspring will still be highly vulnerable (Palombit, 2015). These dependent infants may often be targeted by immigrating males who seek for reproductive opportunities, and can subsequently mate with the victim's mothers. In support for this hypothesis, 55% of mandrill infant deaths occurred in March-May (11 out of 20), which is significantly more often than during any other periods (X^2=17.2, P-value<10^{-3}). For four of them, male infanticide was the most plausible cause of death (unpub. data). In contrast, when females give birth early in the birth season, they often resume cycling at the next mating season, meaning that males do not need to kill their infants to mate with them. Spontaneous abortions may thus represent an adaptive female counter-strategy, as demonstrated in geladas (*Theropithecus gelada*), where females preferentially abort rather than investing into a foetus which would be a likely target of infanticide after a male takeover (Roberts, Lu, Bergman, & Beehner, 2012). Such strategy, called the "Bruce effect", where females abort in presence of an immigrant male (who has not sired their foetus) is relatively well documented among various other non-primate species, such as rodents or mongooses (Inzani et al., 2019; Schwagmeyer, 1979; Zipple, 2020). By contrast with the 'classic' Bruce

effect described in other systems, aborting in 'prevision' of future males' arrival has never been documented to our knowledge, although this hypothesis need further empirical supports.

Infanticide has mainly been considered to evolve among non-seasonal breeding species (Lukas et al., 2014). Indeed, the main benefit of infanticide for the aggressor is to precipitate sexual activity of the female, but this benefit is alleviated when mating is seasonal (R. A. Palombit, 2015). However, infanticide risk has also been demonstrated to promote high reproductive synchrony in voles, *Myodes glareolus* (Poikonen, Koskela, Mappes, & Mills, 2008) and lions (*Panthera leo*) (Packer, Pusey, & Eberly, 2001), and could thus increase the intensity of reproductive seasonality in such species. In mandrills, seasonal spontaneous abortions explain why births are more seasonal than conceptions, and ultimately tighten the population birth peak. This highlights the importance to distinguish strict seasonal breeders (where infanticide is usually not advantageous; but see the case of red deers: Bartos & Madlafousek, 1994) from non-strict seasonal breeders (like mandrills, with a tight birth peak but yet with births occurring year-round, where infanticide can exist) to better understand the interactions between infanticide risk and reproductive seasonality. Our study further emphasizes that characteristics of the social system, such as patterns of male immigration, may have pervasive consequences on population reproductive seasonality.

More generally, this study highlights the importance to take into account other fitness indicators than offspring survival to fully understand the evolution of reproductive seasonality. The strong breeding seasonality of mandrills have emerged in response to the fitness benefits of breeding seasonally for both current (lower miscarriage probabilities) and future reproduction (shorter IBIs), although the natures of their causes are distinct, being resp. social (seasonal infanticide risk) and ecological (seasonal variation in food availability).

Individual variation in reproductive phenology weakens the strength of reproductive seasonality

Although females are not consistent in birth timing across their life, we show that both past reproduction and female social rank influence this trait. Following an infant's (or foetus's) death, female mandrills resume cycling, and conceive, regardless of the season, and it is probably the primary reason why some females give birth at suboptimal timings. Reproductive failures can thus disrupt reproductive seasonality in species where, like mandrills, females recycle rapidly after an infant's death, regardless of the season. Such characteristic may have evolved to offset the costs of infant mortality, via e.g. infanticide or predation, in environment where females can sustain the costs of reproduction even when giving birth in suboptimal periods of the annual cycle.

Dominant females are also more likely to give birth outside the birth peak than subordinate females. Such social effects on individual reproductive phenology have never been reported in primates to our knowledge, and were not observed in captive mandrills, perhaps because food provisioning weakens the effects of rank (Setchell et al., 2002). Similarly, rank affects the birth timing in reindeers (*Rangifer tarandus*), where dominant females, in better condition, give birth earlier in the birth season than subordinate ones (Holand et al., 2004). Two non-exclusive possible explanations may account for rank-related differences in birth timing in mandrills. (i) First, higher-ranking females may have a better access to high quality food items year-round than subordinates (Barton, 1993; Barton & Whiten, 1993). This hypothesis is supported by the important rank-dependent variation detected on IBI: the IBIs' distribution is bimodal, with dominant females giving birth once a year while subordinate ones giving birth every two years on average. Dominant females may thus be able to face the energetic costs of lactation at any time of the year without suffering detrimental effects on their future

reproduction. In other words, for dominant females, the costs of giving birth away from the optimal season may be lower than the costs of waiting for this optimal season. In addition, high-ranking females may reproduce in two consecutive years more often than subordinate females, even if it occurs outside the birth peak, reinforcing this scenario. (ii) Second, social rank may mitigate infanticide risk, as found in capuchin monkeys (Kalbitzer et al., 2017), via rank-related variation in spatial and social positions. The lower probability of miscarriage in dominant females suggest that they are less vulnerable to infanticide than subordinates. This may alter their reproductive schedules, though more information is necessary to understand the exact mechanisms at play.

This study sheds light on the importance of socially-mediated individual variation in reproductive phenology to shape and modulate the intensity of reproductive seasonality at the population-level. More broadly, in species living in large groups, like many primates and herbivores, social competition (over food or mates for example) results in individual variation in reproductive performances and condition (Clutton-Brock & Huchard, 2013; Stockley & Bro-Jørgensen, 2011), which may in turn causes individual variation in reproductive phenology. Such species provide an opportunity for understanding individual variation in seasonal breeding strategies, and their consequences on population demography.

Conclusion

This work contributes to shed new light on the evolution of reproductive seasonality in tropical, long-lived social species. We show that even omnivorous large species can be subject to seasonal variation in food availability in equatorial forests. We further reveal that this seasonal variation in food availability, although less pronounced that in higher latitude, can lead to the

evolution of seasonal breeding, even in environment where food is rarely limited. Indeed, matching early-lactation with the most productive season enhances maternal reproductive pace. Lastly, our results indicate that sociality can have strong and opposite effects on the intensity of reproductive seasonality: birth seasonality is enhanced by infanticide risk but weakened by rank-related variation in birth timing. Both ecological and social factors can thus modulate and shape reproductive timings, and individuals may vary in their phenology strategies in productive environments. Such findings may open new perspectives in our understanding of the diversity of the observed patterns in reproductive phenology in the tropics.

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TABLES

Table 1: Birth timing affects female current reproduction.

The table displays the estimates, 95% confidence intervals (CI), X^2 statistics and P-values for the predictors of the four binomial GLMMs (Models 2A, 2B, 3A and 3B), including female identity and birth cohort as random effects. For Models "A", the fixed effect 'Reproductive phenology' represents if the considered birth (Model 2) or conception (Model 3) occurred within (1) versus outside (0) the birth or conception peaks, while for Models "B", the fixed effect 'Reproductive phenology' represents the deviation (number of days) from the annual mean birth date (Model 2) or annual mean conception date (Model 3). Significant effects are shown in bold. For categorical predictors, the tested category is indicated within parentheses.

Fixed Effect		Estimate	CI		X^2	P-value
			Lower	Upper		
Model 2A: Offspring mortality						
Reproductive phenology	(Within season)	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)	-1.1	-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
Model 3A: Miscarriage						
Reproductive phenology	**(Within season)**	**-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		

Table 2: Birth timing affects female future reproduction.

The table shows the estimates, 95% confidence intervals (CI), X^2 statistics and P-values of the predictors of the two LMMs (Models 4A and 4B) including female identity and birth cohort as random effects. For Model 4A, the fixed effect 'Reproductive phenology' represents if the considered birth occurred 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 annual mean birth date. Significant effects are shown in bold. For categorical predictors, the tested category is indicated within parentheses.

Fixed Effect		Estimate	CI		X^2	P-value
			Lower	Upper		
Model 4A: Interbirth intervals						
Reproductive phenology	**(Within season)**	**-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

Table 3: Influence of female rank, age and past reproduction on birth timing.

The table shows the estimates, 95% confidence intervals (CI), X^2 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 adult females between 2012 and 2020. Significant effects are shown in bold. For categorical predictors, the tested category is indicated within parentheses. The reference category for the past reproduction fixed effect is 'infant survived'.

Fixed Effect		Estimate	CI		X^2	P-value
			Lower	Upper		
Model 5: Probability to give birth within the 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
Past reproduction	(Infant died)	-0.69	-2.10	0.72		
	(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 (early or late in the birth season)						
Female rank		0.29	-6.06	8.18	0.08	0.771
Female age		0.52	-10.36	6.04	0.27	0.606
Past reproduction	**(Infant died)**	**-3.84**	**-76.68**	**-24.89**		
	(Miscarriage)	**-2.23**	**-54.60**	**-3.57**	**19.65**	**$2.01*10^{-4}$**
	(Primiparous)	0.48	-15.86	26.11		

FIGURES

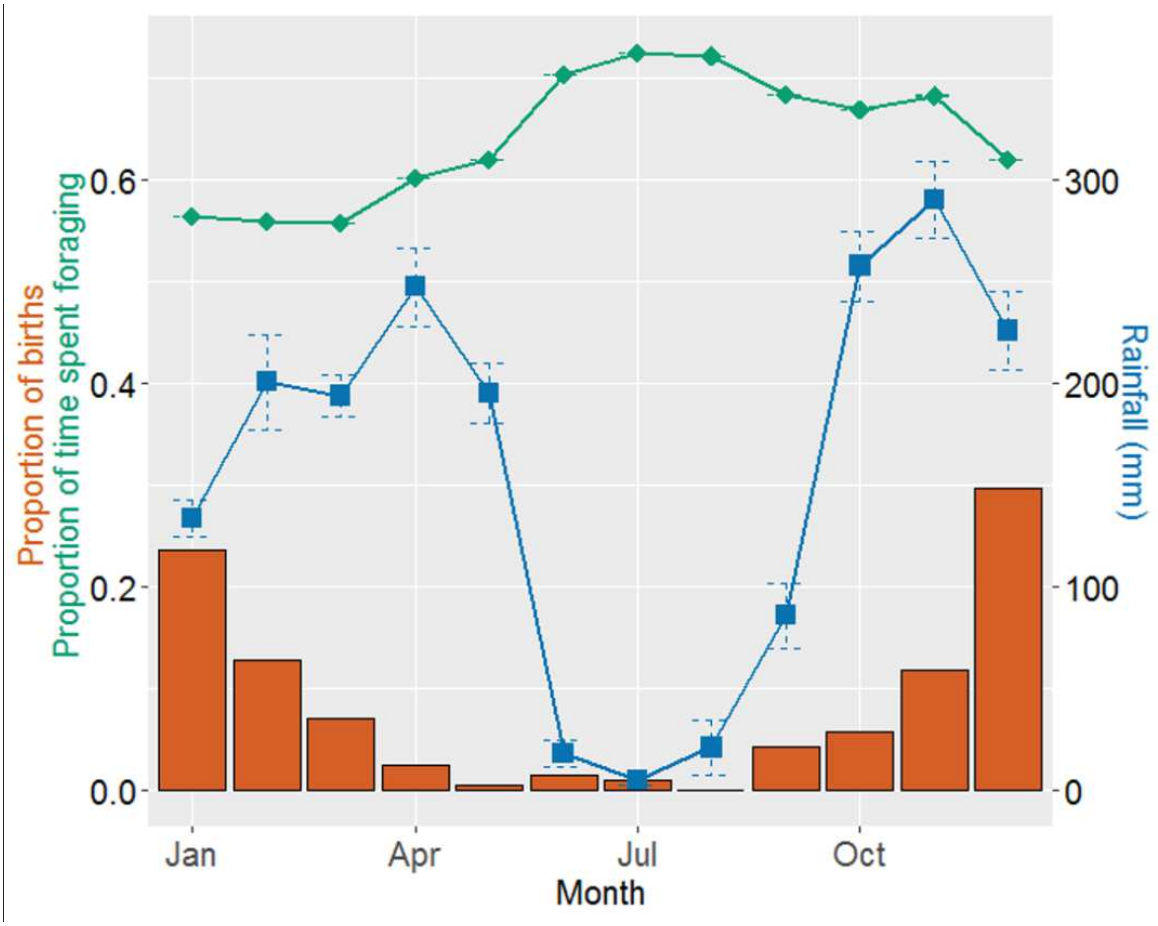


Figure 1: Environmental and reproductive seasonalities of the study mandrills (2012-2020).

Brown 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 are shown using vertical dashed bars.

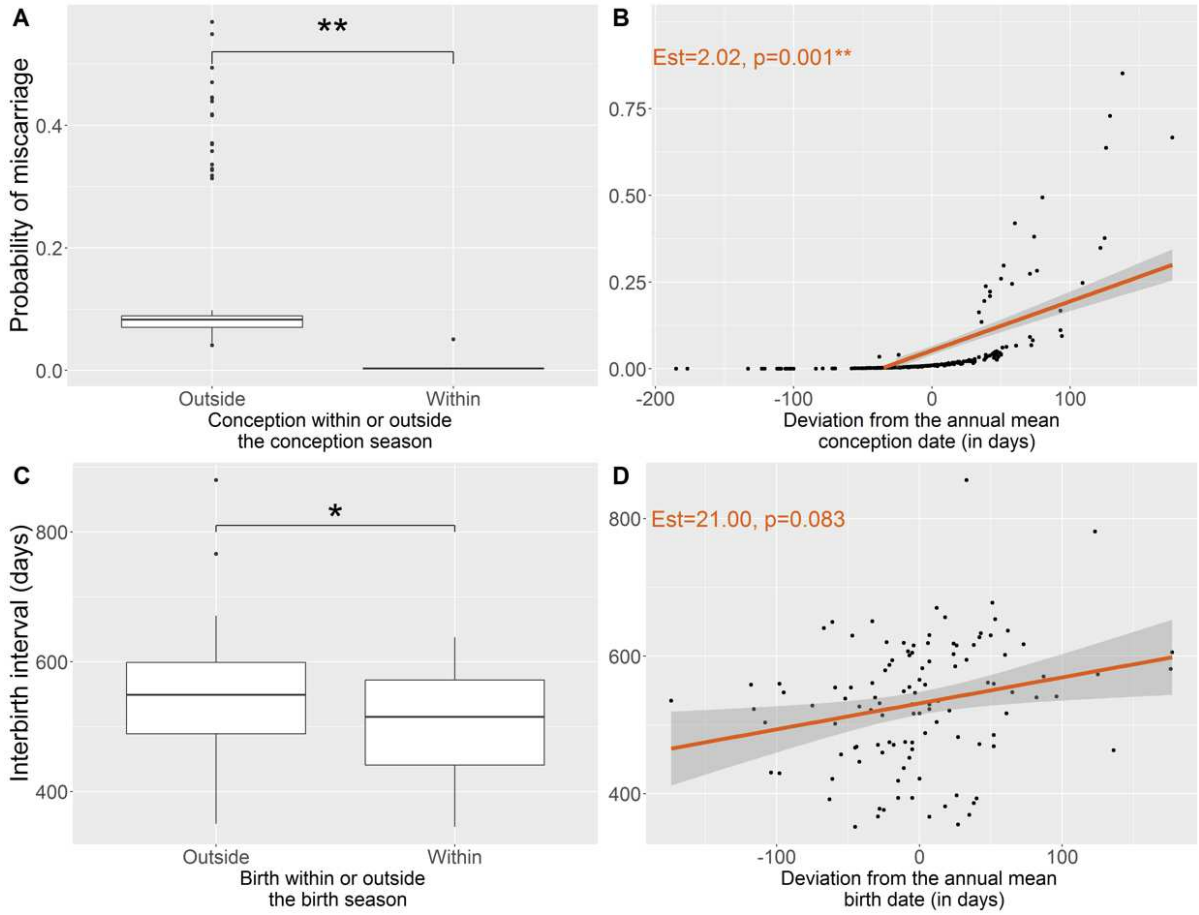


Figure 2: Influence of reproductive phenology on miscarriage probability and interbirth interval lengths.

Miscarriage probabilities are plotted in Panel A in relation to conceiving within or outside the conception season (partial residuals of Model 3A) and in Panel B in relation to the deviation from the mean annual conception date (partial residuals of Model 3B). Similarly, interbirth interval lengths in days are plotted in Panel C in relation to giving birth within or outside the birth season (partial residuals of Model 4A) and in Panel D in relation to the deviation from the mean annual birth date (partial residuals of Model 4B). For graphical purposes, the regression lines in brown are simple linear fits, and the shaded areas display 95% confidence intervals (see also the estimates, 'Est', and P-values, 'P', annotated in brown in the top left corner). For Panels A and C, we represented the P-values[a] of the comparisons between the levels 'within' and 'outside' of the categorical fixed effect of reproductive phenology.

[a]: ·: p<0.10; *: p<0.05 ; **: p<0.01, ***: p<0.001, ****: p<0.0001

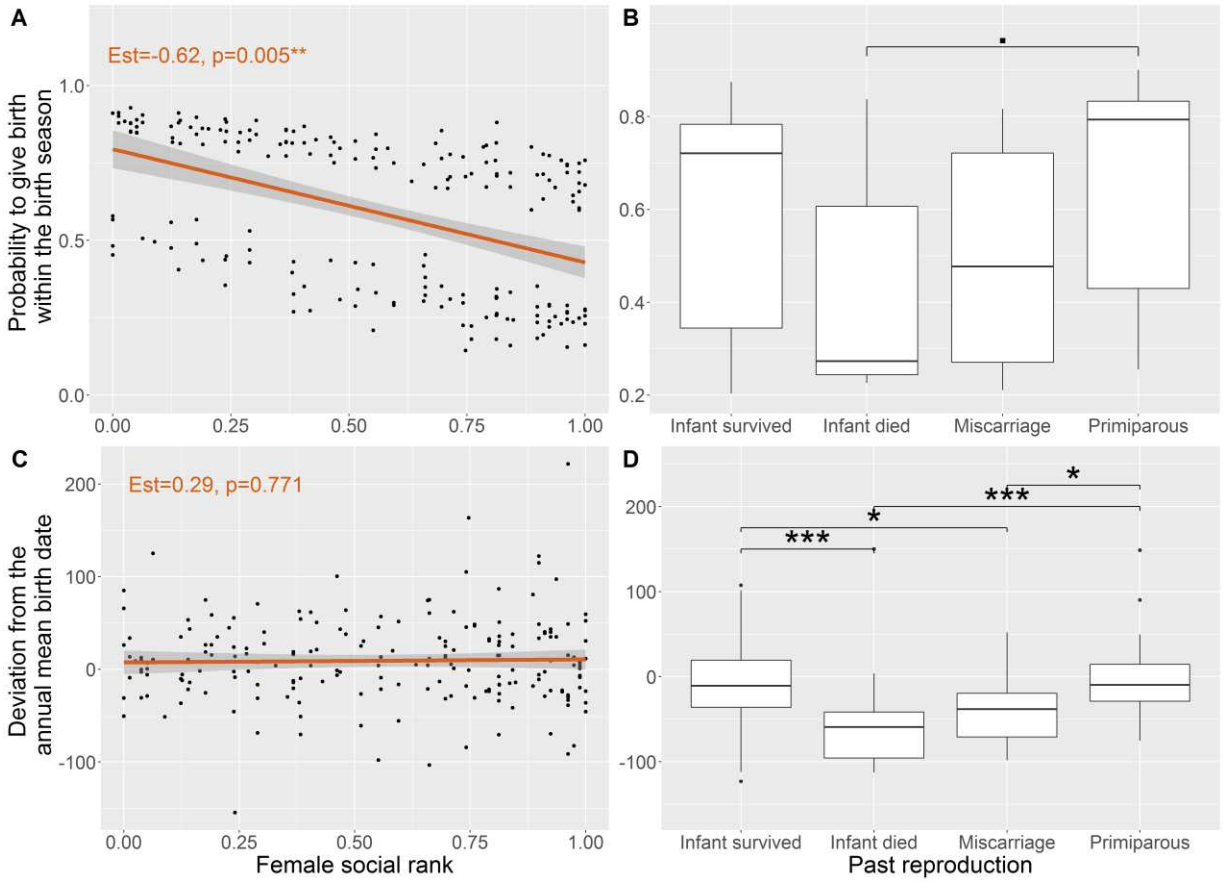


Figure 3: Influence of female social rank and past reproduction on birth timing.

Female probability to give birth within/outside the birth season (partial residuals of Model 5) as a function of female rank (Panel A) and past reproduction (Panel B) and deviation between a given birth date and the mean annual birth date (in days) (partial residuals of Model 6) as a function of female rank (Panel C) and past reproduction (Panel D). For Panels A and C, the brown regression curves show simple linear fits (see also the estimates, 'Est', and P-values, 'P', annotated in brown in the top left corner), and the shaded areas display 95% confidence intervals. For Panels B and D, we represented the P-values[a] of the comparisons between different levels of the categorical fixed effect 'past reproduction'.

[a]: ·: p<0.10; *: p<0.05 ; **: p<0.01, ***: p<0.001, ****: p<0.0001

SUPPLEMENTAL INFORMATION

Table S1: 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 annual mean 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 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, past reproduction	Female rank, female age, past reproduction
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

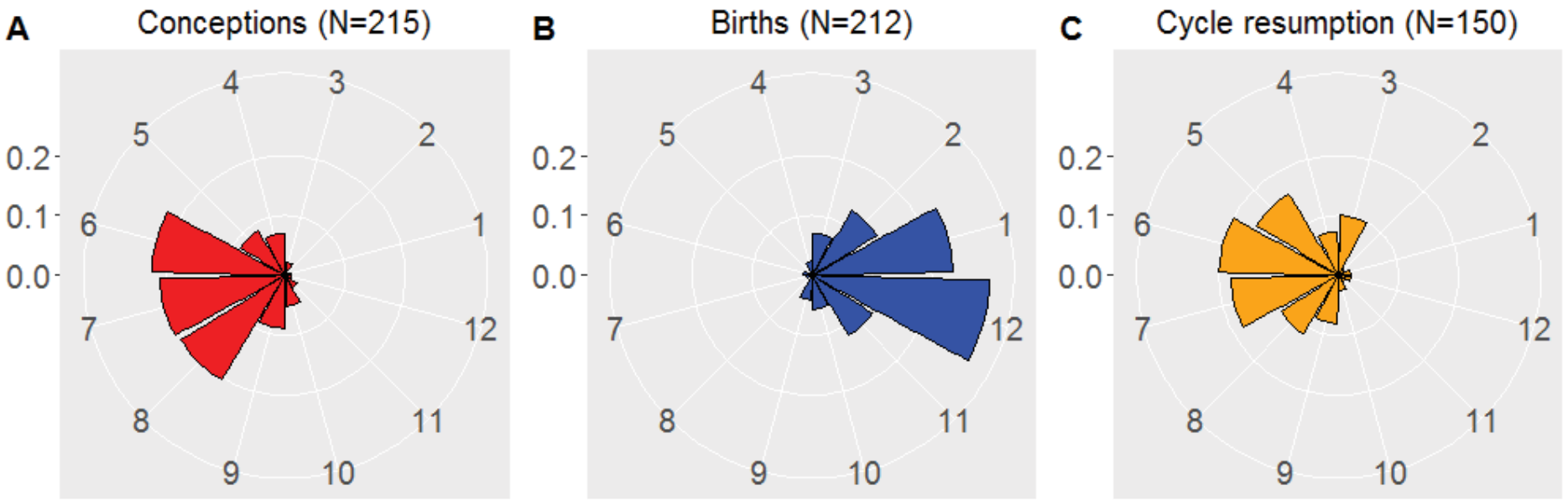


Figure S1: Mandrills are seasonal breeders.

Proportions of conceptions (Panel A), births (Panel B) and cycle resumptions (Panel C) per month (1 for January, 2 for February, etc.) for the reproductive events that occurred between 2012 and 2020 in the study mandrill group.

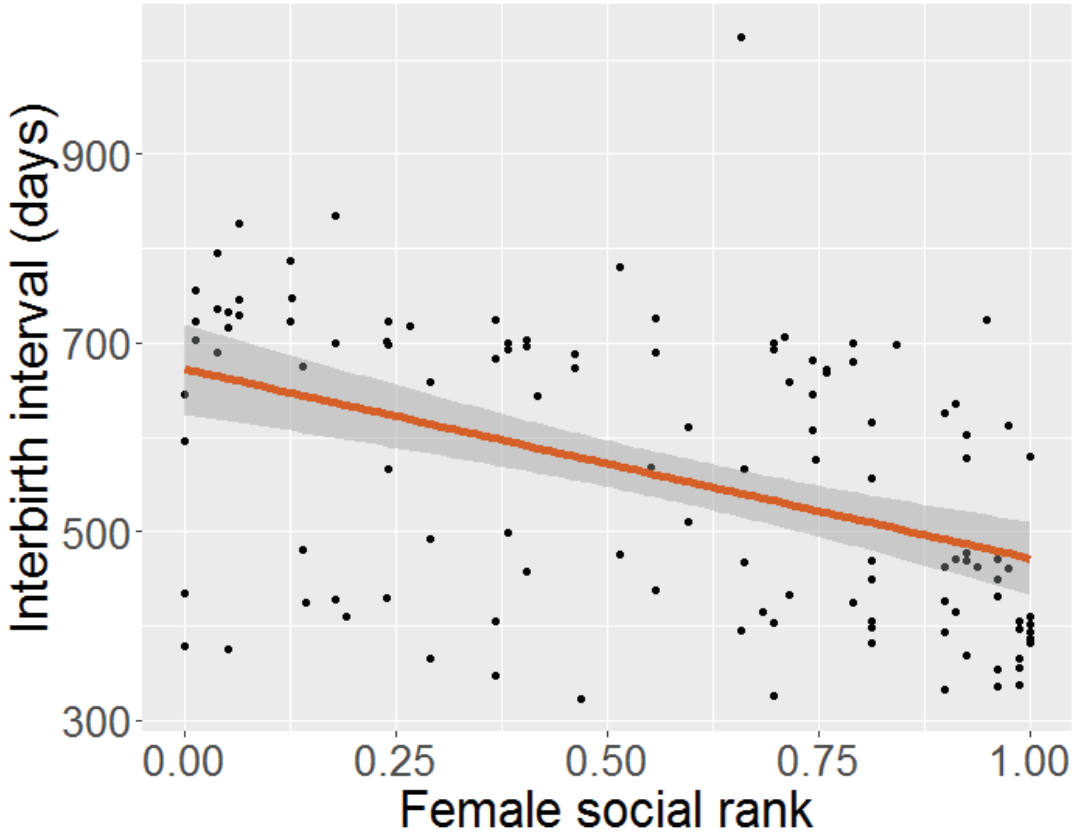


Figure S2: Higher-ranking females have shorter interbirth intervals

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 brown curve shows the linear fit, and the shaded area displays its 95% confidence intervals.

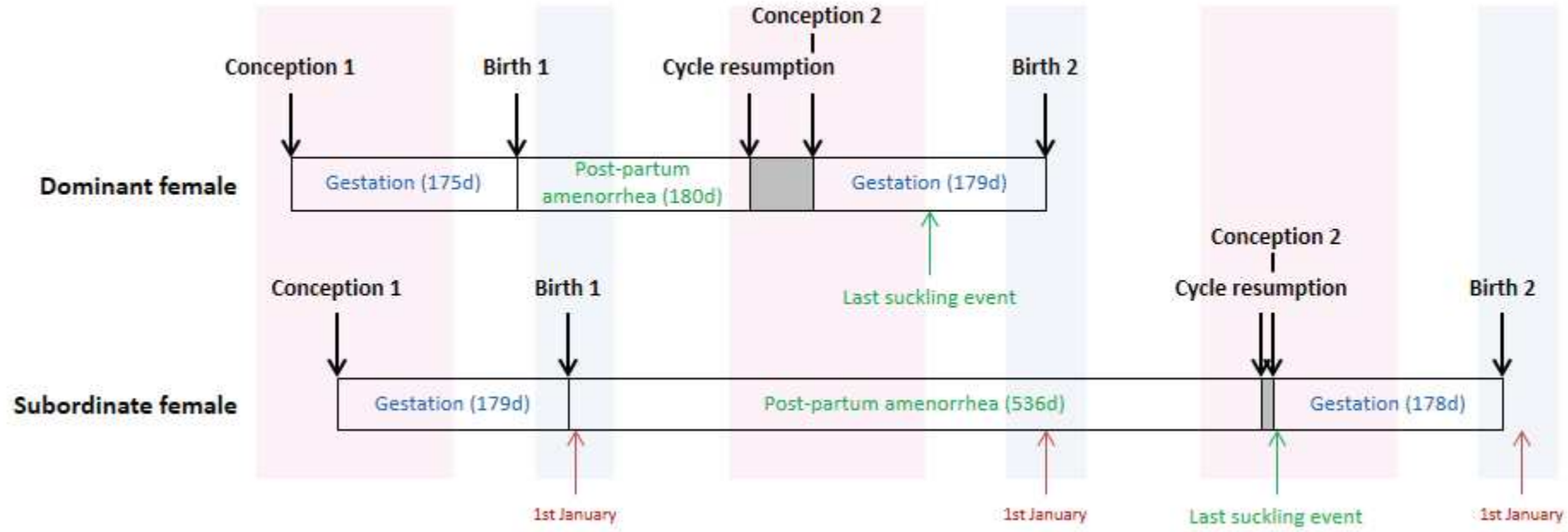
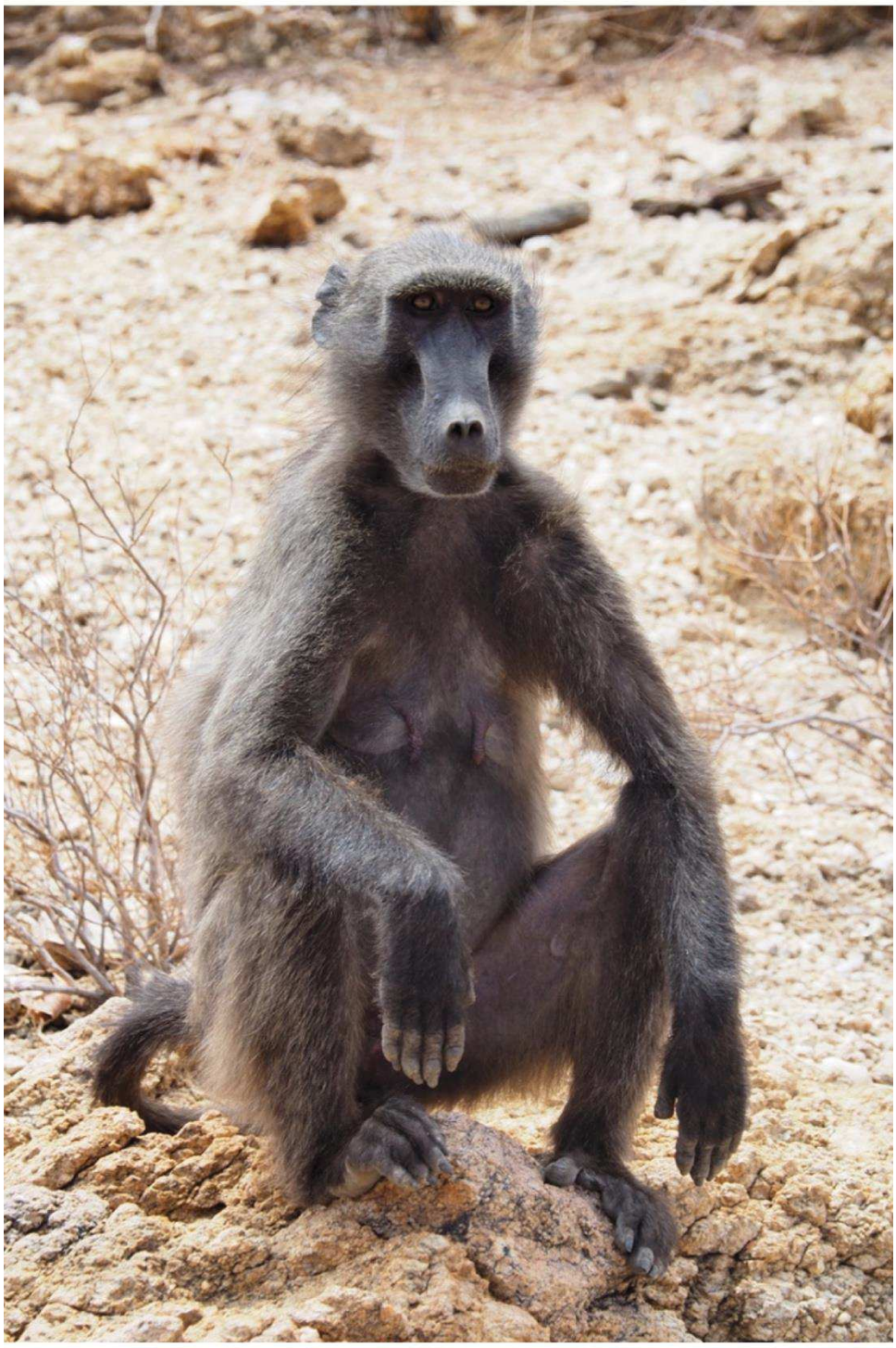


Figure S3: Graphical representation of two real female's cycles from the conception of the first offspring to the birth of the second offspring

The upper part represents the reproductive cycle from a dominant female; while the lower part represents the reproductive cycle: from a subordinate female. Pink squares indicate mating seasons (considered here from the 1st of May to the 30th of September) and blue squares indicate birth peaks (from the 1st of December to the 31st of 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 the same year.

JK



Chapter 6

Climatic unpredictability drives low and flexible reproductive seasonality in large terrestrial African monkeys

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ABSTRACT

Few studies have investigated the ecology and evolution of reproductive seasonality in tropical vertebrates, which show a great diversity in patterns of reproductive phenology. Such diversity may mirror the marked climatic unpredictability (year-to-year variations) characterizing most of the intertropical belt. Here, we gather birth and rainfall seasonality from 16 wild populations of seven African, large-bodied and terrestrial primate species from three genera: *Papio*, *Theropithecus*, and *Mandrillus*. We investigate the influence of multiple components of temporal variation in rainfall on the intensity of reproductive seasonality, as well as which reproductive stage is adjusted with the annual peak of resources. The intensity of birth seasonality varies greatly between and within species, indicating unprecedented flexibility in reproductive seasonality. Across multiple measures of climatic variation, rainfall unpredictability is the only significant predictor of the intensity of reproductive seasonality: important year-to-year variations in the amount of rainfall lead to the loss of reproductive seasonality. Finally, we find very diverse patterns of reproductive phenology, where some (but not all) populations match the lactation peak with the most productive season – a typical mammalian pattern. This study sheds new light on the selective pressures shaping reproductive seasonality in long-lived tropical mammals, by revealing within-species variations, as well as the key influence of climatic unpredictability in favouring a flexible reproductive phenology. Given the phylogenetic ties and the striking life-history and ecological convergences of this taxonomic group with early humans, it also provides an original contribution to our understanding of why humans are non-seasonal breeders.

INTRODUCTION

Many animals are subject to within-year and periodic variation of their environment (Boyce, 1979). These seasonal fluctuations of resource availability and temperatures affect organisms' energy balance, while the greatest energetic costs faced by females take place during certain stage of reproduction, like lactation (Emery Thompson, 2013; Lee, 1996). Consequently, reproductive seasonality, which is the periodic temporal cluster of reproductive events in the annual cycle, is one of the major and most common adaptation to environmental seasonality, as it synchronizes the costliest stage of reproduction in energy with the seasonal food peak, therefore enhancing the condition and survival of both mothers and offspring (F. H. Bronson, 2009; Franklin H. Bronson & Heideman, 1994). A species can be considered either as strict seasonal breeder, if there is a season without any births, or as non-seasonal breeder when births occur year-round (Lancaster & Lee, 1965; Lindburg, 1987). However, a non-seasonal breeding species can still show seasonal variations in birth frequencies if births are not randomly distributed through time, showing one or more birth peak(s) and/or birth valley(s).

Comparative studies investigating the determinants of the intensity of reproductive seasonality in mammals are scarce, and have been mainly conducted at the order-level (ruminants: Rutberg, 1987; Zerbe et al., 2012, carnivores: Heldstab et al., 2018, primates: Di Bitetti & Janson, 2000; Heldstab et al., 2020; Janson & Verdolin, 2005), i.e. looking at interspecific variation in a broad scale. All these studies found a negative relationship between geographical latitude and the breadth of the birth peak in these mammalian orders. However, there are several gaps in our understanding of the determinants of reproductive seasonality at the comparative level, for several reasons. First, this association between latitude and reproductive seasonality only indicates that species living at relatively high latitudes are more likely to breed seasonally than species living in tropical areas, but fails to explain the diverse patterns of reproductive seasonality observed within the tropics (Heldstab et al., 2020; Janson

& Verdolin, 2005). Second, only a few studies have attempted to quantify the extent of variation in reproductive seasonality within different populations of a same species, or between closely relative species with similar diets, sizes and life histories (but see in resp. red deers (*Cervus elaphus*) and African wild dogs (*Lycaon pictus*): Loe et al., 2005; McNutt, Groom, & Woodroffe, 2019). Such comparisons are expected to be particularly insightful to understand the environmental drivers of variation in reproductive phenology, by controlling other sources of variation. Third, latitude is a flawed indicator of environmental seasonality, as it can reflect both the intensity of within-year climatic variation (i.e. climatic seasonality) and environmental productivity. Our understanding of the various components of climatic variation on reproductive seasonality is thus relatively limited.

Most studies have indeed focused on only one such component of climatic variation, which is the intensity of seasonal (i.e. within-year) environmental variation, considering only species diet and latitude as predictors (Di Bitetti & Janson, 2000; Heldstab et al., 2020; Janson & Verdolin, 2005; Zerbe et al., 2012): the more intense the environmental seasonality, the more seasonal the reproduction. However, several other environmental factors must be taken into account. First, environmental productivity, i.e. the overall amount of food availability in a given environment, may modulate the effects of environmental seasonality on reproductive timings: in relatively rich habitats, organisms may be better able to buffer the adverse consequences of the lean season on their condition and survival, therefore decreasing the need to breed seasonally (Janson & Verdolin, 2005). Second, the existence of several seasonal food peaks in the annual cycle, as often encountered in East Africa with two rainy seasons, may extend and flatten the birth peak (Alberts et al., 2005). Third, the predictability of environmental variation could also alter breeding schedules. Indeed, the more intense is year-to-year environmental variation, and the less advantageous reproductive seasonality should be, resulting in longer and

flatter birth peaks and, in extreme cases, in the absence of a birth season, in unpredictable environments.

In support of this, it has recently been shown in 38 ungulate species that the intensity of seasonal breeding decreases with seasonal unpredictability (English, Chauvenet, Safi, & Pettorelli, 2012). Two components of environmental unpredictability, which were not disentangled in the previous study, have recently been suggested to have different impacts on reproductive timings (Heldstab et al., 2020). On the one hand, an environment unpredictable in the magnitude/amplitude of year-to-year variations (relatively to within-year variations) would lead to a high between-year variation in birth frequencies, with lower birth rates in relatively bad years, i.e. with low annual rainfall, as found in several primate populations (Brockman & van Schaik, 2005a; van Schaik & van Noordwijk, 1985; Wiederholt & Post, 2011). On the other hand, an environment unpredictable in the timing of the annual food peak could also lead to low selective pressures favouring reproductive seasonality (de Villemereuil et al., 2020). Disentangling these various components of environmental variation therefore appears critical to understand the evolutionary determinants of reproductive seasonality.

In addition, relatively little is known about how birth timing varies in relation to the annual resource peak in long-lived species. In short-lived species, the full reproductive cycle, from conception to offspring nutritional independence (weaning in mammals) can take place within the same productive season (F. H. Bronson, 2009). However, it is not the case in long-lived species, and females can match various stage of their reproductive cycles with the annual food peak, with different fitness consequences. For example, the capital-income breeder model states that capital breeders are able to store energy and rely on endogenous cues, such as reaching a certain condition-threshold, to onset their reproduction and conceive (Brockman & van Schaik, 2005a). Under this hypothesis, most conceptions are thus expected to occur following an increase of food availability (Brockman & van Schaik, 2005a). Alternatively, the

peak of lactation represents the costliest part of the mammalian reproductive cycle, and synchronizing it with the most productive season can therefore enhance maternal condition and survival (F. H. Bronson, 2009; Franklin H. Bronson & Heideman, 1994). Under this hypothesis, early- or mid-lactation is expected to occur during the annual food peak in primates (J. Altmann, 1980; Brockman & van Schaik, 2005a; Janson & Verdolin, 2005). Lastly, weaning, which occurs after the lactation peak, is often the most vulnerable period of infant life, as infants must learn how to forage for themselves (J. Altmann, 1980; Lee, 1996), and consequently, several species have been shown to time their births in order to match weaning with the seasonal food peak (Brockman & van Schaik, 2005a; Janson & Verdolin, 2005), like most lemurs (Wright, 1999). The factors responsible for whether females adjust one reproductive stage over the others remain unknown.

In this study, we investigate the evolutionary determinants in both the intensity and the timing of reproductive seasonality in three primate genera from the *Papionini* tribe. Within this tribe, we considered the *Papio*, *Theropithecus* and *Mandrillus* genera for several reasons. First they are all relatively large and terrestrial primates (J. Fischer et al., 2019; Swedell, 2011), previously considered as 'baboons' in a broad sense (Bergman, Haile, & Beehner, 2018). Second, they display various patterns of reproductive seasonality. Indeed, on the one hand, most baboon populations are non-seasonal breeders (Bercovitch & Harding, 1993; Swedell, 2011) despite exhibiting seasonal variation in monthly birth frequencies (Cheney et al., 2004; Lycett, Weingrill, & Henzi, 1999), while in the other hand, mandrills (*Mandrillus sphinx*) (Setchell, Lee, Wickings, & Dixson, 2002) and kinda baboons (*Papio kindae*) (Petersdorf, Weyher, Kamilar, Dubuc, & Higham, 2019) are seasonal breeders. Third, they exhibit great ecological flexibility, allowing them to live in various habitats, including arid areas, woodland savannahs, equatorial forests, and grasslands in high altitude (J. Fischer et al., 2019) (see also Figure 1). Fourth, baboons are one of the most studied primates, with data available from different

populations of the same species (J. Fischer et al., 2019). These three genera thus represent a good opportunity to disentangle the effects of various components of environmental variation on reproductive seasonality, while minimizing variations in other factors that are likely to modulate such effects (such as species diet, life history and sociality). Lastly, these species (and in particular from the genus *Papio*) share a variety of features with early humans (Alberts et al., 2005; Brockman, 2005): they are large terrestrial and eclectic omnivorous primates (Alberts et al., 2005; Rhine, Norton, Wynn, & Wynn, 1989), that colonized African savannahs (Bobe, Martínez, & Carvalho, 2020) and are now living in a wide variety of habitats (i.e. not restricted to savannahs) (J. Fischer et al., 2019), able to store large quantities of energy with fat tissues (J. Altmann, Schoeller, Altmann, Muruthi, & Sapolsky, 1993), giving birth to a single offspring every one to three years (J. Altmann & Alberts, 2005; Swedell, 2011), and are mostly non-seasonal breeders (Swedell, 2011). Investigating the environmental determinants of their reproductive seasonality can thus bring new light on the evolution and maintenance of non-seasonal breeding in apes and early humans.

Here we ask three main questions:

(i) What is the extent of inter- and intra-specific variations in patterns of reproductive seasonality, specifically regarding the height and width of the birth peak, as well as its timing in the annual cycle?

(ii) What are the main environmental factors responsible for variation in reproductive seasonality? We disentangled seven components of environmental variation: latitude, environmental productivity, height of seasonal variation, number of rainy seasons, breadth of the rainy season, amount of between-year (unpredictable) variation, and between-year variation in the timing of the rainfall season. Our set of predictions is presented in Table 1.

(iii) In seasonal breeding species, what are the stages of the reproductive cycle timed with the best season? We tested whether females match the seasonal food peak with conceptions under the 'conception hypothesis' (H1), or lactation under the 'lactation hypothesis' (H2). Given the low number of populations with known mean weaning age, we were not able to test the weaning hypothesis (but we will intend to do it in future analyses), stating that females match the seasonal food peak with weaning.

METHOD

1- Sample and data selection

We first searched for data on reproductive seasonality in wild populations of baboons (*Papio* spp.), geladas (*Theropithecus gelada*), drills (*Mandrillus leucophaeus*) and mandrills in the literature (Figure 1). More precisely, we only kept papers providing the number of births per months (but see the exception of yellow baboons, *Papio cynocephalus*, from Mikumi National Park, where births were provided in a three months-period). We obtained birth seasonality data on 16 wild populations from seven species: two on mandrills (personal data; Hongo, Nakashima, Akomo-Okoue, & Mindonga-Nguelet, 2016), three on olive baboons, *Papio Anubis* (Bercovitch & Harding, 1993; Higham et al., 2009; Rowell, 1966), three on yellow baboons (Alberts et al., 2005; Bentley-Condit & Smith, 1997; Rhine, Wasser, & Norton, 1988), one on hamadryas baboons, *Papio hamadryas* (personal data), one on kinda baboons (Petersdorf et al., 2019), five on chacma baboons, *Papio ursinus* (personal data; Barrett, Henzi, & Lycett, 2006; Cheney et al., 2004; Lycett, Weingrill, & Henzi, 1999), and one on geladas (Tinsley Johnson, Snyder-Mackler, Lu, Bergman, & Beehner, 2018) (see Table 2 for references associated with each population, and Figure 1 for their locations). We did not find any monthly birth distributions for two species of interest: drills, albeit studies on a semi-captive population

suggest that they exhibit a seasonal birth peak like mandrills (Kingdon et al., 2012), and guinea baboons (*Papio papio*), albeit studies in captivity suggest that they are non-seasonal breeders (Kingdon et al., 2012; Swedell, 2011).

We also gathered from the literature two species traits that are known to affect the intensity of reproductive seasonality, namely species diet (from Swedell, 2011), and female body size (from Kingdon et al., 2012) (see Table S1).

2- Birth seasonality data

We were interested to quantify two components of reproductive seasonality: the timing of the birth peak/season, and the intensity of birth seasonality. From the monthly distribution of births, we considered that each birth occurred in the middle of the month (i.e. the 15th of each month, except the 14th for February). For the Mikumi population, we similarly considered that births occurred in the middle of the 3 months-period. We then used circular statistic and represent each birth by a vector of length 1 and of angle θ (15*2*pi/365.25 for January, 46*2*pi/365.25 for February, etc.). We computed the mean vector (r-vector) per population, whose angle (converted in a date: μ_{birth}) indicates the mean day of the year in which the births occur (see Table 2), and is thus a measure of birth phenology.

In addition, we computed four measures reflecting the strength of birth seasonality. (i) The length (R) of the r-vector measures the degree of uniformity of the birth distribution across the annual cycle and varies from 0 to 1 (Di Bitetti & Janson, 2000; Janson & Verdolin, 2005; Thompson & McCabe, 2013). When R=0, births are evenly spread across months (i.e. non-seasonal), while when R=1, births all occur at the exact same month of the year (extremely seasonal). We also computed the breadth of the birth peak in a given population using two metrics: (ii) the minimum number of consecutive months in which 50% of births occurred

(called 'BPB 50'), and the (iii) minimum number of consecutive months in which 80% of births occurred (called 'BPB 80') (Heldstab et al., 2018, 2020; Zerbe et al., 2012) (see Table 2). We further ran Rayleigh tests which assess if birth distributions are uniform (H_0: R=0) or not (H_1: R≠0) along the annual cycle. From this test, we categorized for each population the degree of birth seasonality in two levels depending on their P-values (p): (iv) non-seasonal breeders (0, if p>0.05), and seasonal breeders (1, if p <0.05). The different measures of reproductive seasonality are presented per population in Table 2. We found strong correlations between the r-vector and both BPB 50 (cor= -0.91, $p<10^{-4}$) and BPB 80 (cor= -0.99, $p<10^{-4}$). Consequently, and for the following models, we only use R as measure of the intensity of reproductive seasonality, as this measure is more robust to differences in sample size than other metrics, facilitating the comparison of seasonality measures between populations (Janson & Verdolin, 2005).

3- Environmental data

i. Objectives

In order to test our hypothesis, we considered environmental variation through two components: rainfalls and food availability. Indeed, climatic seasonality in Africa (and in most tropical habitats in general) is mainly characterized by variation in rainfall (Alberts et al., 2005; Feng, Porporato, & Rodriguez-Iturbe, 2013; Van Schaik, Terborgh, & Wright, 1993). Although rainfall has also often been used as an indicator of food availability for our studied populations (Alberts et al., 2005; R. A. Hill, Lycett, & Dunbar, 2000; Petersdorf et al., 2019; Tinsley Johnson et al., 2018), we chose to use the Normalized Difference Vegetation Index (NDVI) as an index of food availability. NDVI produces a quantitative index of vegetation productivity with higher values corresponding to a higher degree of vegetation cover (Didan, Barreto

Munoz, Solano, & Huete, 2015). It has previously been used as an indicator of habitat quality for various baboon populations (Dezeure et al., 2020; Zinner, Peí Aez, & Torkler, 2001), and can be an accurate predictor of food availability even among omnivorous species (Pettorelli et al., 2011).

Rainfall and food peak are likely to be lagged by a few months, and this lag duration may vary depending on the habitat/population (Bercovitch & Harding, 1993; Jarvey, Low, Pappano, Bergman, & Beehner, 2018; Dezeure et al., in prep.). Consequently, we used NDVI variation to assess the timing of the seasonal food peak in each population, when investigating the relation between reproductive timing and environmental seasonality. However, NDVI values have to be used with caution when comparing the productivity of environments, as for example, the mean annual NDVI at De Hoop, one of our driest habitat, was almost equalled to the one at Gashaka, one of our wettest habitat. Therefore, we used rainfall variation, and not NDVI, to disentangle various components of climatic variation likely to affect the intensity of reproductive seasonality (such as environmental productivity, predictability and seasonality).

ii. Data extraction

Daily rainfall in a 0.25*0.25 degree resolution (corresponding to between 28*28km at equator and 23*23km at 35° of latitudes) was extracted from satellite data sensors with the Giovanni NASA website (product TRMM 3B42) (Savtchenko, 2016). The GPS coordinates used for this extraction are indicated per population in Table S1, and were assessed either from indications about the home ranges of the habituated groups per population when available in the literature, or from the location (Park, Reserve or nearby city) where the population was observed otherwise (see also Figure 1). Monthly accumulated rainfalls (summed across daily values)

were subsequently computed between January 1998 and December 2019. We therefore gathered 22 years of rainfall per population over the same period of time.

We then extracted the mean NDVI per 16 day-period on a 500 m × 500 m resolution within the same GPS coordinates used for rainfall extraction (Table S1) between March 2000 and March 2017 (given dataset limitations) using MODIS data (MODIS13A1 product) provided by NASA (Didan et al., 2015). Daily NDVI was computed by linear interpolation and then averaged to obtain a monthly value across 18 years.

iii. Decomposition of components of environmental variations

In subsequent analyses, and in order to test our hypotheses, we disentangled various components of rainfall variation across years. We first decomposed monthly rainfall value in three components, as follow: $Rainfall_{m,i} = K_{rain} + Rainfall\ S_m + Rainfall\ NS_{m,i}$, where m is the month of the year (going from January to December) and i is the year (from 1998 to 2019). K_{rain} is a constant, equalled to the mean monthly rainfall across 22 years of records (Figure S1). Rainfall S_m is the seasonal component of rainfall, i.e. the mean monthly rainfall values per month across all 22 years: the months of the rainy season have positive values, while the months of the dry season have negative values (Figure S1). For example, Rainfall S in January is constant between-years, and represents the mean rainfall in January over 22 years. Rainfall S thus represents the seasonal, i.e. within-year periodic, rainfall variation in the annual cycle. Finally, Rainfall $NS_{m,i}$ is the non-seasonal component of rainfall, i.e. the difference between the raw monthly rainfall value ($Rainfall_{m,i}$) and the predictable rainfall variation (K_{rain} + Rainfall S_m) (Figure S1). It represents the unpredictable, i.e. between-year, rainfall variation. Using this decomposition, we assess for each population (see Table 3 for values per population):

- Environmental productivity. It is the mean annual rainfall across all 22 years, equalled to $12*K_{rain}$.
- Height of environmental seasonality. We computed the magnitude of within-year rainfall variation, as the relative standard deviation (SD) of Rainfall S, given by the formula: $\frac{100\times SD(Rainfall\ S)}{12*K\text{rain}}$. The higher the value, the higher within-year rainfall variation.
- Shape of environmental seasonality. Looking at predictable rainfall variation (i.e. K_{rain} + Rainfall S), we first assessed graphically for each population the number of rainy seasons per year. In environments with only one rainy season, we further calculated the rainfall peak breadth (RPB), which is the minimum number of consecutive months of the year during which 80% of the annual rainfall ($12*K_{rain}$) occurs (we also computed the RBP for which 50% of the annual rainfall occurs, and it is highly correlated with this previous metric: cor=0.83, $p=9.01*10^{-4}$). We could not compute the RPB for environments with more than one rainy season, as such measure is meaningless in such contexts.
- Amount of environmental unpredictability. We computed the magnitude of between-year rainfall variation, as the relative standard deviation of Rainfall NS, given by the formula: $\frac{100\times SD(Rainfall\ NS)}{12*K\text{rain}}$. The higher the value, the higher between-year rainfall variation.

In addition, we were interested to quantify environmental unpredictability in terms of timing, i.e. quantifying how much the timing of rainfall varied between-years (and not only the intensity of rainfall between-year variation). First, for each population, we computed the mean rainfall date (as the angle, converted in a date, of the r-vector of the rainfall), thereafter noted μ_{rain}, in the annual cycle using circular statistics on the predictable rainfall variation (K_{rain}+Rainfall S) across 22 years (from 1998 to 2019). μ_{rain} indicates the date where rainfalls

are most concentrated in the annual cycle, in the middle of the rainy season. Second, we computed the mean rainfall date per year, or per semester (for bimodal population). We separated our rainfall data in 22 distinct years, centred on μ_{rain}. So, for example, if μ_{rain} =10th of September, we split up years from March to February. We similarly separated our rainfall data in 44 distinct semesters for the bimodal populations: the first semester going from February to July, and the second one going to August to January, given the distribution of the seasonal component of rainfall in these environments. Third, for each given year (or semester), we computed the mean rainfall date using circular statistics. Fourth, we computed the standard deviation of these yearly mean dates per population, which quantifies the between-year rainfall variation in timing, with higher values corresponding to higher uncertainty in the annual timing of rainfall. For the bimodal populations, we quantified two standard deviations, one per semester, and further computed the mean of these two standard deviations as the measure of between-semester rainfall variation in timing.

Lastly, to assess the seasonal food peak per population, we computed the mean monthly NDVI per month across 18 years (i.e. K_{NDVI} + NDVI S, following the same notation used to disentangle the components of rainfall variations). We then used circular statistics to compute the mean annual NDVI date, μ_{NDVI}, which characterizes the timing of the seasonal food peak per population (see Table 3).

4- Statistical analysis

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

i. Characterization of reproductive and environmental seasonalities

In order to characterize the direction and strength of birth seasonality, we used circular statistics. More precisely, we first estimated the mean direction of the resultant vector (r-vector) of births in the annual cycle (as dates), μ_{birth}, using the function 'circ.summary' from the 'CircStats' package (Agostinelli & Lund, 2018). Second, we used the 'r.test' function from 'CircStats' package to run the Rayleigh test (Agostinelli & Lund, 2018), extracting R, the mean resultant vector length, along with their P-values associated. We similarly computed the mean rainfall (μ_{rain}) and NDVI (μ_{NDVI}) dates in the annual cycle using 'circ.summary'.

ii. Factors affecting the intensity of reproductive seasonality

We considered seven potential environmental determinants of reproductive seasonality, which are listed along with our predictions in Table 1.

For each potential determinant, we plotted R (the r-vector length) depending on the predictor. We further checked the significance between each predictor and R using univariate linear mixed models (LMMs) with the function 'lmer' from lme4 package (Bates, Mächler, Bolker, & Walker, 2015), with R as response variable, the predictor as a fixed effect, and species as random effect. We further computed the conditional and marginal coefficient of determination of these LMMs (pseudo-R-squared) with the function 'r.squaredGLMM' from MuMIn package (Barton, 2019). This is a preliminary design, and we will intent to run proper phylogenetic regressions before submission. Given the low number of populations in this study, and the collinearity between some of our environmental parameters (multivariate models had variance inflated factors >3), we were not able to run stable multivariate models. Indeed, several components of environmental variation were strongly correlated, such as:

- RPB with the height of seasonal environmental variation (cor=-0.95, $p<10^{-4}$), meaning that the higher the height of variations in the seasonal component of rainfall, and the narrower the seasonal rainfall peak in our sampled regions.
- Latitude with environmental productivity (cor=-0.53, p=0.033), meaning that lower latitudes were associated with higher annual mean rainfalls in our sampled regions.
- Environmental productivity with the amount of variation in the non-seasonal component of rainfall (cor=-0.79, $p=2.42*10^{-4}$), meaning that the higher the annual mean rainfall, and the less intense the variations in the non-seasonal component of rainfall.

Given the fact that patterns of mandrill reproductive seasonality were very different from all other populations, and that mandrills are more distantly phylogenetically related from *Papio* spp. than geladas, which is reflected in distinct life histories (see second section of the results), we excluded the two mandrill populations from subsequent analyses but present the results of the models including mandrills in the Supplemental Information.

iii. Timings of conceptions and births in relation with rainfall seasonality

Among seasonal breeding populations (see Table 2), we further investigated how reproductive timings were adjusted with food availability (i.e. NDVI) seasonality. More precisely, we wanted to test two hypotheses: whether females strategically match (H1) conceptions or (H2) lactation with the annual food peak.

For the first hypothesis (H1, 'conception'), we first determined the mean conception date per population with the formula: $\mu_{conc} = \mu_{birth}$ - gestation. We used the mean duration of gestation in days per population when it was provided in the literature, or used a species specific gestation length otherwise (see Table S1). We asked if the seasonal component of NDVI (i.e. K_{NDVI} + NDVI S) during the six months around μ_{conc} (three months before and three months

after) is more important than random, i.e. higher than if females were timing their conceptions regardless of NDVI seasonality. More precisely, we realized an exact two-sample Fisher-Pitman permutation test, using the 'oneway_test' function from the 'coin' package (Hothorn, Hornik, Van De Wiel, & Zeileis, 2006). This function tests if the observed value of NDVI during a specific period (in this case the six months around μ_{conc}) is significantly higher that randomized (i.e. permuted) values of NDVI in the same period. This test randomized monthly NDVI values, so that the NDVI in January could occur in every other month of the year for example. We further tested more precisely if females tended to conceive soon before, or soon after the annual food peak, looking at seasonal NDVI values the three months before μ_{conc} and the three months after μ_{conc} respectively. In addition, we computed the difference, in months, between μ_{conc} and μ_{NDVI} in order to describe the temporal gap between conception and NDVI peaks for each seasonal breeding population.

For the second hypothesis (H2, 'lactation'), we considered the 6 months after birth as the time window corresponding to lactation. Indeed, this window has often been used to characterize infant dependency, and in particular the period of high infanticide risk, in several baboon populations (J. Altmann, 1980; Palombit, 2003). We asked if the seasonal NDVI values (K_{NDVI} + NDVI S) the six months after the annual peak of births (i.e. μ_{birth}) are more important than random, i.e. than if lactation was timed regardless of food availability seasonality. To do so, we similarly ran an exact two-sample Fisher-Pitman permutation tests per population, using the 'oneway_test' function from the 'coin' package (Hothorn et al., 2006). We further tested more precisely if females tended to adjust early-lactation or mid-lactation with the annual food peak, looking at seasonal NDVI values the three months after μ_{birth} or from three to six months after μ_{birth} respectively. In addition, we also computed the difference, in months, between μ_{NDVI} and μ_{birth} in order to describe the temporal gap between NDVI and birth peaks for each seasonal breeding population.

RESULTS

1) Characterization of the variation in patterns of reproductive seasonality

The monthly distribution of births in relation with seasonal variations in rainfall and NDVI – and index of food availability - is shown, for each population, in Figure 2. We first observe large inter-specific variation in the intensity of reproductive seasonality: hamadryas baboons show non-seasonal births (Awash population: R=0.02), while mandrills (Lékédi: R=0.67 and Moukalaba-Doudou: R=0.80 resp.) or kinda baboons (Kasanka: R=0.50) exhibit pronounced birth seasonality characterized by a narrow annual birth peak (Table 2, Figure 2).

We further observe important intra-specific variations in the intensity of birth seasonality in chacma baboons, from nonseasonal breeding (de Hoop: R=0.10; Tokai: 0.22, and Tsaobis: 0.10, respectively) to significant birth seasonality (Drakensberg: R=0.42; Moremi: R=0.37) (Table 2, Figure 2). Intraspecific variations appear less substantial for other species of this sample.

Seasonal birth timing is also surprisingly variable between species: for instance, kinda baboons from Kasanka mainly give birth around July, whereas chacma baboons, with a neighbouring geographical range, give birth between September and November (Table 2, Figure 2).

2) The atypical case of mandrills

The mandrills exhibit the most pronounced breeding seasonality, with more than 50% of births occurring within two months in the two populations considered (Figure 2, Table 2). Different causes may explain this distinct phenology pattern in comparison to other populations included

in our study (Figure 3). First, mandrills form a phylogenetic outgroup compared to other species included. Within the *Papionini* tribe, the genus *Mandrillus* is more closely related to the genus *Cercocebus* (mangabey spp.) than to genera *Papio* and *Theropithecus* (Figure 3). *Papio* and *Theropithecus* genera are more closely related to *Lophocebus* (mangabey spp.) and *Rungwecebus* (kipunji) genera than to the genus *Mandrillus* (Figure 3). Such phylogenetic distance is reflected in life-history and ecological differences that may influence reproductive phenology. For example, female mandrills are smaller on average than the *Papio* spp. and geladas, which is associated with a faster life history pace; mandrills also have a different, largely frugivorous diet (Figure 3). These traits may all contribute to explain observed differences in the intensity of reproductive seasonality between mandrills on the one hand, and *Papio* spp. and geladas on the other hand. This is a preliminary draft, and we will either remove mandrills from this study, or add species from the missing genera (*Cercocebus*, *Lophocebus* and *Rungwecebus*) to consider the entire *Papionini* tribe when reworking on this manuscript.

3) What are the ecological factors affecting the intensity of reproductive seasonality?

We therefore excluded mandrills to further investigate the links between environmental variables and the intensity of reproductive seasonality. We found an effect of the amount of environmental unpredictability and of habitat productivity, two correlated environmental predictors (cor=-0.794, $p<10^{-3}$) on the intensity of reproductive seasonality indexed by R (Table 4): the higher the amount of between-year rainfall variations and the lower the mean annual rainfall, the lower the intensity of reproductive seasonality (Figure 4). Lastly, we did not find any effect of latitude, height of rainfall seasonality, number of rainy seasons, breadth of the rainfall peak or unpredictability in the timing of the annual peak of rainfall on the intensity of reproductive seasonality (Table 4). Including mandrills in these analyses did not alter these results (Table S2).

4) Which stage of the reproductive cycle is timed with the annual food peak?

Females time conceptions in the middle of the food peak in two (Kasanka & Moremi) of nine seasonal breeding populations (Table 5), supporting the 'conception' hypothesis (H1). More precisely, conceptions immediately followed the annual food peak in three populations (Lékédi, Amboseli & Moremi), and immediately preceded it in one population (Kasanka) (Table 5). The timing separating the conception peak from the food peak was highly variable across populations (Table 5), but in most populations, the conception peak occurred from 1 to 4 months after the annual food peak (except for the Mikumi, Kasanka & Simien populations).

Females time lactation (i.e., six months following birth) with the annual food peak in four (Lekedi, Moukalaba-Doudou, Drakensberg & Moremi) populations (Table 5), supporting the 'lactation' hypothesis (H2). More precisely, females match early-lactation (i.e., three months following birth) in one population (Drakensberg), while they match mid-lactation (i.e., three to six months following birth) in two populations (Lekedi & Moremi) (Table 5). For most populations, the annual birth peak occurs two to five months before the annual food peak (except for the Mikumi, Kasanka, & Simien populations, Table 5).

DISCUSSION

Here, we revealed strong inter- and intra-specific variation in both the intensity of reproductive seasonality and the annual timing of births in relation with environmental seasonality in baboons and relatives. Our study further emphasizes the importance of an overlooked aspect of environmental variation on the intensity of reproductive seasonality: its unpredictability. Lastly,

we did not detect any general pattern of reproductive phenology, meaning that baboons and relatives match different stages of their reproduction with the annual food peak.

Inter- and intra-specific variation in reproductive seasonality

At the genus level, we found a wide diversity of intensities of reproductive seasonality: around half (6 out of 13) of the sampled *Papio* populations can be considered as seasonal breeders, i.e. with a significant birth peak in the annual cycle (like the kinda baboon), whereas others are non-seasonal breeders, meaning that they don't exhibit any significant variation in their monthly birth frequencies (like the hamadryas baboon). Such diverse patterns of reproductive seasonality within a single genus has rarely been reported in non-primate mammalian genera (see for example *Cervus*: English et al., 2012; Loe et al., 2005; Rutberg, 1987, *Damaliscus*: Rutberg, 1987, *Ovis*: Rutberg, 1987, *Ursus*: Spady, Lindburg, & Durrant, 2007, *Mustela*: Heldstab et al., 2018, *Vulpes*: Heldstab et al., 2018). However, even if it has never been highlighted in previous comparative studies, important intra-genus variation in the intensity of reproductive seasonality seems to exist in several primate genera with large distribution ranges, such as *Alouatta* (Di Bitetti & Janson, 2000; Janson & Verdolin, 2005), *Cercopithecus* (Heldstab et al., 2020; Janson & Verdolin, 2005), *Cebus* (Janson & Verdolin, 2005) or *Macaca* (Heldstab et al., 2020; Janson & Verdolin, 2005).

Interestingly, we further reveal intraspecific variation in the intensity of reproductive seasonality. Only chacma baboons exhibit substantial variation in breeding seasonality, probably because it is the only species for which we could gather data from more than three populations with a reasonable number of births. It is possible that other baboon species with relatively large distributional ranges, such as yellow, olive and hamadryas baboons, also exhibit between-population variation in breeding strategies. Only one study previously quantified such

intraspecific variation in the intensity of reproductive seasonality, in African wild dogs (*Lycaon pictus*): they reproduce seasonally in relatively high latitudes in order to match their pup-rearing periods with the coolest period of the year, whereas they reproduce year-round in equatorial areas, where seasonal fluctuations of temperatures are low (McNutt et al., 2019). These findings indicate that population-level factors may be responsible for variation in reproductive seasonality on top of species-level ones, as well as suggest a weak phylogenetic signal in this taxonomic branch. We have planned to run phylogenetic regressions and quantify phylogenetic inertia before submitting this manuscript for publication.

Lastly, intra-genus and intra-specific variation in reproductive seasonality reflects the proximate cues used by *Papio* spp. to adjust their reproduction. Unlike species using strict photoperiodic cues to onset their reproduction (Bradshaw & Holzapfel, 2007; Paul, Zucker, & Schwartz, 2008; Spady et al., 2007), many monkeys, including the taxonomic group under study, use alternative cues (Heldstab et al., 2020; but see the exception of lemurs: Rasmussen, 1985), which remain poorly understood, but are likely based on some aspect of environmental variation. As most mammalian species, baboons and relatives exhibit a condition-induced reproduction, where conceptions (and/or cycle resumption after lactation) are more likely to occur when females are in better condition (Alberts et al., 2005; Beehner, Onderdonk, Alberts, & Altmann, 2006). However, we found that (i) even in the driest habitats (Tsaobis or De Hoop), baboons can conceive year-round, and that (ii) kinda baboons (and mandrills) exhibit a striking strong breeding seasonality (and this breeding seasonality is lost in zoos for mandrills: Heldstab et al., 2020). Therefore, this condition-threshold cannot be the only cue used as previously thought (Brockman & van Schaik, 2005a) in our populations, and they may use other unknown environmental cues (such as the onset of rainy season) to adjust their reproductive timings, explaining the diversity of observed intensities of reproductive seasonality.

Environmental unpredictability as a main driver of flexible reproductive seasonality

Higher climatic unpredictability weakens the intensity of reproductive seasonality

Here, we showed that environmental unpredictability was the only significant predictor of the intensity of reproductive seasonality in our populations: more precisely, higher amounts of between-year rainfall variation lower reproductive seasonality. Only one other study in mammals showed that the birth peak breadth is higher in environments with higher year-to-year stochastic environmental variations among 70 ungulate populations (English et al., 2012). Indeed, most studies investigating the effects of climate on reproductive seasonality exclusively considered environmental seasonality, i.e. the magnitude of within-year environmental variation. The impact of between-year environmental variation, through stochastic variation or climatic events such as el Niño and fruit mast years (in South-East Asia) for example (Brockman & van Schaik, 2005a; van Schaik & van Noordwijk, 1985; Wiederholt & Post, 2011), on the intensity of reproductive seasonality has only been suggested in primates (Clauss, Zerbe, Bingaman Lackey, Codron, & Müller, 2020).

The wide habitat range of baboons and relatives (Figure 1) may have favoured a low and flexible reproductive seasonality in these species, rather than a fixed given reproductive strategy (e.g. a strict breeding season controlled by photoperiod). Indeed, the fitness benefits associated with seasonal breeding - enhancing maternal condition and offspring survival - may be alleviated in unpredictable environments, where droughts can extend over the rainy season. In such environments, other adaptations may be more advantageous, such as an ability to store energy (Brockman & van Schaik, 2005a; van Schaik & van Noordwijk, 1985), to expand the dietary repertoire (Grueter, 2017), to increase daily foraging time (Alberts et al., 2005; Grueter, 2017), or to flexibly adjust lactation duration (van Noordwijk, 2012). As such, *Papio* species share a variety of such features: they can store energy, have an eclectic omnivorous diet and typically rely on fallback food during the dry season (J. Altmann et al., 1993; S. A. Altmann,

2009; Swedell, 2011). The importance of climatic unpredictability on shaping low and flexible reproductive seasonality has been overlooked, although it may be generalized to other long-lived mammals living (i) in tropical areas, (ii) across a wide range of habitats, and/or (iii) in highly unpredictable environments.

However, we only partially explain the variation in intensity of reproductive seasonality (20% of variation in the intensity of reproductive seasonality is explained with the amount of rainfall unpredictability), and it is likely that other factors, such as feeding competition, access to paternal care or predation risk impacting reproductive synchrony in these social species (Boinski, 1987; Chapter 4), or life history traits like interbirth intervals or infant mortality (Clauss et al., 2020; van Noordwijk, 2012), may also play major roles in the evolution of their reproductive seasonalities.

No effect of other environmental components on reproductive seasonality

Climatic unpredictability can break into two components: (1) the amount/magnitude of year-to-year variation (i.e., if the rainy season is more rainy or drier than usual), (2) year-to-year variation in the timing of the rainy season (i.e., if the rainy season occurs earlier or later than usual) (Clauss et al., 2020); but these components have never been disentangled in empirical studies so far. Although we did not detect any significant effect of unpredictability in the timing of the rainy season, this study opens new avenues to investigate various environmental components that are likely to affect reproductive seasonality, and our methodology can be re-used in future studies.

Environmental productivity was the only other significant predictor of the intensity of reproductive seasonality in this study, and was negatively correlated with the amount of year-to-year rainfall variation, so in the opposite direction compared to our prediction. Indeed, even

in dry areas like at Tsaobis or De Hoop, baboons can breed year-round. The significant correlation of environmental productivity is thus likely to be artefactual, due to the fact that in our sampled habitats, the most productive areas are also the most predictable.

Lastly, our decomposition of rainfall components further calls for a more rigorous definition of the term seasonality, especially when it is used in a quantitative way. Indeed, a 'more seasonal' environment can either be an environment with higher within-year variation (i.e. the amplitude of variation between the 'best' and the 'worst' month of the year), with higher within-year over between-year variation (i.e. the amplitude of within-year variation controlling for the intensity of unpredictable variations), with a shorter productive season (i.e. the rainfall peak breadth), or with only a unimodal season (i.e. one rainy, or one warm season per year). However, we did not find any significant effect of environmental seasonality on reproductive seasonality in this study, as the amount of environmental unpredictability is a stronger predictor of reproductive seasonality than all the other environmental variation components explored.

Absence of clear patterns to explain the observed diversity in reproductive phenology

We did not find a general pattern of reproductive timing in relation with environmental seasonality, meaning that baboon females can match different reproductive stages with the annual food peak depending on populations, and possibly individuals.

Weak support for the 'conception' hypothesis

In most seasonal breeding populations, conception peak did not occur during or soon after the annual food peak, which goes against the 'conception' hypothesis. The underlying mechanism

in favour of this hypothesis is that females may be able to onset their reproduction and/or conceive only above a condition-threshold (Brockman & van Schaik, 2005a; Jönsson, 1997), once their condition is sufficient to ensure the survival of their future offspring's and their own. In *Papio* and relatives, females are, however, able to conceive year-round, even in relatively poor habitats. They may have evolved other adaptations to environmental seasonality that enhance this ability to be over their condition-threshold (and so to breed) year-round, such as their omnivorous diet, the use of fallback food (Alberts et al., 2005; S. A. Altmann, 2009), and/or very low condition thresholds.

Partial support for the 'lactation' hypothesis

We found partial support for the 'lactation' hypothesis. Indeed, in some populations, early- or mid-lactation peak tends to coincide with the annual food peak, and in most populations, the birth peak occurs two to five months before the annual food peak. Baboon females might thus match the energetically costliest phase of their reproductive cycle, i.e. the peak of lactation (Brockman & van Schaik, 2005a; Lee, 1996; van Schaik & van Noordwijk, 1985), with the annual food peak. This strategy has been shown to increase maternal reproductive pace in two studied populations, namely the Tsaobis baboons (Chapter 3) and the Lékédi mandrills (Chapter 5). Other large tropical mammals follow this pattern. For example, female herbivores from the Serengeti National Park give birth before or during the rainy season (Sinclair, Mduma, & Arcese, 2000).

However, it remains unclear which stage of lactation is matched with the annual food peak, and this stage may vary across populations. Data quantifying maternal energy expenditure during lactation (Rosetta, Lee, & Garcia, 2011), or a comparison of isotopic measures of trophic levels between mother and infants (Reitsema, 2012; Reitsema, Partrick, & Muir, 2016) would

be necessary, for each population, to determine when the lactation peak occurs. Indeed, given the wide variation in interbirth intervals ('IBI's) among the studied populations (Swedell, 2011), the exact timing of lactation peak may similarly vary, limiting the possibility to establish such timings in this comparative analysis. For example, maternal energy intake is maximal when infants are around two months old in a captive population of olive baboons (Garcia, 2014), versus 4-6 months old in wild geladas (Dunbar & Dunbar, 1988; Dunbar, Hannah-Stewart, & Dunbar, 2002) and Amboseli baboons (J. Altmann, 1980), and around 6-9 months old for the Drakensberg baboons (Barrett et al., 2006; Lycett et al., 1999). In addition, strong between-individual (age- and rank-related) variations in post-partum amenorrhea (PPA) and IBI durations have been found in numerous *Papio* and relatives populations (Gesquiere, Altmann, Archie, & Alberts, 2017; Packer, Collins, Sindimwo, & Goodall, 1995; Roberts, Lu, Bergman, & Beehner, 2017; Setchell et al., 2002), and may further affect the population's reproductive phenology (Dezeure et al, in prep.).

Unexplored factors and the potential importance of weaning

First, weaning could be another critical stage to time with the annual food peak, responsible for the unexplained part of variation in reproductive phenology, as it is a highly vulnerable period of life for most primate infants (Janson & Verdolin, 2005). Indeed, weaning is the phase of the reproductive cycle adjusted with the annual food peak in most seasonal-breeding Malagasy lemurs (Wright, 1999), and the timing of weaning is also important in baboons (J. Altmann, 1980; Lycett et al., 1999; Rhine et al., 1988), as the amount of 'weaning' food available may vary seasonally and be critical for infant survival (J. Altmann, 1980). However, as lactation peak, high inter-individual variation is often observed and getting an estimation of weaning age per population is thus difficult.

Second, and more broadly, various unexplored factors can potentially affect reproductive timing and further limit our ability to detect a clear pattern. For example, for populations living at high altitudes like the geladas from Simien and the chacma baboons from Drakensberg, seasonal variation in temperatures also constrain reproductive phenology (Lycett et al., 1999; Tinsley Johnson et al., 2018). Moreover, the existence of more than one optimal birth timing in the annual cycle can further modulate reproductive phenology. For example, in the Tsaobis chacma baboons, females may either synchronize the lactation peak (around 5-6 months after birth) or late-weaning (for infants that are 13-16 months old) with the annual food peak, which respectively enhance maternal reproductive pace or infant survival (Chapter 3). Other populations could show similar reproductive trade-offs, weakening reproductive seasonality and complicating patterns of reproductive phenology in these long-lived tropical species.

At high latitudes, most, if not all, mammalian species match lactation with the best season of the year (F. H. Bronson, 2009; Franklin H. Bronson & Heideman, 1994), but in tropical and long-lived species, the reproductive stages that are matched with the annual food peak appear more variable (Brockman & van Schaik, 2005a; Janson & Verdolin, 2005; Sinclair et al., 2000). The few studies that have investigated the determinants of reproductive timing in relation to climate in tropical species have highlighted the importance of body size, energy storage and environmental predictability (Brockman & van Schaik, 2005a; Janson & Verdolin, 2005; van Schaik & van Noordwijk, 1985). Here we found that baboons and relatives exhibit a wide diversity of strategies in reproductive timing in relation with food availability seasonality, suggesting that other factors must be taken into account.

Consequences for the reproductive resilience to climate change of baboons and relatives

In an ecological timescale, climate change is strongly increasing rainfall unpredictability in the tropics, both in timing and magnitude (Feng et al., 2013). Our study suggests that baboons should be relatively resilient to future climate change with regard to their reproduction, as they can flexibly adjust their reproductive timing in response to such unpredictable changes, to the extent where they can lose reproductive seasonality entirely, and unlike species relying on photoperiodic cues (Bradshaw & Holzapfel, 2007; Paul et al., 2008). Although baboons may be better able to deal with an increase of environmental unpredictability, their reproductive performances (birth rates, fertility, offspring and adult mortality) will nevertheless likely be altered by directional changes linked with global warming, such as a continuous increase in temperatures and in the frequency of droughts (S. E. Hill & Winder, 2019).

Consequences for understanding the evolution of non-seasonal breeding in Anthropoid primates including humans

Baboons and relatives represent a good model for understanding the evolution of behavioural and reproductive plasticity of early humans (J. Fischer et al., 2019) and in particular, the evolution of non-seasonal reproduction in this lineage. Although most great apes are nonseasonal breeders (Brockman & van Schaik, 2005b; Campos et al., 2017), suggesting that their common ancestor also bred year-round, humans are distinct from other apes by exhibiting much faster reproductive paces, and by living in a wider variety of environments, rather than being restricted to tropical forests (Wells & Stock, 2007). The selective pressures having shaped the reproductive phenology in the human lineage versus in other apes are therefore probably very different, and the taxonomic group studied here may provide valuable insights to understand the adaptation of early humans to diverse and unpredictable environments.

Indeed, our results suggest that, facing new highly unpredictable environments when expanding in African savannah environments, baboons may have evolved a variety of adaptations including low and flexible reproductive seasonality. Adaptations shared by baboons and early humans to keep reproducing at times of food scarcity include a generalist omnivorous diet and the frequent use of fallback food (Alberts et al., 2005; S. A. Altmann, 2009), a well-buffered social system (Brockman, 2005; J. Fischer et al., 2019), an increased ability to store fat (J. Altmann et al., 1993; Emery Thompson, 2013), or an ability to switch their home ranges to more suitable areas (Alberts et al., 2005). Here, we found that environmental unpredictability was the only environmental predictor of the intensity of seasonal breeding in baboons, and that equatorial forests (Gashaka, Lékédi and Moukalaba) tend to be just as seasonal as other environments, but more predictable (at least nowadays). Previous authors proposed that the transition from rainy forests to savannahs was associated to an increase in environmental seasonality, which favoured the evolution of reproductive flexibility (Brockman, 2005). Instead, our study suggests that the increased environmental unpredictability associated with such transition may have driven the evolution of low reproductive seasonality in baboons. Similar adaptations to environmental unpredictability may have allowed early humans to thrive and maintain fast reproductive paces during their colonization of a wide variety of environments.

Conclusion

Our work revealed substantial variation in patterns of reproductive seasonality across species of large African terrestrial monkeys, and unprecedented variation within species, highlighting an exceptional flexibility in their reproductive phenology. We further show that among multiple dimensions of climatic seasonality, rainfall unpredictability is the only successful predictor of the intensity of reproductive seasonality, with important year-to-year variations in rainfall

leading to the loss of seasonal reproduction. Patterns of breeding phenology are similarly diverse and flexible across those populations that breed seasonally, suggesting that they can match various reproductive stages with the annual food peak, perhaps due to demographic, life-history or social heterogeneities. This study sheds new light on the selective pressures shaping reproductive seasonality in long-lived tropical mammals, by revealing the key influence of climatic unpredictability in favouring a flexible reproductive seasonality. Given the phylogenetic ties and the striking life-history and ecological convergences of our taxonomic group with early humans, it also provides an original contribution to our understanding of why humans are non-seasonal breeders.

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FIGURES



Figure 1: Distribution of the studied species in Africa, and locations of the populations considered in this study

1: Lékédi. 2: Moukalaba-Doudou. 3: Gashaka-Gumti. 4: Gilgil. 5: Queen Elizabeth. 6: Amboseli. 7: Mikumi. 8: Tana River. 9: Awash. 10: Kasanka. 11: De Hoop. 12: Drakensberg. 13: Moremi. 14: Tokai. 15: Tsaobis. 16: Simien. The species distributions and images come from Julia Fischer et al., 2017; Kingdon et al., 2012. The equator is represented with a full blue line, while the tropics are represented with dashed blue lines.



Figure 2: Monthly distribution of births in relation with rainfall and NDVI seasonalities

The proportion of births per month (left side of the y-axis) is represented with red bars. In addition, the darker red bar indicates the month for which the mean birth date (μ_{birth}) occurs for seasonal breeding populations. We indicated in darker red the value of the r-vector length (R) for each population (top-left corner of each panel). We represent the mean monthly rainfall (equalled to K + Rainfall S, in mm) in blue (right side of the y-axis), and the mean monthly NDVI (equalled to KNDVI + NDVI S divided by 2 for graphical purposes) in green (left-side of the y-axis). The species' and population' names are indicated on top of each panel, along with the number of births observed (N).

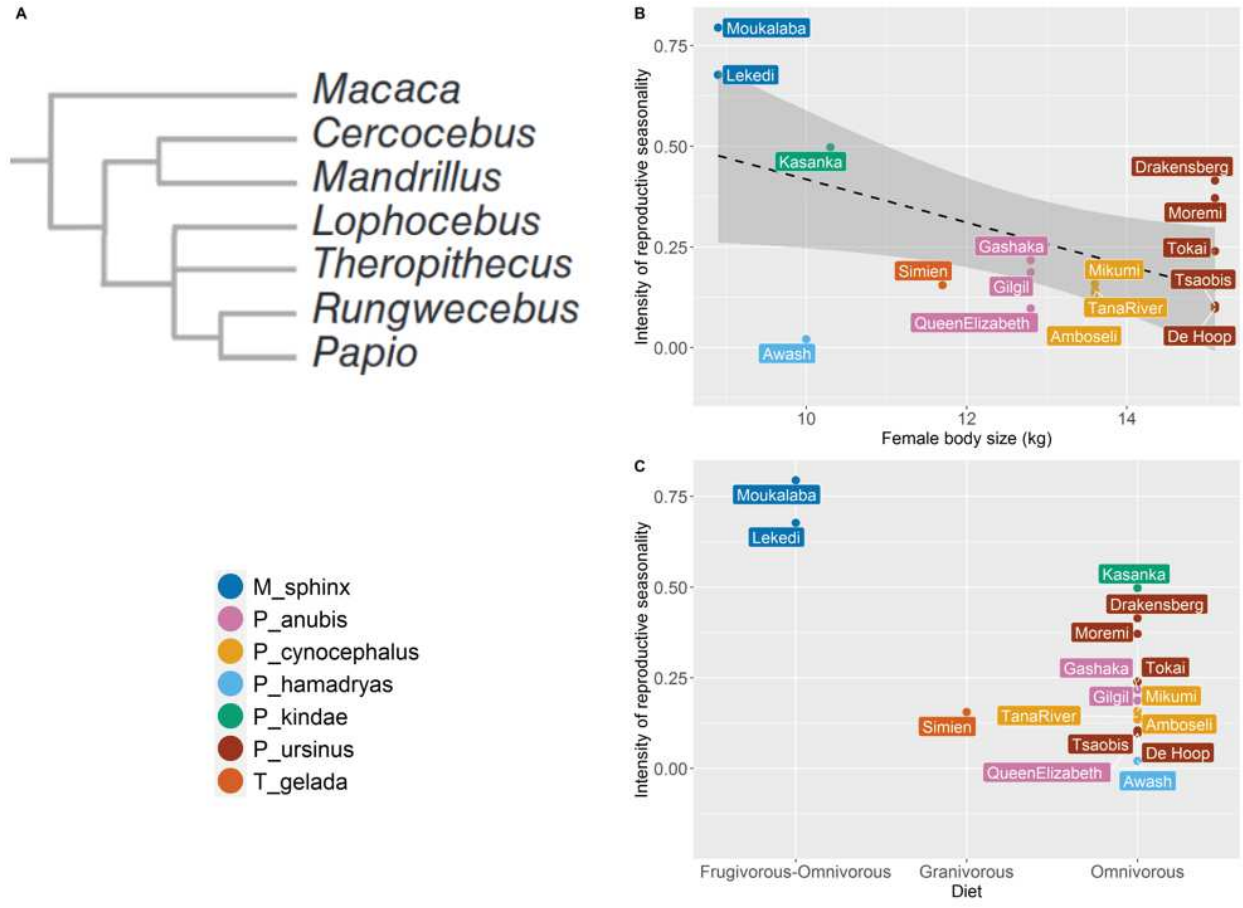


Figure 3: The atypical case of mandrills

Panel A: phylogeny of the *Papionini* tribe (from: Roos & Zinner, 2017). Panel B: intensity of reproductive seasonality (R) in relation to female mean body size (per species, in kg). The dashed black line represents the linear regression, and the shaded area around it displays 95% confidence intervals. Panel C: intensity of reproductive seasonality (R) in relation to diet. For Panels B and C, each point represents one population (annotated with the name of the population), and the colour indicates the species (see legend at the bottom left).

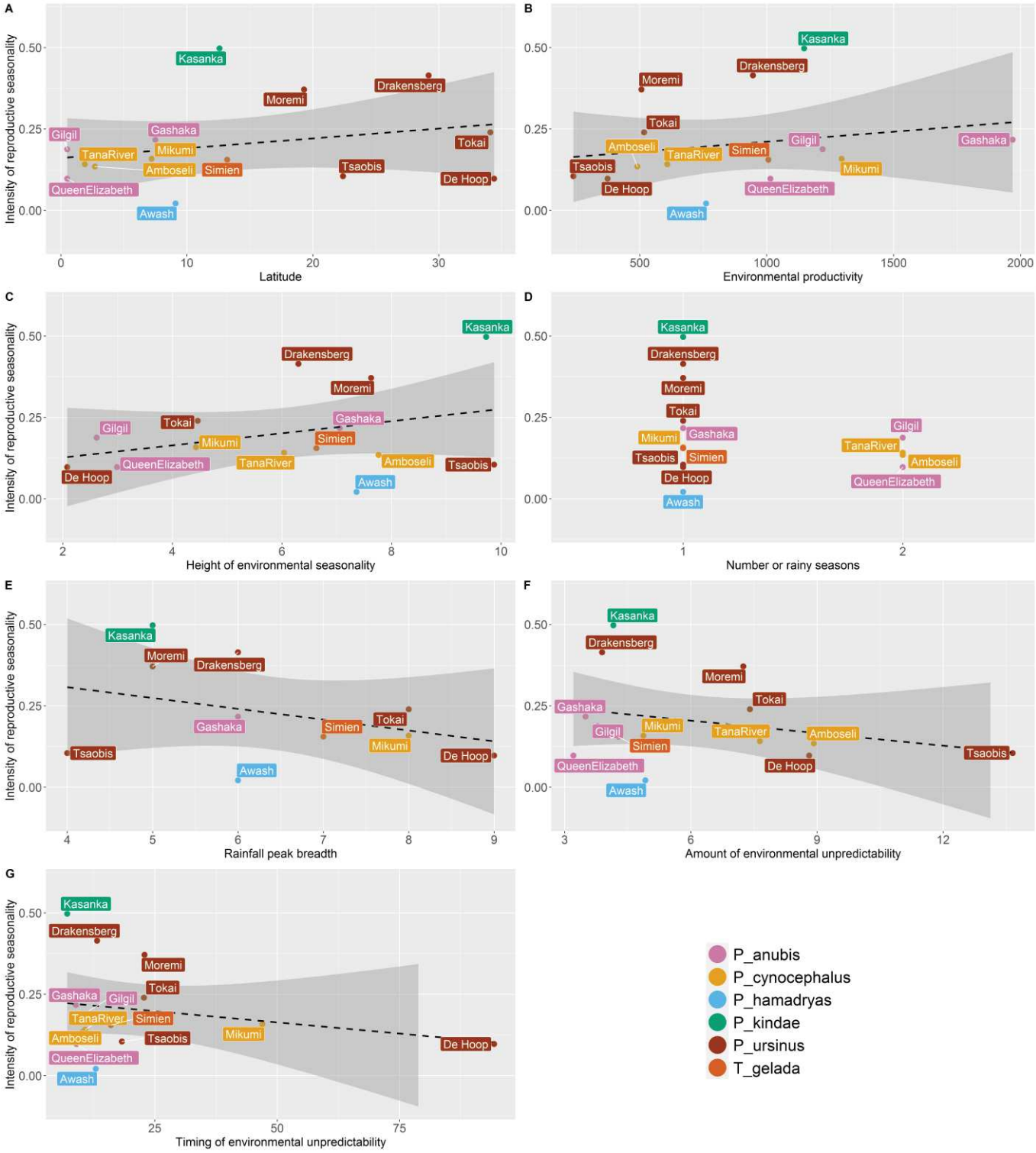


Figure 4: Effects of environmental variations on the intensity of reproductive seasonality

We plotted the intensity of reproductive seasonality (R) depending on latitude (Panel A), mean annual rainfall (in mm, Panel B), the intensity of variation in the seasonal component of rainfall (Panel C), the number of rainy seasons (Panel D), the rainfall peak breadth (RPB, Panel E), the intensity of variation in the non-seasonal component of rainfall (Panel F) and the between-year variation in rainfall timings (Panel G). For each panel, one point represents a population (with the population name annotated), and the colour indicates the species (see legend at the bottom). The dashed black line represents the linear regression, and the shaded area around it displays 95% confidence interval.

TABLES

Table 1: Main predictions about the effects of various environmental components on the intensity of reproductive seasonality (R)

Predictor		Description	Prediction	Results
Latitude		Latitude, in degrees	When latitude increases, R increases	No
Environmental productivity		Mean annual rainfall ($12*K_{rain}$)	When environmental productivity increases, R decreases	Yes (opposite effect)
Environmental seasonality	Height of rainfall peak	Relative standard deviation of the seasonal component of rainfall (Rainfall S)	When the amount of within-year rainfall variation increase, R increases	No
	Modality of annual rainfall distribution	Number of rainy seasons (1 or 2)	When there is more than one rainy season, R decreases	No
	Breadth of the annual rainy season (broadness)	Rainfall peak breadth (RPB): minimum number of consecutive months with >80% of annual rainfall (only for environments with one rainy season)	When RPB increases, R decreases	No
Environmental unpredictability	Amount	Relative standard deviation of the non-seasonal component of rainfall (Rainfall NS)	When the amount of rainfall unpredictability (between-year variation) increases, R decreases	Yes
	Timing	Standard deviation of the yearly mean rainfall dates (or the average of the two standard deviations of mean rainfall dates per semester for bimodal environments)	When the level of rainfall unpredictability in term of timing increases, R decreases	Marginal effect

R refers here to the r-vector length, i.e. to the intensity of reproductive seasonality

Table 2: Birth seasonality of the populations considered in this study

Species	Population	N	R	P-value (Rayleigh)	Seasonal breeding?	BPB 80 (months)	BPB 50 (months)	μ_{birth}	References
Mandrillus sphinx	Lekedi	218	0.6766	$<10^{-5}$	Seasonal	5	2	1-Jan	personal data
	Moukalaba-Doudou	208	0.7940	$<10^{-5}$	Seasonal	3	2	8-Jan	Hongo et al. 2016
Papio anubis	Gashaka-Gumti	32	0.2167	0.2237	Non-seasonal	8	4	17-Dec	Higham et al. 2009
	Gilgil	118	0.1873	0.0159	Seasonal	9	5	23-Feb	Bercovitch & Harding 1993
	Queen Elizabeth	35	0.0971	0.7216	Non-seasonal	9	5	17-Jan	Rowell 1966
Papio cynocephalus	Amboseli	496	0.1344	0.0001	Seasonal	9	6	12-Oct	Alberts et al. 2005
	Mikumi	164	0.1584	0.0163	Seasonal	9+	6+	24-Jul	Rhine et al. 1988
	Tana River	35	0.1413	0.5004	Non-seasonal	9	6	25-Nov	Bentley-Condit & Smith 1997
Papio hamadryas	Awash	218	0.0208	0.9097	Non-seasonal	10	6	21-Jun	personal data
Papio kindae	Kasanka	70	0.4971	$<10^{-5}$	Seasonal	6	4	16-Jul	Petersdorf et al. 2019
Papio ursinus	De Hoop	30	0.0969	0.7574	Non-seasonal	9	5	20-Oct	Barrett et al. 2006

	Drakensberg	37	0.4143	0.0014	Seasonal	6	4	23-Nov	Lycett et al. 1999
	Moremi	122	0.3710	$<10^{-5}$	Seasonal	7	4	27-Sep	Cheney et al. 2004
	Tokai	52	0.2394	0.0507	Non-seasonal	8	5	21-Dec	personal data
	Tsaobis	215	0.1046	0.0949	Non-seasonal	9	5	18-Nov	personal data
Theropithecus gelada	Simien	354	0.1550	0.0002	Seasonal	9	5	8-Oct	Tinsley Johnson et al. 2018

[+] Approximated birth peak breadths for Mikumi, given that the number of births was only provided per 3 months-period (not per month)

Table 3: Components of environmental variation per population

Species	Population	Latitude (°)	Mean annual rainfall (mm)	Height of rainfall seasonality	Number of rainy season(s)	Rainfall peak breadth (months)	Amount of rainfall unpredictability	Timing of rainfall unpredictability (days)	μ_{rain}	μ_{NDVI}
Mandrillus sphinx	Lekedi	1.8	1913	4.96	1	7	3.17	12.16	12-janv	11-Apr
	Moukalaba-Doudou	2.5	1482	6.26	1	6	3.76	13.37	20-janv	30-Mar
Papio anubis	Gashaka-Gumti	7.5	1969	7.06	1	6	3.50	8.88	31-juil	5-Aug
	Gilgil	0.5	1220	2.62	2	NA	3.79	10.29	29-Apr	23-Jun
	Queen Elizabeth	0.5	1015	2.99	2	NA	3.21	9.00	06-nov	8-Dec
Papio cynocephalus	Amboseli	2.7	490	7.77	2	NA	8.93	10.29	31-janv	14-Mar

	Mikumi	7.2	1296	4.43	1	8	4.87	46.98	25-Feb	13-Apr
	Tana River	1.9	608	6.04	2	NA	7.64	10.78	12-janv	4-Mar
Papio hamadryas	Awash	9.05	762	7.36	1	6	4.92	12.95	22-juil	23-Aug
Papio kindae	Kasanka	12.6	1148	9.73	1	5	4.16	7.11	19-janv	26-Feb
Papio ursinus	De Hoop	34.4	373	2.08	1	9	8.82	94.32	17-juin	29-May
	Drakensberg	29.2	946	6.30	1	6	3.89	13.22	12-janv	5-Feb
	Moremi	19.3	507	7.63	1	5	7.25	22.91	26-janv	20-Feb
	Tokai	34.1	517	4.46	1	8	7.41	22.79	05-juil	22-Jun
	Tsaobis	22.4	239	9.87	1	4	13.65	18.29	19-Feb	9-Apr
Theropithecus gelada	Simien	13.2	1007	6.63	1	7	4.28	16.03	24-juil	23-Aug

Table 4: Influence of several components of rainfall variation on the reproductive seasonality of *Papio* and *Theropithecus* populations

The table shows the estimates, 95% confidence intervals (CI), X^2 statistics and P-values of the predictors of the LMMs including species as random effect, R as response variable (the r-vector length), and each predictor as the only fixed effect of a univariate model. The two *Mandrillus* populations have been discarded from these models (see Table S2). Significant effects are indicated in bold. For the 'number of rainy seasons' predictor, the tested category is indicated between parentheses.

Predictor	Estimate	CI		X^2	P-value
		lower	upper		
Latitude	-0.002	-0.131	0.126	0.001	0.969
Habitat productivity	**0.074**	**0.007**	**0.142**	**4.649**	**0.031**
Height of environmental seasonality	0.031	-0.034	0.095	0.885	0.347
Number or rainy seasons (2)	-0.056	-0.219	0.107	0.454	0.500
Rainfall peak breadth	-0.039	-0.127	0.049	0.765	0.382
Amount of environmental unpredictability	**-0.084**	**-0.136**	**0.031**	**9.708**	**0.002**
Timing of environmental unpredictability	-0.046	-0.110	0.018	1.971	0.160

Table 5: Reproductive timings in relation with food availability seasonality

For each seasonal breeding populations, we indicated the statistics and P-values of the Fisher-Pitman permutation test (Z test) investigating if there is more NDVI (our proxy of food availability) than random during different stages of female reproductive cycle, predicting that either conceptions (H1) or lactation (H2) would match the annual food peak. For the conception hypothesis (H1), we looked at the NDVI values either around the mean conception dates ('Conception' column: three months before and after μ_{conc}), before the mean conception dates ('Before conception' column: three months before μ_{conc}), or after the mean conception dates ('After conception' column: three months after μ_{conc}). For the lactation hypothesis (H2), we looked at NDVI values either six months after births ('Lactation' column: six months after μ_{birth}), the three months after births ('Early lactation' column: three months after μ_{birth}), or from three to six months after births ('Mid lactation' column: three to six months after μ_{birth}). Significant effects are indicated in bold. In addition, we indicated the deviation, in months, between the mean conception date (μ_{conc}) and the mean NDVI date (μ_{NDVI}), and between the mean NDVI date (μ_{NDVI}) and the mean birth date (μ_{birth}).

Species	Population	Conception hypothesis							Lactation hypothesis						
		Conception		Before conception		After conception		μ_{conc}-μ_{NDVI} (month)	Lactation		Early lactation		Mid lactation		μ_{NDVI}-μ_{birth} (month)
		Z test	P-value	Z test	P-value	Z test	P-value		Z test	P-value	Z test	P-value	Z test	P-value	
Mandrillus sphinx	Lekedi	-0,616	0,277	**-1,772**	**0,032**	1,061	0,841	2,93	**-2,432**	**0,005**	-1,036	0,173	**-1,772**	**0,032**	3,32
	Moukalaba	1,585	0,947	-1,081	0,177	2,911	1,000	3,55	**-2,405**	**0,006**	-1,474	0,064	-1,304	0,114	2,70
Papio anubis	Gilgil	-0,514	0,314	-0,994	0,186	0,400	0,627	2,10	-1,382	0,089	-0,602	0,286	-0,994	0,186	3,98
Papio cynocephalus	Amboseli	-1,616	0,056	**-1,701**	**0,050**	-0,164	0,459	1,12	-0,439	0,334	0,743	0,768	-1,250	0,109	5,03
	Mikumi	-0,744	0,242	0,599	0,732	-1,458	0,077	-2,50	2,635	0,999	2,443	0,996	0,599	0,732	8,65
Papio kinda	Kasanka	**-2,707**	**0,002**	-1,030	0,168	**-2,096**	**0,005**	-1,28	1,419	0,920	2,669	1,000	-1,030	0,168	7,36
Papio ursinus	Drakensberg	1,209	0,881	-0,897	0,177	2,294	0,996	3,35	**-2,694**	**0,002**	**-2,213**	**0,009**	-0,897	0,177	2,40

	Moremi	**-2,312**	**0,012**	**-2,649**	**0,005**	-0,021	0,468	1,25	**-1,838**	**0,031**	0,528	0,691	**-2,649**	**0,005**	4,77
Theropitethecus gelada	Simien	2,291	0,994	2,201	1,000	0,445	0,677	-4,50	1,922	0,974	0,019	0,482	2,201	1,000	-1,51

SUPPLEMENTAL INFORMATION

Table S1: Location, mean female body size, diet and mean gestation duration per population.

Species	Population	Country	GPS coordinates (West,South, East,North)	Female body size[1] (kg)	Diet [2]	Gestation[3] (days)	References
Mandrillus sphinx	Lekedi	Gabon	13.03, -1.81, 13.04, -1.80	8.9	Frugivorous-Omnivorous	175	personal data
	Moukalaba-Doudou	Gabon	10.24,-2.60, 10.35,-2.50	8.9	Frugivorous-Omnivorous	175*	
Papio anubis	Gashaka-Gumti	Nigeria	11.58,7.51, 11.66,7.56	12.8	Omnivorous	185	
	Gilgil	Kenya	36.23,-0.61, 36.45, -0.48	12.8	Omnivorous	180	
	Queen Elizabeth	Uganda	29.70, -0.57, 29.80, -0.47	12.8	Omnivorous	180*	
Papio cynocephalus	Amboseli	Kenya	37.27, -2.71, 37.32, -2.62	13.6	Omnivorous	178	
	Mikumi	Tanzania	37.37, -7.29, 37.49, -7.19	13.6	Omnivorous	178*	
	Tana River	Kenya	40.13, -1.94, 40.13, -1.93	13.6	Omnivorous	182	

Papio hamadryas	Awash	Ethiopia	39.96, 9.00, 40.07, 9.12	10.0	Omnivorous	182	Swedell 2011
Papio kindae	Kasanka	Zambia	30.21,-12.58, 30.22,-12.55	10.3	Omnivorous	178*	Rogers et al. 2019
Papio ursinus	De Hoop	South Africa	20.52,-34.45, 20.60,-34.39	15.1	Omnivorous	190	Weingrill et al. 2004
	Drakensberg	South Africa	29.44,-29.28, 29.54, -29.15	15.1	Omnivorous	190*	
	Moremi	Botswana	22.86, -19.42, 23.01, -19.27	15.1	Omnivorous	183	Cheney et al. 2004
	Tokai	South Africa	18.39, -34.08, 18.43, -34.05	15.1	Omnivorous	190*	
	Tsaobis	Namibia	15.67, -22.46, 15.88, -22.30	15.1	Omnivorous	190	personal data
Theropithecus gelada	Simien	Ethiopia	38.31, 13.20, 38.42, 13.28	11.7	Granivorous	183	

[1] data coming from Kingdon 2012 (except for kinda baboons, see reference column)

[2] data coming from Swedell 2011

[3] data coming from Roberts et al. 2017 (or see references column)

* Mean gestation length was not available for these populations. So, we used mean gestation length of other population of the same species with the highest sample size. We considered that the gestation length of kinda baboons was similar to the ones of yellow baboons.

Table S2: Influence of several components of environmental variation on the intensity reproductive seasonality

The table shows the estimates, 95% confidence intervals (CI), X^2 statistics and P-values of the predictors of the LMMs including species as random effect, R as response variable (the r-vector length), and one predictor at a time (fitted as the only fixed effect). These models are similar to the ones presented in Table 4, except that they also include the two mandrill populations. Significant effects are indicated in bold. For the 'number of rainy seasons' predictor, the tested category is indicated between parentheses.

Predictor	Estimate	95% CI		X^2	P-value
		lower	upper		
Latitude	-0.036	-0.174	0.101	0.268	0.604
Habitat productivity	**0.084**	**0.005**	**0.162**	**4.386**	**0.036**
Height of environmental seasonality	0.024	-0.037	0.084	0.024	0.772
Number or rainy seasons (2)	-0.060	-0.227	0.106	0.505	0.477
Rainfall peak breadth	-0.033	-0.112	0.046	0.669	0.413
Amount of environmental unpredictability	**-0.084**	**-0.138**	**-0.031**	**9.34**	**0.002**
Timing of environmental unpredictability	-0.045	-0.097	0.007	2.834	0.092

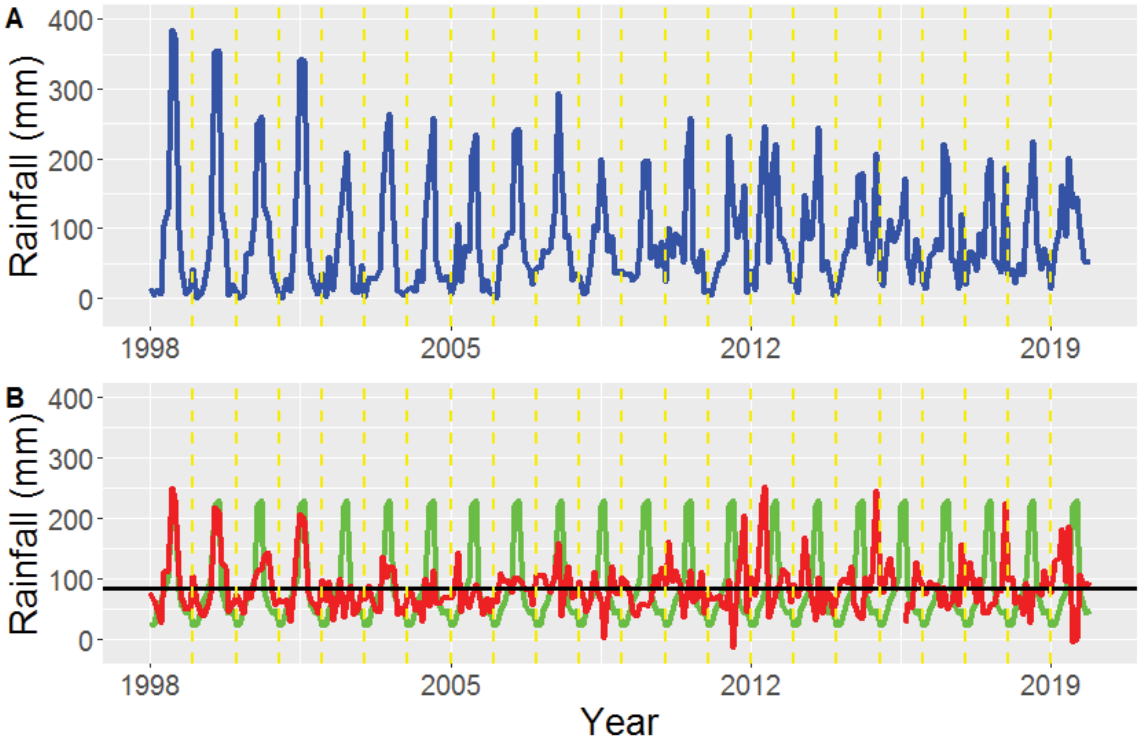
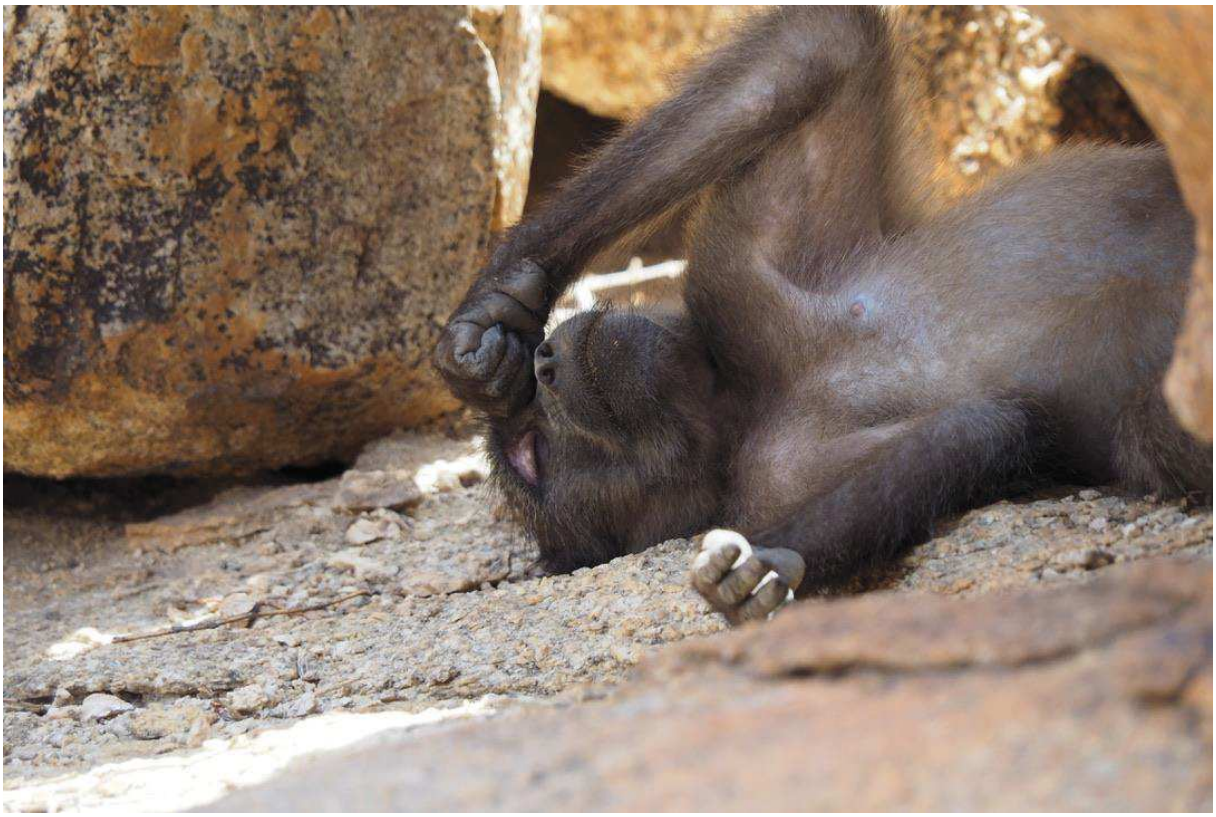


Figure S1: Example of rainfall variation decomposition

We represented in Panel A the average monthly cumulative rainfall (raw data, in mm) recorded at Simien National Park (example from the gelada population) over 22 years (from January 1998 to December 2019) in blue. In Panel B, the black horizontal line indicates the mean monthly rainfall (K_{rain}), the green curve represents the predictable (seasonal, i.e. repeatable pattern between years) rainfall variation (K_{rain} + Rainfall S), and the red curve represents the unpredictable (between-year) rainfall variation (K_{rain} + Rainfall NS) over 22 years of records.

GENERAL DISCUSSION



This manuscript sheds light on the evolutionary determinants of reproductive seasonality. Indeed, this study highlights both ecological and social determinants of the intensity of reproductive seasonality, considering various components of mothers' and offspring' fitness. It also brings new evidence on the optimal strategies of breeding phenology, and in particular on which phase of the reproductive cycle (pregnancy, lactation, weaning) should be synchronized with the seasonal food peak in order to maximise either offspring survival, early development, or maternal reproductive pace. This work therefore helps us understanding the apparent paradoxical reproductive seasonalities of two tropical, long-lived and social primate populations, chacma baboons and mandrills.

In this section, I will first discuss the consequences of reproductive seasonality (birth timing and synchrony) found in our two studied populations, on offspring development, mother-offspring relationship, and on both mother and offspring fitness. I will then explain how this work contributes to a better understanding on the reproductive phenology of long-lived tropical mammals. Finally, I will discuss the main determinants of the intensity of reproductive seasonality, with a particular interest to environmental variation, life history and sociality. Lastly, I suggest new avenues and perspectives arising from this manuscript.

I°) Developmental, behavioural, and fitness consequences of birth timing

A- Consequences of reproductive seasonality on offspring development

First, our study on infant baboon coloration (Chapter 2) emphasizes the importance of food availability during pregnancy for offspring early growth and development, looking at the colour transition of infant baboons, from pink skin and black fur when born, to grey skin and fur when eight months old and older. Even if we did not find any direct effect of seasonal birth timing when controlling for food availability during pregnancy on infant coloration, our results suggest that the timing of pregnancy can affect offspring development. Such finding confirms several lines of evidence showing the benefits of good maternal condition during prenatal life on offspring early growth and survival (Emery Thompson, 2013; Martorell & Gonzalez-Cossio, 1987). Therefore, matching pregnancy with periods of food abundance could be adaptive for species able to store energy, by maximising maternal condition at birth, and so early-lactation. However, coloration transition can be influenced by other factors (like infanticide risk: Bădescu et al., 2016) that may not affect other aspects of infant development, such as growth rates. Therefore, we would need to determine the correlation between infant coloration and other developmental milestones like weaning age, to confirm the evolutionary significance of matching pregnancy with the seasonal food peak (see Chapter 2).

During this PhD, I also ran preliminary analyses that are not presented in this manuscript, and which looked at the influence of birth timing on various other indicators of offspring development, including weight (using trapping data) and feeding efficiency (using observational data on the number of bites per minute on a given food item) in chacma baboons.

While weight-for-age was unaffected by birth timing, it appears that feeding efficiency was: infants born at certain times of the year had higher feeding efficiency than others, i.e. fed on certain berries at higher rates (controlling for their age and for the season of observation). Further analyses would be needed to better understand such results, but our dataset was limited in sample size. It is likely that birth timing affects various aspects of infant development, and that the timing of weaning in relation to seasonal variation in food availability is critical for infant development (J. Altmann, 1980). In addition, birth synchrony (i.e. being born in a large cohort of infants) could also affect social development: for example, infants born in large cohorts would have faster social development and would be better socially integrated within the group than the ones born in asynchrony. Indeed, infants born in synchrony would have more conspecifics with the same age, and might be half-paternal siblings, which may both enhance the frequencies of social plays and other social interactions between them (Lynch, Di Fiore, Lynch, & Palombit, 2017). However, there are few empirical data investigating such associations (Ims, 1990), and I aim to investigate the effect of birth timing and synchrony on various developmental indicators in the future.

B- Consequences of reproductive seasonality on mother-offspring relationships

i. Maternal care buffers environmental seasonality

In baboons, mothers increase their level of care during the lean season (Chapter 3). Similar results were found in the mandrill populations (looking at suckling frequencies), but have been later discarded from Chapter 5 (in order to submit this article). Given their large relative size, and their ability to store more energy, mothers in most species are presumably less vulnerable

to food shortage than weanlings, who have higher relative energy expenditure due to growth and faster metabolism, as well as lower experience at extracting solid food, especially during droughts. This strategy represents another adaptation (than seasonal reproduction) to environmental seasonality, and might be common in primates (van Noordwijk, 2012). Indeed, wild female primates, including baboons, had been showed to increase the time spend foraging in their activity budget during both lactation and during the harsh season (Alberts et al., 2005; Barrett et al., 2006; Muruthi, Altmann, & Altmann, 1991; van Noordwijk, 2012). It suggests that lactating females may in general attempt to increase (or at least stabilize) their energy intake during the lean season, in order to increase the care for their offspring. Such a strategy could enhance non-seasonal reproduction, or at least promote the ability to breed-year round (which is the case in our two populations).

In both study populations, mothers did not adjust their maternal care depending on their infant's birth timing, meaning that they increase maternal care during the lean season regardless of their infant's age. The main difference between the two populations is that this strategy was sufficient to buffer the adverse consequences of environmental seasonality on offspring mortality in mandrills, but not in baboons (Chapter 3). The absence of maternal care adjustments for offspring born in suboptimal timings (late in the birth season) was also found in the seasonal breeding bighorn sheep (Whiting, Stewart, Bowyer, & Flinders, 2010), leading to higher offspring mortality (for males only) (Feder et al., 2008). Investigating how mothers adjust care in relation to season and their offspring's birth timing can help us to understand the fitness consequences of reproductive seasonality. Indeed, the level of maternal care adjustments according to environmental seasonality and/or birth timing can modulate the intensity of reproductive seasonality.

ii. Seasonal birth timing and mother-infant conflict

We use tantrum frequencies to quantify the consequences of seasonal birth timing on mother-infant relationships during weaning (Chapter 3). Indeed, tantrums represent a typical primate behavioural manifestation of mother-infant conflicts (Maestripieri, 2002) and indicate a mismatch between the actual maternal care provided and the optimal level of care needed in the infant perspective. This work brings new results in the relatively limited literature investigating (i) the temporal evolution of mother-infant conflicts during weaning, and (ii) the main factors affecting inter-individual variations in the intensity of such conflicts.

First, it has previously been shown that tantrums usually peak when mothers resume cycling in several macaque populations (Berman, Rasmussen, & Suomi, 1993; Gomendio, 1991; Gore, 1986; Worlein, Eaton, Johnson, & Glick, 1988). It is not the case in our studied populations, as tantrum frequencies peak when infants are around 5-8 months old in baboons (while cycle resumption occurs around 12 months on average). It seems that **tantrum frequencies are maximal during the onset of weaning**, i.e. when maternal rejection rates increase as infant's independent feeding also increase (Barrett & Henzi, 2000; Collinge, 1987).

Second, we found that the intensity of mother-infant conflict was strongly driven by birth timing in baboons, with **higher level of tantrums for infants born 'early', i.e. before the population birth peak** (baboons are non-seasonal breeders and the peak refers here only to the highest frequency of births in the annual cycle). A similar pattern was found in the seasonal breeding rhesus macaque (*Macaca mulatta*), where early-born infants show higher rates of distressed behaviours than late-born infants (Vandeleest & Capitanio, 2012). Why do early births maximise mother-infant conflict? In baboons, females giving birth early exhibit shorter IBI and higher offspring mortality. Such timing matches late weaning with the dry season, generating stress for the infants who react by throwing more tantrums (Chapter 3). Such

finding confirms various studies that have shown an increase of tantrum behaviours when mothers exhibit relatively short post-partum amenorrhea or subsequent interbirth intervals, in humans (Fouts, Hewlett, & Lamb, 2005) and vervet monkeys (*Cercopithecus aethiops*) (Hauser & Fairbanks, 1988).

Our work further showed that birth timing and infant's age both affect tantrum frequencies, but not environmental seasonality. The level of tantrum has been found to increase during periods of food scarcity in wild populations of chacma baboons (Barrett & Henzi, 2000), or in populations with relatively lower level food quality in vervet monkeys (Hauser & Fairbanks, 1988). Here, we suggest that **birth timing can mediate the adverse effects of environmental seasonality on mother-infant conflictual relationships**. Indeed, our results suggest that infants would throw more tantrums only when they are weaned, and/or when their mothers resume cycling, during the wrong harsh season. Barrett & Henzi (2000) found in the only other study looking at baboon tantrum frequencies that only 3 infants out of 10 displayed such behaviour, exclusively during the dry harsh season. We suppose that these three infants were actually born in suboptimal birth timings. While few previous studies have investigated the sources of inter-individual variations in the level of tantrums (but see: Vandeleest & Capitanio, 2012), our work finds support for a major role of birth timing, supporting the idea that tantrums are signals of infant needs, requesting more investment from its mother (Barrett & Henzi, 2000). Such finding may also apply to several other primate populations living in wild habitat with seasonal fluctuations in food availability. Further studies would however be needed to better understand the evolution of tantrum behaviours, by quantifying the correlation between infant condition and tantrum frequencies for instance.

Taken together, our results suggest that females may be able to compensate, via increased maternal care, for the lean season during most stages of lactation, except when late-weaning occurred during the lean season, certainly because females may have already recycled,

i.e. restarted their subsequent reproduction at this stage. Consequently, infants respond to such limitations by throwing more tantrums. Looking at both suckling and tantrum frequencies, i.e. at actual maternal investment versus offspring requests on their mother, can thus shed light on the maternal physiological limits during lactation, in relation with environmental variation. Our work calls for observational and comparative studies investigating the main determinants of variation in tantrum frequencies, as important between-individual and -population variations seem to exist, along with their consequences on maternal reproduction and offspring condition and survival (Barrett & Henzi, 2000; Hauser & Fairbanks, 1988; John E. Lycett, Henzi, & Barrett, 1998; Maestripieri, 2002).

C- Fitness consequences of birth timing

We found several fitness consequences, on both offspring and mothers, of birth timing through this work. First, birth synchrony was associated with fitness costs for mother baboons: when giving birth in synchrony, subordinate females had longer IBIs, i.e. slower reproductive pace. This finding thus confirms several evidence from numerous social species (see introduction) that the timing of birth in relation with timings of other females within the same group, and not necessarily in relation with season, can have strong fitness consequences. However, this is the first empirical evidence of fitness costs associated with reproductive synchrony on a wild primate (but see costs on offspring survival for captive macaques: Silk, 1989) .

In both populations, we further showed that births timing adjusting the **peak of lactation** (around 2-3 months after birth in mandrills, versus 5-6 months in chacma baboons) with the seasonal food peak also **accelerate maternal reproductive pace** (Chapter 3 & 5). Indeed, the peak of lactation is the energetically costliest phase of the reproductive cycle. Adjusting this phase with the seasonal food peak may therefore contribute to alleviate the costs of lactation

and enhance maternal condition during the second half of lactation. In addition, the onset of weaning typically coincides with the peak of lactation, and matching it with abundant resources can contribute to hasten the transition to feeding independence by granting infants access to an optimal amount of weaning foods (J. Altmann, 1980). Both earlier weaning and better maternal nutritional condition are likely to enhance cycle resumption (P. C. Lee, 1987; P. C. Lee, Majluf, & Gordon, 1991; Saltzman, Tardif, & Rutherford, 2011), and explain the benefits of such reproductive phenology on maternal reproductive pace. This pattern is likely to be generalized in numerous, if not all, mammalian species, and it has often been argued that species must time lactation peak with the best season of the year (F. H. Bronson, 2009; Franklin H. Bronson & Heideman, 1994; Carnegie et al., 2011). In fast-lived mammalian species, when lactation is shorter than, or approximately equal to, the length of the good season, lactation is expected to occur within the seasonal food peak.

However, our study on chacma baboons (Chapter 3) provides evidence that for long-lived species, with lactation duration extending beyond the length of the good season, synchronizing the peak of lactation with the seasonal food peak would not systematically **maximise offspring survival**. Indeed, **late-weaning**, occurring a few months after the lactation peak, is the period when primate infant vulnerability is maximal as they must learn how to ensure their own provisioning (J. Altmann, 1980; Janson & Verdolin, 2005; Rhine, Wasser, & Norton, 1988; van Schaik & van Noordwijk, 1985). As such, mothers may preferentially match late weaning with the seasonal food peak in order to enhance offspring survival. Our study on mandrills further suggests that some species and populations may have evolved other adaptations than seasonal reproduction (such as an ability for pregnant mothers to keep nursing infants that are not fully weaned even during the lean season, or to extend lactation for offspring that are born in suboptimal timings) to ensure the survival of their offspring during late-weaning. Nonetheless, in mandrills, we found another fitness costs on current reproduction:

females conceiving outside the mating season were more likely to abort than the ones conceiving within the mating season.

These various fitness consequences associated with distinct birth timing raise the question of which phase of their reproductive cycle females chose to time with the seasonal food peak, and what are the factors likely to affect variation in strategies of breeding phenology.

II°) Evolutionary determinants of reproductive phenology: why giving birth in such timing?

In long-lived species with a relatively long reproductive cycle (from conception to weaning), females cannot squeeze the full development of their offspring within the same seasonal food peak. They consequently need to match specific stage(s) of their cycle with seasonal food peak(s). We found associations between several fitness measures and birth timing (see I-C), which bring new insights on the selective pressures shaping reproductive phenology. More precisely, this work shows that females can match with the seasonal food peak either (i) pregnancy in order to enhance their offspring early-life development, (ii) lactation peak in order to enhance their reproductive pace and condition, or (iii) late weaning in order to enhance their offspring survival.

First, our study on infant baboon coloration (Chapter 2) emphasizes the importance of pregnancy on offspring early-life development. However, pregnancy is not the energetically costliest phase of the reproductive cycle for female primates (as for most mammalian species) (Emery Thompson, 2013; P. C. Lee, 1996). Consequently, timing the onset of pregnancy with the seasonal food peak might only be a proximate consequence of a reproductive physiology

controlled by a condition threshold, where females can only onset their reproduction after an increase in their energy balance, i.e. after an increase of food availability (Brockman & van Schaik, 2005a). A such, **the overall quantity of food available in the environment might be a major factor to understand the timings of conception and pregnancy**: in poor habitats, pregnancy might be more likely to happen soon after or during the seasonal food peak; whereas in rich habitats, conception timing may be more flexible, and females might strategically adjust other phases of their reproductive cycles with the seasonal food peak. Such hypothesis is supported in our two study populations (Chapter 4 & 5), although we failed to detect the same pattern with the preliminary results of the comparative analysis from 16 wild populations of *Papio*, gelada and mandrills (Chapter 6). Baboons, in the broad sense (Bergman, Haile, & Beehner, 2018), may have specific features (diet flexibility, fall-back food, large size) enhancing their ability to onset their reproduction and conceive year-round, and as such, conceptions tended not to be adjusted to environmental seasonality. However, a broader comparative analysis investigating the effects of habitat quality on the timing of conception in relation with environmental seasonality should be conducted to confirm whether this pattern is found in other species from other taxa. If not conceptions, species may strategically match another stage of their reproductive cycle with the seasonal food peak in order to enhance both maternal and offspring fitness.

Indeed, in both studied population, we showed that timing the peak of lactation with the seasonal food peak accelerates maternal reproductive pace (Chapter 3 & 5). In fast-lived mammalian species, when lactation is shorter than, or approximately equal to, the length of the good season, lactation always occurs within the seasonal food peak (F. H. Bronson, 2009; Franklin H. Bronson & Heideman, 1994). Most long-lived mammals living in high latitudes (outside the tropics) also time lactation peak with the most productive season: such as most ungulate species (Côté & Festa-Bianchet, 2001; Holand et al., 2004; Rutberg, 1987; Zerbe et

al., 2012), or bears (Spady, Lindburg, & Durrant, 2007) for instance. Here, through our comparative analysis on various seasonal breeding populations of 'baboons', we found that in most cases, birth peak occurs a few month (between 0 and 5) before the peak of food availability (Chapter 6). This strategy is thus not specific to our two studied populations among 'baboons'.

However, this comparative analysis revealed that, even if lactation peak tends to be preferentially timed with the seasonal food peak, it is by no means the only strategy encountered. Indeed, a good example of the importance of weaning on the selective pressures affecting reproductive phenology has been provided by our population study on chacma baboons (Chapter 3). The moderate birth peak of this population tends to occur in between the birth timing maximising maternal current reproduction (late-weaning during the seasonal food peak) and future reproduction (lactation peak with the seasonal food peak). This is not specific to our population, as birth timing has been suggested to be selected to time weaning within the most productive seasonal in other baboon populations (J. Altmann, 1980; J.E. Lycett et al., 1999; Rhine et al., 1988), and most lemur species (Wright, 1999). In addition, in some human (V Lummaa, Lemmetyinen, Haukioja, & Pikkola, 1998) and baboon (Rhine et al., 1988) populations, the birth peak does not coincide with the birth timing maximising offspring survival, and such an apparent paradox suggest that the existence of reproductive trade-off over birth timing is common in long-lived species.

The critical question is thus now: what are the factors likely to explain which stage of her reproductive cycle a female would chose to time with the seasonal food peak? So far, only two theoretical frames attempted to hypothesize the main factors likely to affect variation in reproductive phenology: the capital-income model (Brockman & van Schaik, 2005a; Janson & Verdolin, 2005), and the classic versus alternative model (van Schaik & van Noordwijk, 1985). In these models developed for primates, species size, ability to store energy, and environmental predictability had been suggested to impact reproductive phenology strategies. Capital

breeders, i.e. species able to store energy, using endogenous cues to onset their reproduction, and of relatively large sizes, should time conception during or soon after an increase of food availability (Brockman & van Schaik, 2005a; Janson & Verdolin, 2005). Whereas income breeders, using external cues to control their reproduction (such as photoperiodic cues), and of relatively small size, should match mid-lactation (i.e. the peak of lactation) with the peak of food availability (Brockman & van Schaik, 2005a; Janson & Verdolin, 2005). In addition, it has been suggested that in predictable environments, species must time mid-lactation with the food peak ('classic' strategy), while in unpredictable environments, species must time conception with the food peak ('alternative' strategy) (van Schaik & van Noordwijk, 1985). However, and as developed in the introduction of this manuscript, these theoretical frameworks have received weak empirical supports, and several conceptual critics (Clauss et al., 2020; Lewis & Kappeler, 2005; Stephens et al., 2009). Our study on mandrills is another empirical evidence suggesting that the heuristic power of this model is limited: mandrills can be considered as capital breeders, albeit they time early-lactation, and not conception, with the seasonal peak of food availability. In addition, our comparative analysis do not bring any supports to these hypotheses (Chapter 6), as we revealed that (i) despite sharing comparable sizes and storage capacities, baboons and relatives use diverse reproductive phenology strategies, and that (ii), environmental predictability do not tend to explain the variation in birth timing in relation with environmental seasonality.

Taken together, our results on both populations suggest that overall habitat productivity can also be an important factor affecting strategies of breeding phenology, as it may modulate the strength of selective pressures during late weaning. Indeed, in harsh habitats, like at Tsaobis, females might time late-weaning with the most productive season, whereas in rich habitats, like in the Lékédi forest, females might time the peak of lactation with the most productive season. Similarly, in Madagascar, which is known to be an unpredictable and harsh environment,

several lemur species adjust their reproductive events in order to time weaning with the best season (Wright, 1999). However, we were not able to test this hypothesis given the low number of seasonal breeding 'baboon' populations available (Chapter 6), and it is likely that other factors, such as extrinsic infant mortality (Chapter 6) may also account.

More broadly, this manuscript points to the fact that optimal reproductive phenology is more complex than previously thought (F. H. Bronson, 2009), and that matching lactation peak with the most productive season is by no means the universal adaptive strategy in mammals. **The reproductive phenology of long-lived species living in the tropics remain thus unclear and would need further investigations.**

III°) Evolutionary determinants of reproductive seasonality

In this section, I discuss various factors affecting the intensity of reproductive seasonality in the light of this work. I respectively explore the importance of (i) environmental fluctuations, with a focus on environmental seasonality and unpredictability, (ii) life histories, and in particular of life history trade-off and extrinsic infant mortality, and lastly (iii) sociality, and more precisely of female competition, female rank and infanticide, on reproductive seasonality.

A- Environmental fluctuations

i. Environmental seasonality, even in the tropics and in rich habitat

It has often been assumed that organisms living in the tropics rely on resources relatively stable year-round, i.e. with low sensitivity to seasonal climatic fluctuations, resulting in the absence

of reproductive seasonality for most tropical species (Baker, 1938; Stouffer, Johnson, & Bierregaard, 2013; Wikelski et al., 2000). The first crucial finding of this work is the existence of **seasonal variation in food availability even for omnivorous species living in tropical regions**. Indeed, in both tropical study sites, we found evidence indicating that important seasonal (i.e. periodic within-year) variation in rainfalls leads to variation in available resources. The fact that such variations occur in baboons and mandrills, despite their omnivorous diet and their widespread distribution (i.e. almost everywhere in sub-Saharan Africa) (Swedell, 2011; chapter 6), suggests that most primate species, if not all, live on resources that vary seasonally. Indeed, it confirms that climatic (i.e. mainly rainfall within the tropics) variations affect plant phenology in tropical (including equatorial) habitats, which in turn modulate the seasonal amount of food available for primates (Van Schaik et al., 1993). More generally, the fact that seasonality in food availability is felt by species with such features suggest that most vertebrates in the world live from resources exhibiting a certain degree of seasonality (Franklin H. Bronson & Heideman, 1994). The only exceptions may be accounted for populations living in captivity or anthropological disturbed environments (close to habitations, crops, dumpsters) where food may be available in high amount year-round without any variation.

Consequently, we found some direct evidence of the influence of environmental seasonality on the reproductive timing of chacma baboons: conception probabilities increased following the seasonal peak in food availability at Tsaobis (Chapter 4). In Lékédi forest, mandrills' conceptions, births and cycle resumptions, all exhibit strong seasonality. Therefore, even among large omnivorous species able to store energy, environmental seasonality (in resource availability) affects reproductive timing, which leads to some degree of reproductive seasonality. It confirms several examples of species exhibiting strong breeding seasonality, despite (i) their tropical environment, like Malagasy primates (Meyers & Wright, 1993; Wright,

1999), (ii) their large size, as for example Bactrian camels (*Camelus bactrianus*), with gestation period of over a year (Skidmore, 2011), and (iii) their omnivorous diet, such as brown bears (*Ursus arctos*) (Spady et al., 2007), making reproductive seasonality the norm rather than the exception in mammals (F. H. Bronson, 2009).

The case of mandrills is even more interesting. Indeed, living in a rich equatorial forest, they can successfully breed year-round (without any costs on their offspring' post-natal survival), and they onset their reproduction and conceive mainly during the lean season (Chapter 5). This highlights a second crucial input of this work: **even in rich environments, with high (yet variable) amount of food available year-round, reproductive seasonality can emerge**. One could have assumed that in rich habitats, where seasonal variations in food availability do not cause severe food limitations, females would reproduce year-round. From a mechanistic perspective, indeed, female mandrills can onset their reproduction and conceive year-round. In this rich environment, their energy balance may be positive even in the lean season, allowing them to be over their condition-threshold (internal cues to control reproduction, see introduction) year-round. However, ultimately, our chapter 5 shows that as long as there are seasonal variations in food availability, and regardless of the absolute quality of the habitat, it might be advantageous to adjust reproductive timings in relation to the seasonal food peak in order to maximise maternal reproductive success (with shorter interbirth intervals associated with certain birth timing), leading to reproductive seasonality. This finding is not specific to mandrills, and can be expanded to the several cases of tropical (or even equatorial) seasonal breeders, such as white-faced capuchins (*Cebus capucinus*) (Carnegie et al., 2011), Sanje mangabeys (*Cercocebus sanjei*) (Thompson & McCabe, 2013) or long-tailed macaques (van Schaik & van Noordwijk, 1985) for example.

As it seems that most species perceive some seasonal variation in food availability, two main evolutionary paths can lead to the absence of seasonal breeding. First, seasonal

reproduction represents only one adaptation among others to environmental seasonality. Species may use other strategies, such as the ability to store energy, to use fall-back food during the harsh season, to increase allo-parental care during the lean season, or to decrease the costs in energy associated with reproduction (through slower reproductive pace for example) (Brockman & van Schaik, 2005a; Heldstab, van Schaik, & Isler, 2017; Jönsson, 1997; Stephens, Houston, Harding, Boyd, & Mcnamara, 2014; van Woerden, van Schaik, & Isler, 2010). Second, other ecological or social factors can lead to the decrease of reproductive seasonality. For example the level of environmental unpredictability, species life histories and benefits of reproductive asynchrony may also decrease the intensity of reproductive seasonality, and are discussed below in the light of this work (see also Figure 1).

ii. Environmental unpredictability: magnitude and timing of between-year variation

We disentangled two components of environmental unpredictability, namely the amount of between-year rainfall variation, and the year-to-year variation in the timing of the rainy season, to explore their effects on the reproductive seasonality of several populations of different species of wild baboons and closely related species (Chapter 6). The amount of rainfall unpredictability was the only environmental predictor of the level of reproductive seasonality: when between-year variation in the amount of rainfall increased, the intensity of reproductive seasonality decreased. Indeed, the fitness benefits associated with seasonal breeding may be alleviated in unpredictable environments, where the rainy season might not be good some years. In such environments, other adaptations might be more advantageous than seasonal reproduction, such as an ability to store energy (Brockman & van Schaik, 2005a; van Schaik & van Noordwijk, 1985), to expand the dietary repertoire (Grueter, 2017), to increase foraging

time per day (Alberts et al., 2005; Grueter, 2017), or to shorten/extend lactation duration (van Noordwijk, 2012) (see Chapter 6). The unpredictability of the environment can thus be a major climatic factor explaining the evolution of flexible reproductive phenology, typically characterized by low or facultative reproductive seasonality, in baboons, but also in humans and other species with high ecological flexibility (Chapter 6).

We did not find any effect of environmental unpredictability, in the amount of year-to-year variation in food availability, on the timing of reproductive events (conceptions and cycle resumptions) in the Tsaobis baboons (Chapter 4), but we did on offspring survival. The intensity of between-year environmental variation may thus also affect reproductive success, as shown for several primate species exhibiting lower birth rates in relatively bad years, i.e. with low annual rainfall (Brockman & van Schaik, 2005a; van Schaik & van Noordwijk, 1985; Wiederholt & Post, 2011).

It has been argued that between-year variations in seasonal timing (instead of intensity) should mainly affect reproductive timings, with earlier rains associated with earlier reproductive events for instance. As such, numerous studies investigating the effect of climate change on bird reproductive phenology in temperate regions showed that the earlier onset of warm temperatures in late-winter causes earlier laying dates (Charmantier & Gienapp, 2014; Marcel E. Visser & Both, 2005). Therefore, we could intuitively argue that an increase of environmental unpredictability in terms of magnitude (i.e. the amount of between-year environmental variation) would lead to higher between-year variation in birth frequencies, while an increase of environmental unpredictability in terms of timing would lead to lower reproductive seasonality (when considering several years). This hypothetical framework has been proposed by Heldstab et al. (2020) to explain the apparent paradoxical reproductive seasonality of Malagasy primates, which are more seasonal in their births than any other primate species (Heldstab et al., 2020; Wright, 1999), while Madagascar exhibits strong inter-annual

variations in rainfall and resources available. The timing of the onset of the different Malagasy seasons is supposed to show relatively little between-year variations, explaining the emergence of such a pronounced, inflexible reproductive seasonality. We failed to find support for this assumption in our comparative analysis on baboons and relatives, as we did not find any effect of the unpredictability of the timing of the rainy season on reproductive seasonality (Chapter 6). However, our work calls for comparative analyses disentangling the effects of these two components of environmental unpredictability on the intensity of reproductive seasonality on a wider panel of populations living in a wider range of habitats, in order to test if both aspects of environmental predictability can affect reproductive seasonality.

B- Species life history

i. Reproductive trade-off over birth timing in long-lived species

The most studied evolutionary trade-off is certainly the one between survival and reproduction for a given individual (S C Stearns, 1989). In long-lived species, females must allocate their energy between their current and future offspring, leading to another type of trade-off (Rivalan et al., 2005). The literature investigated mainly the negative relationship between offspring quantity and quality (Conde-Agudelo, Rosas-Bermudez, Castaño, & Norton, 2012; Krist, 2011), or more precisely between maternal reproductive pace (or 'birth spacing') and offspring survival and growth (Emery Thompson et al., 2016; S. D. Lee, Ruiz-Lambides, & Higham, 2019). Meanwhile, facing environmental seasonality, females must 'chose' when to give birth, and this seasonal timing can have fitness consequences on both mothers' current and future reproduction (see I-C). In long-lived species, and in particular in species with long lactation time, the lactation peak, which is the costliest phase in energy of maternal reproductive cycle (Emery Thompson, 2013; P. C. Lee, 1996), can occur a few months before late-weaning, which

is the most vulnerable period of life for offspring survival (Janson & Verdolin, 2005; van Schaik & van Noordwijk, 1985).

As such, we showed that birth timings maximising offspring survival are not the ones maximising maternal reproductive pace in chacma baboons (Chapter 3). These two optimal birth timings are separated by approx. four months, and synchronize respectively late-weaning and lactation peak with the seasonal food peak. Such a trade-off between current and future reproduction over birth timing results in lower reproductive seasonality in this population. Indeed, females vary in their strategies to solve this reproductive trade-off, resulting in a flat birth peak between these two optima. In contrast, in our second study population (mandrills), birth timings maximising maternal reproductive pace are aligned with the ones maximising current reproduction. This is probably due to the ability of mandrills (like the white-faced capuchin, another tropical primate: Carnegie et al., 2011), to breed year-round without any costs on offspring survival in this rich environment. As such, the absence of trade-off between current and future reproduction over birth timing in mandrills results in higher reproductive seasonality, with a strong selective pressure favouring seasonal breeding.

The fact that the birth timing can cause reproductive trade-offs may thus impact the intensity of reproductive seasonality. This work calls for more studies investigating the effect of birth timing not only on offspring and mother survival, but also on mother future reproduction in the case of long-lived species. Indeed, we found that in both populations, maternal pace was strongly influenced by birth timing, and surprisingly, almost all studies investigating the fitness consequences of reproductive seasonality omitted this component of maternal fitness (but see: Brinkhof, Cavé, Daan, & Perdeck, 2002). The studies investigating the trade-off between current and future reproduction over reproductive timing are thus rare. One example comes from Pacific herrings (*Clupea palasii*), where the best time to hatch in the offspring's perspective (i.e. the time that maximises offspring condition in early-life) is

different from the best time to spawn in the parent's perspective (i.e. the time that maximises parental condition and survival, and so future reproduction), and the difference between these two optimal timings is driven by variation in food availability (Ljungström, Francis, Mangel, & Jørgensen, 2019). However, the consequences of such trade-off for breeding seasonality are not discussed in this paper (Ljungström et al., 2019).

Although such reproductive trade-offs are expected to be widespread across long-lived animals, they could possibly also affect the intensity of reproductive seasonality among faster-lived species. For example, it has been shown that in the European coot (*Fulica atra*), early laying dates are associated with an increased probability of a second brood within the same season (maximising thus parents' reproductive pace) but also with a decrease of parental survival probability (Brinkhof et al., 2002): this trade-off between current and future reproduction can also affect the intensity of reproductive seasonality in this species, depending on individual variation in breeding schedules' strategies. However, as explained above, the studies taking into account multiple fitness components are rare, and we do not know how common and widespread this reproductive trade-off might be in animals. In addition, theoretical models would be needed to better understand the consequences of such reproductive trade-off on the intensity of reproductive seasonality.

ii. Extrinsic offspring mortality

So far, the possible effect of extrinsic offspring mortality on reproductive seasonality has been mainly studied through the lens of the relationship between predation risk and reproductive synchrony. For example, in impalas (*Aepyceros melampus*), reproductive seasonality is intense in environments with highly seasonal food resources, whereas predation risk decreases the intensity of reproductive seasonality in environments where food is less seasonal, as impalas

may benefit from asynchronous births in order to better hide their lambs by night (Moe, Rutina, & Du Toit, 2007). In our population, predation events are rare, but we showed an effect of reproductive history (whether or not previous reproduction ended with a failure – miscarriage or infant mortality) on reproductive phenology in mandrills (Chapter 5). Knowledge on the main causes of infant death is, however, essential to predict the effects of such mortality on reproductive seasonality.

Indeed, on the one hand, extrinsic and non-seasonal offspring mortality (pre- and post-natal) can disrupt reproductive seasonality in species where females onset their reproduction soon after their infant's death regardless of the season. This work therefore suggests that extrinsic and stochastic infant mortality (from predation, disease, or infanticide for instance) can be an important factor affecting reproductive seasonality. However, the hypothesis that higher extrinsic infant mortality would lead to lower reproductive seasonality has never been tested in other populations. On the other hand, seasonal offspring mortality caused by food shortages during the lean season or seasonal diseases (as found in several wild primate populations: Gogarten et al., 2012) may have the opposite effect, and lead to higher reproductive seasonality. Indeed, seasonal birth timings associated with higher infant survival may be more strongly selected and consequently lead to more intense reproductive seasonality.

More broadly, the ability to resume cycling at any time of the year cycle following offspring's death (as is the case in *Cercopithecinae*) is linked to the absence of a strict birth season, and high extrinsic offspring mortality could be the selective pressure favouring such a life-history trait. Indeed, a strict reproductive seasonality, where reproduction is photoperiod-induced for example, would force females to wait for the next optimal season to conceive again following their offspring's death. Such a cost could outweigh the benefits of breeding seasonally when extrinsic infant mortality is high. A comparative analysis would be needed to infer the determinants of this ability to resume cycling year-round or not.

C- Sociality

i. Female competition and reproductive synchrony

In chapter 4, we brought the first empirical evidence at Tsaobis that **reproductive asynchrony at the group-level can contribute to the evolution of non-seasonal reproduction at the population level**. Indeed, in our population, reproductive synchrony was associated with a slower reproductive pace, a lower likelihood to conceive and to onset reproduction for subordinate females. More precisely, we further found indirect evidence suggesting that this reproductive asynchrony may have been generated in response to female-female competition over paternal care (Chapter 4). Various species of polygynous birds also exhibit high level of female competition over paternal care (Slagsvold & Lifjeldt, 1994). It has been argued, but rarely supported (see the exception of the red-winged blackbird: Yasukawa, Leanza, & King, 1993; Yasukawa, Mcclure, Boley, & Zanocco, 1990) that a secondary female should delay nesting to reduce the overlap with the females who had already conceived with the same male, in order to increase paternal care for the nestlings of the secondary female (Slagsvold & Lifjeldt, 1994). Even if it has never been tested in our knowledge, such strategies could affect reproductive seasonality at the population level, explaining the evolution of a wider and more flexible reproductive season in these seasonal breeders.

A variety of female mammals suppress the reproduction of other females in response to various socioecological conditions (Beehner & Lu, 2013; Wasser & Barash, 1983). Females can compete over a wide diversity of resources, such as food, mates, paternal care, burrows or territories, and such competition can result in reproductive suppression (Beehner & Lu, 2013; T. Clutton-Brock & Huchard, 2013; Stockley & Bro-Jørgensen, 2011; Wasser & Barash, 1983). Indeed, for example, in numerous social species, like mongooses, meerkats, wild dogs, hyenas,

wolves, and several primate species, females can suppress the breeding of others (before or after conceptions) when resources are limited and consequently when competition is intense (Beehner & Lu, 2013; T. Clutton-Brock & Huchard, 2013; Stockley & Bro-Jørgensen, 2011; Wasser & Barash, 1983). Reproductive timings in these species are thus necessarily constrained in time, however, the consequences of such reproductive suppression on reproductive synchrony and seasonality remain poorly understood. Nevertheless, a prominent example comes from banded mongooses, where dominant females actively suppress the reproduction of subordinates (Nichols et al., 2012), leading to the evolution of extreme birth synchrony (Hodge et al., 2011), as subordinates' pups are less likely to be killed by dominant females when born in synchrony with the dominants' pups.

More precisely, if the resources initially causing female competition and reproductive suppression do not vary seasonally (such as the number of adult males in the social group for females competing over mates or paternal care for example), reproductive suppression would generate reproductive asynchrony that would weaken the strength of reproductive seasonality at the population-level (as found in Chapter 4). In contrast, if the resources responsible for female competition vary seasonally (when females compete mainly over food for instance), females would more often prevent others to breed during the harsh season, given that in most cases food is difficult to monopolize during the good season (as found in banded mongooses: Nichols, Bell, Hodge, & Cant, 2012). This seasonal reproductive suppression should ultimately increase the strength of reproductive seasonality. Indeed, without this active suppression, the births of the 'suppressed' females would occur in other seasons than the optimal one only. A better understanding of the influence of seasonal variations in resource availability on the intensity of reproductive suppression is therefore needed to quantify its potential effects on reproductive seasonality.

More broadly, our work highlights the importance to take into account reproductive suppression as a factor likely to affect breeding seasonality in numerous social species.

ii. Female rank and reproductive phenology

In this work, female social rank appears as a major individual factor mediating reproductive performances and phenology. We first showed that high-rank females exhibit shorter interbirth intervals ('IBI's) in our two populations, confirming previous studies from other baboon and mandrill populations (Cheney et al., 2004; Gesquiere, Altmann, Archie, & Alberts, 2017; Packer, Collins, Sindimwo, & Goodall, 1995; Setchell et al., 2002). IBIs can be closer to an integer number of years for some individuals, favouring the emergence of stronger reproductive seasonality (although it was not the case in our two populations). In mandrills, individual variations in IBIs might further result in two different strategies for females of different ranks: dominant females would attempt to give birth in consecutive years, despite IBIs a bit longer than 365 days on average, while subordinate females would only give birth once every two years. These rank-dependent strategies are likely to explain the higher probability of dominant females to give birth outside the birth season in mandrills (see Chapter 5). This lower reproductive seasonality of dominant females weaken the intensity of reproductive seasonality at the population level.

We also found individual rank-related variation in the probabilities of current reproductive failure (pre and post-natal offspring mortality) in both populations, with dominant females being less likely to abort (in mandrills, Chapter 5) or to lose an infant before weaning (in baboons, Chapter 4). It confirms previous results in other baboon populations in the case of post-natal mortality (J. Bulger & Hamilton, 1987; Packer et al., 1995). However, it is the first report of dominant females having lower likelihood to miscarry in a species from the *Papionini*

tribe (the opposite direction for this effect, with dominant being more likely to abort, was found in a population of yellow baboons: Packer et al., 1995). These rank-related variations of reproductive success are common among mammalian social species (T. Clutton-Brock & Huchard, 2013; Stockley & Bro-Jørgensen, 2011), including meerkats, mongooses, several ungulate and carnivore species (such as red deers, hyenas or lions), and also elephants. Such rank-related variations in reproductive success can thus modulate the selective pressures affecting optimal birth timing, and ultimately affect individual variation in reproductive phenology.

Lastly, female rank can further modulate the consequences of competition over food or mating opportunities on reproductive timing. Subordinate females are more constrained that dominant ones, and may therefore adjust their reproduction depending on dominant females' reproductive schedule, either to delay and stagger their reproductive timings (as we showed in chacma baboons, Chapter 4), either to synchronize their reproductive timings with dominant females (as showed for banded mongooses: Hodge et al., 2011).

More generally, our work highlights the importance to consider individual variation in reproductive timing to understand the observed pattern at the population-level. The consequences of individual variation in reproductive suppression on reproductive seasonality have been overlooked, and further work on other social species should quantify individual strategies in birth timing and its consequences on reproductive seasonality. In addition, for other taxa and species (not necessarily living in large social groups), other individual parameters, such as female's age or genetic (Garel et al., 2009; Marcel E. Visser et al., 2011), should be considered as they might similarly affect reproductive strategies, including phenology, and ultimately population reproductive seasonality. A model taking into account individual variation in life histories, social competition, and access to food, and thus condition, to determine the optimal breeding seasonality strategy depending on a variety of social and

external environmental variations would be necessary to better understand the potential effects of rank on reproductive seasonality in a variety of mammal species.

iii. Infanticide and reproductive seasonality and synchrony

Infanticide by males has mainly been considered to evolve among non-seasonal breeding species, as an infanticide attack would not bring any benefits to the male aggressor in the case of seasonal breeding species (Ryne A. Palombit, 2015). Indeed, the main benefit of infanticide for the aggressor is to precipitate the sexual activity of the mother of the killed infant, but this benefit is alleviated when sexual receptivity is primarily determined by photoperiodic or other seasonal cues (R. A. Palombit, 2015). In line with this, a comparative study showed that infanticide is more common among non-seasonal breeding species (Lukas & Huchard, 2014). However, the association between infanticide and reproductive seasonality is complex and may vary across contexts and populations. For example, infanticide by males occurs in the seasonally breeding red deers (Bartos & Madlafousek, 1994). In addition, the causal relationships between infanticide and reproductive seasonality remain unclear and may be species-specific. Indeed, one may assume that higher extrinsic mortality rates (from infanticide, but also from other stochastic events like predation, see III-B-ii) would lead to the evolution of female ability to resume cycling immediately after their offspring's death (as in our study populations). These two mechanisms, namely infanticide promoting non-seasonal reproduction (through an ability to onset reproduction year-round) and non-seasonal reproduction promoting infanticide, may have co-evolved in a self-reinforcing feedback loop.

A relatively common social counter-strategy used by females against male infanticides may consist in synchronizing reproductive events, and is encountered in several species, including banded mongooses as already mentioned above (Hodge et al., 2011). In addition, in voles, it has been shown that while asynchronous breeding is the optimal strategy in non-

infanticidal populations (in order to decrease food competition), synchronous breeding becomes the adaptive strategy when infanticide is common in the population (Poikonen, Koskela, Mappes, & Mills, 2008). In lions, females benefit from breeding synchronously as their offspring are communally defended against infanticidal male intruders (Packer, Pusey, & Eberly, 2001). Infanticide could thus promote reproductive synchrony, and would therefore lead to an increase of the intensity of reproductive seasonality in such populations.

Lastly, whenever infanticide (or infanticide risk) is seasonal, it can further impact population reproductive seasonality, as found in mandrills. Indeed, infanticide risk might cause an increase of abortions when conceptions occurred late in the mating season, resulting in a tighter birth peak (Chapter 5). This is suggestive of a Bruce effect, where females terminate pregnancies after exposure to unfamiliar males, as first demonstrated in mice (*Mus musculus*) (Parkes & Bruce, 1962), and also encountered in geladas (Roberts, Lu, Bergman, & Beehner, 2012). In mandrills, if a birth occurs late in the birth season, the resulting <6 month-old offspring will still be breastfed, and thus highly vulnerable at the arrival of the first immigrant males around March-April, who represent infanticide threats (Ryne A. Palombit, 2015). This potential 'preventive' Bruce effect, which is a counter-strategy to infanticide, leads to a shortened birth peak (Chapter 5). In geladas however, infanticide following male takeovers is responsible for a second birth peak (in addition to an 'ecological' birth peak), as male takeovers are seasonal in this species (Tinsley Johnson et al., 2018).

This work contributes to show that the relationship between reproductive seasonality and infanticide is more complex than previously thought. While infanticide may have evolved in non-seasonal breeding species, it can also reinforce breeding seasonality in some other species. The association between infanticide and reproductive seasonality appears deeply modulated by the ecology, life-history and social system of a species, leading to potentially divergent scenarios.

General conclusion

This work emphasizes the fact that looking only at climatic seasonality effects on offspring survival is far from sufficient to fully understand the evolution of reproductive seasonality. Specifically, in our case studies, looking exclusively at post-natal offspring mortality in relation to birth timing would lead us to conclude that mandrills should be non-seasonal breeders while baboons should be seasonal breeders. First, climatic unpredictability, and not only seasonality, may be a major factor affecting the intensity of reproductive seasonality, especially in the tropics. Second, taking into account life history and sociality is critical to understand the fitness consequences of reproductive seasonality, and so the evolution of reproductive seasonality. Indeed, our findings bring evidence that both ecological and social determinants interplay with species life histories to shape the reproductive seasonality of mammals (Boinski, 1987; Canu et al., 2015; Moe et al., 2007; Rutberg, 1987; Sinclair et al., 2000; Tinsley Johnson et al., 2018). The Figure 13 shows an attempt to represent/sum up the various evolutionary determinants, environmental, social but also additional factors at the species (life history pace, size, predation) or individual level (rank, age, condition), responsible for the diverse intensities of reproductive seasonality – from non-seasonal breeding to extremely seasonal breeding - observed in the animal kingdom.

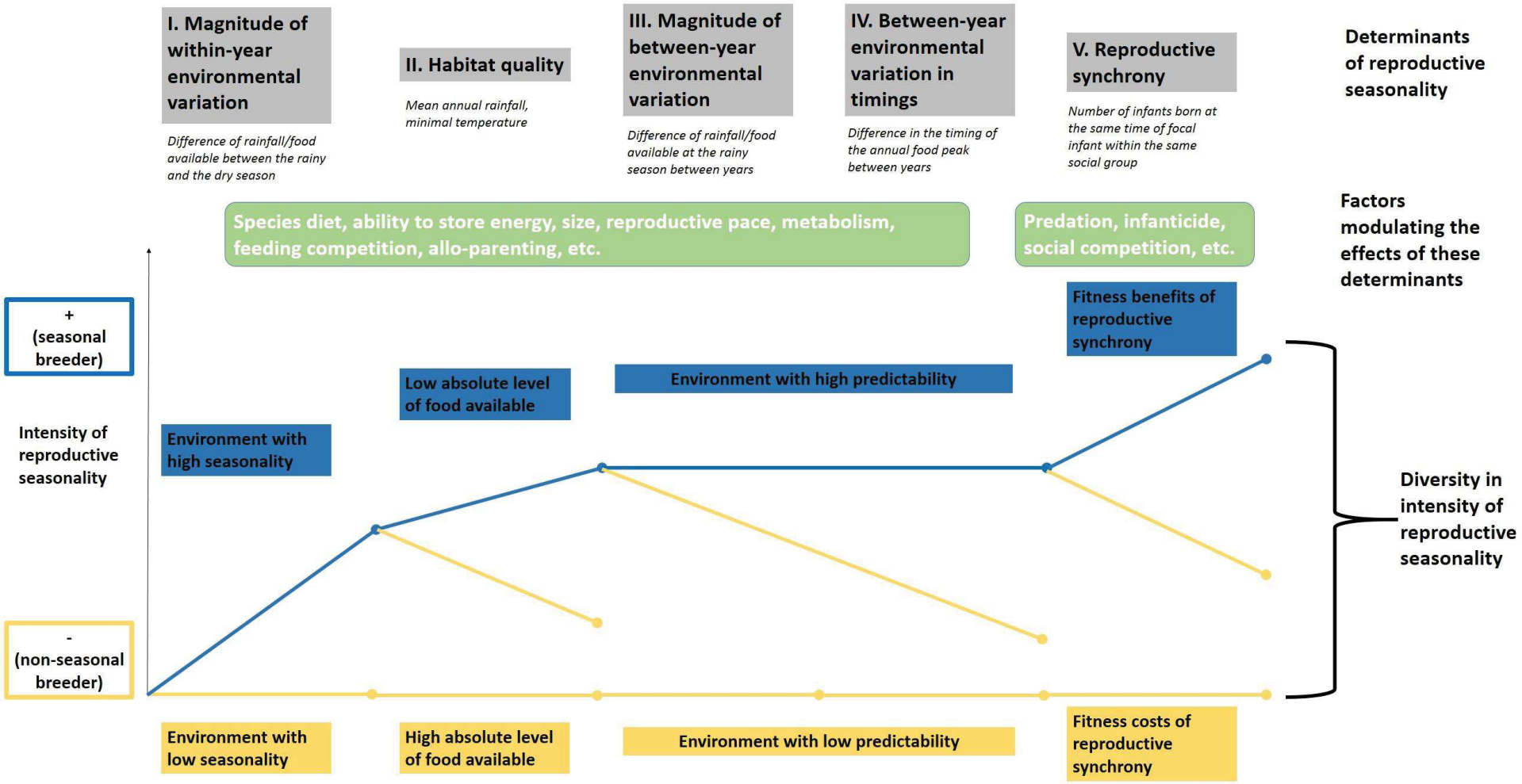

I. Magnitude of within-year environmental variation
Difference of rainfall/food available between the rainy and the dry season
II. Habitat quality
Mean annual rainfall, minimal temperature
III. Magnitude of between-year environmental variation
Difference of rainfall/food available at the rainy season between years
IV. Between-year environmental variation in timings
Difference in the timing of the annual food peak between years
V. Reproductive synchrony
Number of infants born at the same time of focal infant within the same social group
Determinants of reproductive seasonality
Species diet, ability to store energy, size, reproductive pace, metabolism, feeding competition, allo-parenting, etc.
Predation, infanticide, social competition, etc.
Factors modulating the effects of these determinants
+ (seasonal breeder)
Intensity of reproductive seasonality
- (non-seasonal breeder)
Environment with high seasonality
Low absolute level of food available
Environment with high predictability
Fitness benefits of reproductive synchrony
Diversity in intensity of reproductive seasonality
Environment with low seasonality
High absolute level of food available
Environment with low predictability
Fitness costs of reproductive synchrony

Figure 13 (previous page): Evolutionary determinants of the intensity of reproductive seasonality in mammals

This figure is an attempt to summarize the several factors likely to affect the intensity of reproductive seasonality, in light of this work. The sequential part, from I. to IV. is only for illustrative purposes, as the different effects of several components of environmental variations affect altogether, and not necessarily sequentially, reproductive seasonality.

I. The more intense seasonal variation, the more intense is seasonal reproduction. Environmental seasonality is the main factor promoting the evolution of reproductive seasonality. If we consider an initial situation with no reproductive seasonality, environmental seasonality can thus only enhance, more or less, reproductive seasonality, depending on the level of within-year periodic environmental variation.

II. Habitat quality can further impact reproductive seasonality, as species living in relatively poor habitats on average, could be limited to breed at certain times of the year. In contrast, in richer habitats, organisms may be more likely to buffer environmental seasonality, promoting their ability to breed year-round. Habitat quality therefore mainly acts in interaction with environmental seasonality to affect reproductive seasonality, and the level of food available during the harsh season may be the critical factor affecting the intensity of reproductive seasonality. We did not find support for such an effect of habitat quality on baboons and relatives' reproduction, presumably given their ability to buffer environmental seasonality through their omnivorous diet and ability to use fallback food during the harsh season, allowing them to conceive year-round regardless of habitat quality.

III & IV. Environmental unpredictability, i.e. between-year environmental variation, in both the magnitude (III) and the timing (IV) of seasonality can affect reproductive seasonality. The higher the unpredictability, the lower the intensity of reproductive seasonality. Highly predictable environments would however not increase the intensity of reproductive seasonality. Indeed, in a theoretical case where the environment is 100% predictable, but without any seasonal environmental variation (i.e. perfectly stable), the predictability by itself would not enhance a species to breed seasonally. Only environmental seasonality would.

V. Finally, once environmental variation acts on the evolution of reproductive seasonality, fitness benefits or costs associated with reproductive synchrony could modulate the intensity of reproductive seasonality. However, in the absence of selection for seasonal reproduction, selection for reproductive synchrony would not lead to the emergence of annual birth seasons, but to randomly timed episodes of synchronous births.

All these environmental effects (I to IV) are likely to be influenced by various additional factors, either specific to a species, such as diet, ability to store energy, life history, size, or specific to an individual, such as body condition, rank, parity, reproductive history, etc (see green box). Examples of selective pressures affecting reproductive synchrony are provided in the second green box.

IV°) Perspectives

A- Paternal care and reproductive seasonality

This work on chacma baboons raises the possibility that paternal care acts as the ultimate cause of female-female competition and suppression responsible for reproductive asynchrony. Paternal care positively impacts offspring developmental pace and survival in a variety of social and mating systems (Braun & Champagne, 2014; Huck & Fernandez-Duque, 2013; Qvarnström & Price, 2001), including the promiscuous societies of baboons (Charpentier, Van Horn, Altmann, & Alberts, 2008; and see Chapter 1).

In the light of our work, it would be interesting, in order to confirm that females compete over paternal care, to test two hypotheses in the Tsaobis population: (i) infants associated with a dominant male (at the time of conception, and/or at the time of early-lactation and weaning) have higher fitness benefits (on growth and survival) than the ones associated with lower-ranking males. Such benefits would explain why sexually receptive females compete with each other. The benefits to conceive with a dominant male may be particularly important on infant survival, as dominant males may better prevent infanticides than lower ranking one. Although such an effect would be difficult to detect given the low frequency of infanticidal events.

(ii) There is competition between lactating females and between weanlings over access to paternal care (on the same male), i.e. the benefits of paternal care are diluted when a same male must share his 'care' between several lactating females/infants. Such dilution would explain why females who already conceived with a given male harass and suppress the reproduction of other females trying to conceive with the same male (Baniel et al., 2018). Under such a scenario, we would for instance expect that infants in larger cohorts (i.e. with a high

number of other infants associated with the same male) have slower development than those in smaller cohorts (i.e. the infant is the only one associated with a given male). Competition between lactating females over access to a male has been found in another baboon population (R. A. Palombit et al., 2001), but its consequences on infant fitness and maternal reproductive pace remain unknown.

B- Allo-parenting and reproductive seasonality

The potential importance of allo-parenting on reproductive seasonality has recently received some support. Indeed, allo-parenting care may represent another adaptation to environmental seasonality, buffering the costs of the harsh season on mothers condition (Heldstab et al., 2017). A recent comparative study found that cooperative breeding species live in more arid and unpredictable environments (Lukas & Clutton-Brock, 2017), supporting the existence of a relationship between allo-parenting care and environment seasonality. Allo-maternal care can take a variety of forms in animals including primates, but its major aspects are infant transport and baby-sitting (Tecot, Baden, Romine, & Kamilar, 2013). The existence of individual variation, and the factors responsible for such variation, in allo-parental care received remain unknown in baboons, as allo-parental care has never been investigated nor thought to exist.

An interesting perspective would be to investigate if females giving birth in asynchrony, and/or outside the ecological birth peak, tend to receive more allo-care than others, as a strategy to buffer suboptimal and harsh environmental conditions on mothers. Indeed, mandrill and baboon live in large multifemale multimale groups where high genetic relatedness exists between females, who are philopatric (Swedell, 2011). Social bonds and allo-maternal care in such cohesive social units might thus be an additional factor responsible for the absence of reproductive seasonality in most baboon and relative species. Here, we could expect that

females may be better able to buffer the adverse consequences of giving birth in suboptimal timing when their infants receive more allo-maternal care.

One of the main factor responsible for individual variation in the level of allo-maternal care received may further be the social integration of the mother within the group. Indeed, we could hypothesize that females with higher social integration and stronger social bonds, would have infants receiving higher level of allo-maternal care than others (regardless of environmental conditions). Such effect could be a mechanism, among others, explaining the positive effects of maternal social bonds on offspring survival found in several baboon populations (Silk, Alberts, & Altmann, 2003; Silk et al., 2009). All in all, we could predict that females with stronger social bonds would be able to reproduce year-round with lower fitness costs than females with weaker social bonds. Social bonds, allo-parental care, and reproductive seasonality could thus been associated, albeit such assumption has rarely been found yet.

C- Climate change and reproductive seasonality

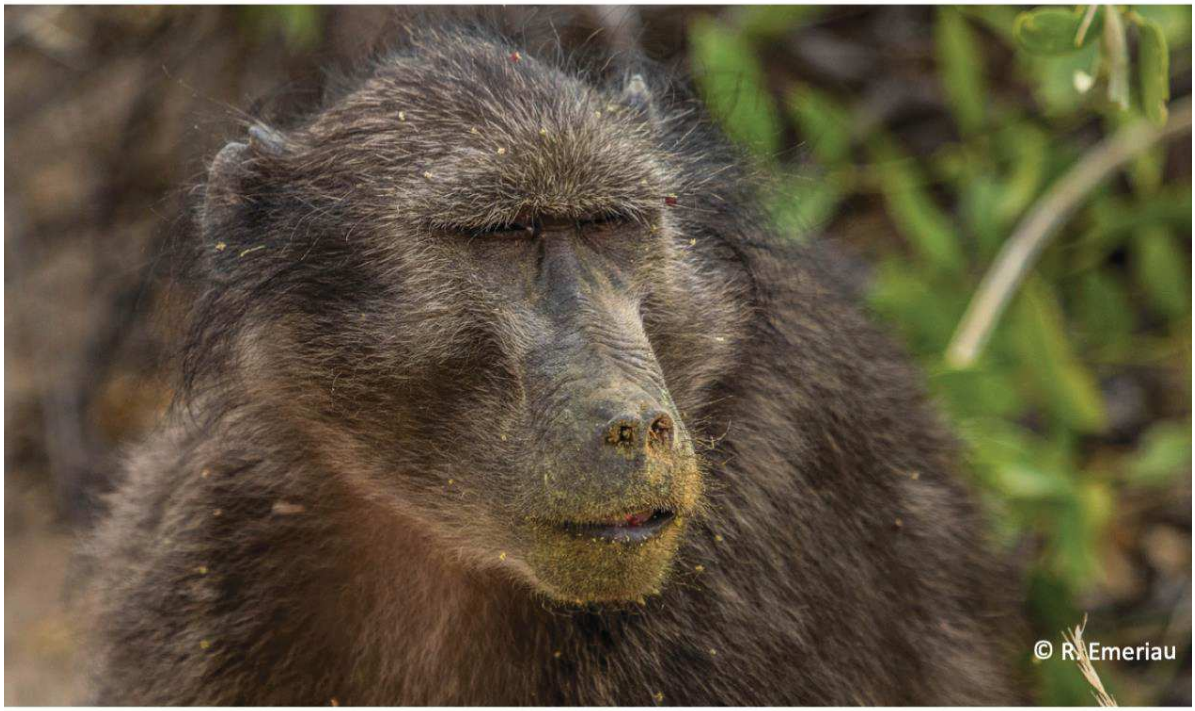
In our work, we showed that the intensity of environmental seasonality, but also its unpredictability (both in the timing and in the magnitude) affect the reproductive phenology and the intensity of reproductive seasonality of wild primate populations, regardless of habitat quality and of their diet (as even omnivorous species are affected). Climate change is affecting the intensity of environmental seasonality, but also increasing its unpredictability, changing both the timing and intensity of the seasons (Dai, 2013; Easterling et al., 2000; Feng et al., 2013). Only one study to date investigated and found adverse effects of climate change on the reproduction and demography of a non-seasonal breeding and large mammalian species, namely *Bos Taurus* (Burthe et al., 2011). Our comparative study emphasized the high flexibility of baboons and relatives' reproductive timings (Chapter 6), and these species must thus be

relatively resilient to the effect of climate change through environmental seasonality and predictability. However, a recent study found that three baboon species (out of six) are at risk of substantial habitat loss because of the increase of droughts and ambient temperatures due to global warming despite their expected resilience (Hill & Winder, 2019). In shorter-term, most primate species are under the threats of other anthropological disturbances than climate change, such as habitat degradation, loss and fragmentation, hunting and poaching for bush meat trade, or more broadly the geographical and demographic expansion of human population (Estrada, Garber, & Chaudhary, 2020). The impact of climate change on primate fecundity and demography might be underestimated in comparison to the more conspicuous and direct effects of hunting and/or land use changes, because its effect is harder to quantify, and need long-term projects following the same population (Wich & Marshall, 2016). In addition, in longer-term, climate change is likely to be one of the main factor affecting primate distribution and demography (Korstjens & Hillyer, 2016; Wich & Marshall, 2016). Our work therefore calls for more studies investigating the impact of climate on the reproductive phenology of mammals and in particular primates, a taxonomic group where a lack of such data may hinder efficient conservation plans in action (Korstjens & Hillyer, 2016; Zhang et al., 2019).

In addition, various studies highlighted the fact that animals can use a wide variety of environmental or social cues to induce reproduction (Franklin H. Bronson & Heideman, 1994; Paul et al., 2008) (see also Introduction). However, no comparative analysis intended to determine the main factors affecting which cues species use to adjust their reproduction. Such studies would be crucial to better understand the consequences of climate change on reproductive phenology, and therefore on populations' demography. Indeed, the species with photoperiodic (and possibly other environmental, like temperature or rainfall) cues should be less resilient to climate change, and may not be able to flexibly adjust their reproductive timing depending on environmental fluctuations. It has been argued that tracking selection through

plasticity in birth dates might be particularly challenging for mammals (de Villemereuil et al., 2020), but this study focused on ungulates living exclusively at high latitudes, where environmental seasonality is marked, and used to be predictable before climate change (i.e. with low between-year environmental variation). We may argue that mammalian species, like baboons or humans (Chapter 6), that have evolved in unpredictable environments are more likely to be able to flexibly adjust their reproduction timing in response to current and future climate change.

FRENCH SUMMARY OF THE PHD



INTRODUCTION

La reproduction saisonnière est définie comme étant le regroupement temporel et périodique d'évènements reproductifs (naissances, conceptions, etc.) dans le cycle annuel entre individus d'une même espèce. Elle se compose de deux principales caractéristiques : son intensité (à quel point le regroupement est étroit), et sa phénologie (quand a lieu ce regroupement). On observe une grande diversité d'intensité de saisonnalité reproductive dans le règne animal, en particulier chez les mammifères. En effet, certaines espèces, comme les chèvres des montagnes (*Oreamnos americanus*, donnant naissance durant seulement un mois chaque année) (Côté & Festa-Bianchet, 2001), ont une reproduction hautement saisonnière, alors que d'autres, comme les êtres humains (*Homo sapiens*), se reproduisant toute l'année sans, ou avec peu, de variations dans les fréquences mensuelles de naissance (F H Bronson, 1995; Ellison et al., 2005), et ont donc une reproduction non-saisonnière.

La plupart des études regardant les facteurs responsables des variations de saisonnalité reproductive se sont uniquement concentrés sur un facteur : la saisonnalité environnementale. En effet, les variations intra-annuelles et périodiques (de période d'un an) de facteurs climatiques, comme la pluie ou la température, sont à l'origine des saisons. Et ces saisons provoquent la fluctuation de nourriture disponible pour un organisme donné dans un environnement donné (Boyce, 1979). Cette saisonnalité de l'environnement est ainsi bien souvent la cause ultime et/ou proximale de la saisonnalité reproductive (F. H. Bronson, 2009; Franklin H. Bronson & Heideman, 1994).

D'un point de vue ultime, la reproduction est une période de vie coûteuse en énergie pour les femelles, puisqu'elles doivent assurer la survie et croissance de leur(s) petit(s). Ceci est particulièrement marqué chez les mammifères, puisque par exemple, une femelle adulte musaraigne (*Blarina brevicada*) pesant environ 11g doit trouver de la nourriture en quantité suffisante pour produire 55g de lait en moyenne à ses petits en fin de lactation (Pearson, 1944). Ainsi, ajuster ses timings reproductifs en fonction des fluctuations saisonnières de nourriture est souvent adaptatif (F. H. Bronson, 2009), et la phénologie reproductive est sous forte pression de sélection (de Villemereuil et al., 2020). De fait, plusieurs études ont confirmé l'importance de la saisonnalité environnementale pour expliquer l'intensité de la saisonnalité reproductive : plus un environnement est saisonnier, et plus la reproduction est saisonnière. Par exemple, il a été montré que l'intensité de la reproduction saisonnière au sein des mammifères augmente avec la latitude, utilisée comme indicateur du niveau de variation intra-annuelle des ressources disponibles, à la fois au niveau intra-spécifique (exemple des

lycaons, *Lycaon pictus* : McNutt, Groom, & Woodroffe, 2019), et inter-spécifique (ruminants : Rutberg, 1987; Zerbe et al., 2012 ; carnivores : Heldstab et al., 2018 ; primates : Di Bitetti & Janson, 2000; Heldstab et al., 2020; Janson & Verdolin, 2005). De plus, il a aussi été montré les primates du nouveau monde frugivores ont une saison de naissance plus courte que les folivores, étant données que les variations saisonnières de fruits sont plus importantes que celles de feuilles (Di Bitetti & Janson, 2000).

D'un point de vue proximal, deux principales causes de la saisonnalité de la reproduction ont été avancées : la condition de la femelle (de la mère, via un seuil de condition qu'il est nécessaire de surpasser pour pourvoir être fertile) (Brockman & van Schaik, 2005a; Clauss et al., 2020), et des signaux environnementaux, et en particulier la photopériode, c'est à dire la durée des jours (Bradshaw & Holzapfel, 2007; Franklin H. Bronson & Heideman, 1994). Dans les deux cas, des variations saisonnières environnementales peuvent expliquer comment les organismes se reproduisent saisonnièrement.

Toutefois, la saisonnalité environnementale à elle seule ne peut expliquer la diversité des phénologies reproductives qui existent dans le règne animale. D'autres facteurs, jusque-là négligés, doivent également affecter les timings reproductifs des mammifères, et sont pris en compte dans cette thèse (voir Figure 4 de l'introduction générale). Parmi ces facteurs, on retrouve l'imprévisibilité de l'environnement (c'est à dire les variations interannuelles environnementales), l'écologie de l'espèce (notamment sa capacité à stocker de l'énergie, la prédation, le régime alimentaire, etc.), les traits d'histoire de vie (taille, rythme reproducteur). De plus, chez les espèces sociales, la synchronie reproductive peut aussi impacter la saisonnalité reproductive. La synchronie de la reproduction a été défini par Ims (1990) comme étant le phénomène causé par des interactions biologiques produisant un regroupement plus serré des événements de reproduction que la saisonnalité environnementale seule. D'autres facteurs que ceux impactant la saisonnalité de la reproduction peuvent jouer sur les coûts et bénéfices associés à la synchronie de la reproduction, comme la compétition entre femelles pour la nourriture, ou pour l'accès à la reproduction, ou l'existence d'allo-parentage par exemple (Ims, 1990).

OBJECTIFS

Le principal but de cette thèse est de mieux comprendre les déterminants évolutifs et les conséquences en termes de valeurs sélectives de la saisonnalité de la reproduction, en se concentrant sur deux populations de primates sauvages, les babouins chacma (*Papio ursinus*) de Namibie, et les mandrills (*Mandrillus sphinx*) du Gabon. Nous utilisons dans ce travail une combinaison de données de long-terme d'histoire de vie, de morphologie, écologique et comportementale afin de quantifier les variations individuelles de phénologie et de synchronie reproductive, ainsi que ses conséquences sur différentes composantes de valeurs sélectives à la fois des mères et des jeunes.

MODELES D'ETUDE (chapitre 1)

Nos deux populations d'étude, les babouins chacma (Tsaobis, Namibie) et les mandrills (Lékédi, Gabon) vont contribuer à combler certaines lacunes de la littérature sur la reproduction saisonnière qui est pour l'instant largement biaisée vers des espèces de petites tailles vivant en climats tempérés et arctiques (F. H. Bronson, 2009; Franklin H. Bronson & Heideman, 1994). Ces populations sont d'autant plus pertinentes pour nos questions dans la mesure où bien qu'elles partagent de nombreux points communs en termes de morphologie, écologie, et d'organisation sociale (Swedell, 2011), et qu'elles soient proches dans la phylogénie (Kingdon et al., 2012), elles exhibent des saisonnalités reproductives différentes et paradoxales. En effet, les babouins ont une reproduction non-saisonnières alors qu'ils vivent dans en environnement hautement saisonnier (avec une saison des pluies et une longue saison sèche, bien marquées), et en revanche, les mandrills ont une reproduction hautement saisonnière alors qu'ils vivent dans une forêt équatoriale, avec probablement peu de variations environnementales.

RESULTAT

Je présente ici les résumés (abstracts) de chaque manuscrit présenté dans cette thèse.

Chapitre 2 : Transitions développementales des couleur du corps des jeunes babouin chacma : Implications pour estimer l'âge et le rythme développemental (publié à l'American Journal of Physical Anthropology)

Chez de nombreuses espèces de primates, et d'autres mammifères, un des traits de développement morphologique le plus remarquable est la transition de couleur du pelage (et

peau) natal vers le pelage (et peau) adulte (Ross & Regan, 2000; Treves, 1997). Étudier la chronologie et l'âge de ces transitions de coloration peut-être une méthode facile et non-invasive pour (i) estimer l'âge des enfants pour lesquelles la date de naissance est inconnue, et (ii) détecter des différences inter-individuelles de rythme développemental pour les enfants d'âge connu.

En utilisant une combinaison de photographies et de d'observations de terrain sur 73 enfants babouin chacma d'âge connus, nous avons (a) noté leur couleur de peau de rose à gris sur six parties du corps ainsi que leur couleur de fourrure de noir à gris ; (b) validé notre méthode d'estimation d'âge en utilisant un sous-groupe d'observations sur 22 enfants d'âge connu précisément, et (c) quantifié les déterminants écologiques, sociaux et individuels de variations de transition de couleur de peau et fourrure entre individus.

Nos résultats montrent que les transitions de couleur de peau peuvent être utilisé pour estimer l'âge des jeunes babouins chacma de moins de sept mois (nombre de jour médian entre l'âge réel et l'âge estimé = 10, range = 0-86). Nous dévoilons également que la nourriture disponible pendant la grossesse, mais pas pendant le début de lactation, joue sur les transitions de couleur des enfants, et agit donc sur le rythme développemental.

Cette étude souligne ainsi le potentiel d'étudier les variations intra- mais aussi inter-individuelles de transition de couleur pendant le début de vie des jeunes afin d'estimer l'âge quand celui-ci n'est pas connu, et le rythme développemental quand celui-ci est connu.

Chapitre 3 : La saisonnalité de la reproduction génère un compromis reproductif chez un mammifère longévif (en cours de soumission)

Les bénéfices évolutifs de la saisonnalité reproductif sont souvent mesurés à partir d'une seule composante de la valeur sélective d'un individu, comme la survie des jeunes jusqu'à l'indépendance alimentaire (F. H. Bronson, 2009). Pourtant, différentes composantes de la valeur sélective pourraient être maximisées par des timings de naissance distincts. Cela devrait générer des compromis reproductifs qui pourraient être primordiaux pour comprendre les variations de timing reproducteurs entre individus, populations et espèces.

Dans cette étude, nous utilisons des données de démographies et comportementales de long-terme de babouins chacma sauvages vivant un en environnement saisonnier pour tester la significativité adaptative des variations saisonnières des fréquences des naissances. Comme

les humains, les babouins sont des omnivores éclectiques (Rhine, Norton, Wynn, & Wynn, 1989), donnant naissance tous les 1 à 3 ans à un seule jeune se développant lentement (J. Altmann, 1980; J. Altmann & Alberts, 2005), and se reproduisent tout au long de l'année (Swedell, 2011).

Nous identifions deux timings de naissance optimaux distincts, séparés de quatre mois, qui maximise la survie des jeunes ou minimise les intervalles entre naissances (IBIs), en synchronisant respectivement la fin ou le début du sevrage avec le pic annuel de nourriture. Les naissances sont plus fréquentes entre ces deux optima, en faveur d'un compromis adaptatif entre reproduction actuelle et future. De plus, les enfants nés proches du timing favorisant le rythme reproductif maternel (au lieu de la survie des jeunes) font plus de crises de colères, une manifestation typique du conflit mère-enfant (Barrett & Henzi, 2000; Maestripieri, 2002).

Les compromis maternels sur les timings de naissance, se traduisant également par un conflit mère-enfant après la naissance, pourraient être communs parmi les espèces longévifs ayant un développement, de la naissance jusqu'à l'indépendance alimentaire, se déroulant sur plusieurs saisons. De tels compromis peuvent affaiblir sensiblement les bénéfices de se reproduire saisonnièrement, et nos résultats ouvrent ainsi de nouvelles avenues pour comprendre l'évolution de la phénologie reproductive chez des animaux longévifs, y compris les humains.

Chapitre 4 : Déterminants évolutifs de la reproduction non-saisonnière de babouins chacma sauvages (prêt pour soumission)

La phénologie reproductive varie grandement de fortement saisonnière à non-saisonnière chez les animaux, parfois même parmi des espèces proches dans la phylogénie et/ou spatialement (sympatrique). L'intensité de la saisonnalité reproductive est souvent considérée comme un résultat de l'intensité de la saisonnalité environnementale, mais ceci ne permet pas d'expliquer les nombreux cas de reproduction non-saisonnière dans un environnement saisonnier.

Ici, nous étudions les déterminants évolutifs de la non-saisonnalité de la reproduction chez un primate sauvage, le babouin chacma, vivant dans un habitat tropical saisonnier, caractérisé par une forte imprévisibilité climatique. Nous testons trois hypothèses, proposant

respectivement que la non-saisonnalité de la reproduction a évolué en réponse à (i) l'imprévisibilité climatique (c'est-à-dire en réponse aux fortes variations climatiques inter annuelles) ; (ii) la compétition reproductive entre femelles du même groupe, favorisant l'asynchronie reproductive ; et (iii) des variations individuelles liées aux rangs des femelles des timings de naissance optimaux.

Nous avons trouvé du soutien uniquement pour l'hypothèse d'asynchronie reproductive : (i) la synchronie des naissances est coûteuse pour les femelles subordonnées, en allongeant leurs intervalles entre naissances, et (ii) les femelles ajustent leur phénologie de la reproduction (périodes de fertilité et conceptions) en fonction des autres femelles du groupe, et décalent leurs conceptions dans le temps.

Ces résultats indiquent de la compétition autour de la reproduction entre femelle, répondant à de la suppression reproductive d'un point de vue mécanistique, et certainement à de la compétition pour l'accès aux soins paternels d'un point de vue ultime, génère de l'asynchronie de la reproduction au niveau du groupe. Ceci contribue à affaiblir l'intensité de la saisonnalité de la reproduction au niveau de la population. Cette étude souligne donc l'importance de la socialité comme médiateur de l'évolution et modalités de phénologie reproductive chez des organismes grégaires, un résultat d'une grande portée pour comprendre les paramètres démographiques clés jouant sur les réponses de populations à l'augmentation des fluctuations climatiques dans le contexte du changement climatique global.

Chapitre 5 : Déterminants évolutifs de la reproduction saisonnière d'un primate longévif et social vivant en forêt équatorial (prêt pour soumission)

La saisonnalité de la reproduction est la norme chez les mammifères de régions tempérées où la saisonnalité environnementale est marquée, mais est moins fréquente, et souvent moins prononcée, chez des espèces vivant à basses latitudes. Notre compréhension des déterminants évolutifs façonnant les patrons de phénologie reproductive des espèces tropicales, est au mieux, fragmentaire. De plus, chez des espèces longévives pour lesquelles les cycles reproducteurs ne peuvent pas tenir au sein d'une seule saison, quelle(s) phase(s) de ce cycle, de la conception du jeune jusqu'à son indépendance, les femelles choisissent d'ajuster au pic saisonnier de nourriture, et avec quelles conséquences sur leurs valeurs sélectives, reste mal connue(s).

Ici, nous étudions les conséquences reproductives des variations des timings de naissance chez un primate longévif et à reproduction saisonnière endémique du bassin du Congo (le mandrill), en utilisant des données d'histoire de vie et comportementales provenant d'une population sauvage.

Premièrement, nous caractérisons les patrons de saisonnalités reproductive et environnementale, en montrant que la reproduction est hautement saisonnière, et que les ressources disponibles pour les mandrills sont affectées par les variations saisonnières des pluies. Deuxièmement, nos résultats montrent que ce pic étroit de naissances maximise la reproduction future (diminue les intervalles entre naissances) des femelles en ajustant le pic de lactation au pic saisonnier de nourriture disponible. Pourtant, et contrairement à la plupart des espèces à reproduction saisonnière, les femelles peuvent concevoir tout au long de l'année sans coûts détectables sur la survie de leurs jeunes, ce qui pourrait expliquer l'absence d'une saison de naissance stricte, comme souvent observée chez des espèces vivant dans des habitats riches. Troisièmement, nous révélons des variations de phénologie reproductive causées par la socialité : l'infanticide, provoquant vraisemblablement des avortements spontanés saisonniers, favorise un pic étroit de naissances, alors que le rang social des femelles diminue l'intensité de la saisonnalité reproductive, dans la mesure om les femelles dominantes se reproduisent moins saisonnièrement que les subordonnées.

Globalement, ces résultats soulignent les patrons flexibles de phénologie de la reproduction chez des espèces longévives vivant dans des environnements riches et tropicaux, proposant ainsi un éclairage nouveau sur l'évolution de la saisonnalité de la reproduction chez ces espèces. Ces résultats peuvent en outre aider à mieux prédire les conséquences démographiques des changements de saisonnalité environnementales provoquées par le changement climatique global pour des mammifères tropicaux longévifs.

Chapitre 6 : Saisonnalité de la reproduction et variations environnementales des *Papio* et proches cousins (en préparation)

Peu d'études ont étudié l'écologie et l'évolution de la saisonnalité de la reproduction chez les vertébrés tropicaux, qui montrent pourtant une grande diversité de phénologie de la reproduction. Cette diversité peut refléter l'imprévisibilité climatique marquée (variations inter-annuelles) qui caractérise la majeure partie de la zone intertropicale. Ici, nous rassemblons la saisonnalité des naissances et environnementale de 16 populations sauvages de

sept espèces de primates africains, de grande taille et terrestres de trois genres: *Papio*, *Theropithecu*s et *Mandrillus*. Nous étudions l'influence de multiples composantes de la variation temporelle des précipitations sur l'intensité de la saisonnalité de la reproduction, ainsi que la phase du cycle reproductif de la femelle ajusté avec le pic annuel des ressources. L'intensité de la saisonnalité des naissances varie considérablement entre les espèces et au sein de celles-ci, ce qui indique une flexibilité sans précédent de la saisonnalité de la reproduction chez ces populations. Au travers de nos multiples mesures de la variation climatique, l'imprévisibilité des précipitations est le seul prédicteur significatif de l'intensité de la saisonnalité de la reproduction: d'importantes variations inter-annuelles de la quantité de précipitations entraînent la perte de la saisonnalité de la reproduction. Enfin, nous trouvons des patrons très divers de phénologie de la reproduction, où certaines populations ajustent le pic de lactation avec la saison la plus productive - un modèle commun chez les mammifères. Cette étude apporte un éclairage nouveau sur les pressions sélectives qui façonnent la saisonnalité de la reproduction chez les mammifères tropicaux à rythme de vie lent, en révélant des variations intra-spécifiques, ainsi que l'influence clé de l'imprévisibilité climatique, ayant favorisé l'évolution d'une phénologie de la reproduction flexible. Enfin, compte tenu des convergences écologiques et des nombreuses caractéristiques partagées entre ce groupe de primates anthropoïdes terrestres africains et les premiers humains, cela contribue à une meilleure compréhension des pressions climatiques favorisant l'évolution d'une saisonnalité de la reproduction faible et flexible chez les premiers humains.

DISCUSSION GENERALE

1/ Conséquences des timings de naissance sur le développement, le comportement et la valeur sélective des mères et leurs petits

Au travers de cette thèse, nous avons révélé de nombreuses conséquences de la saisonnalité de la reproduction, et plus exactement de l'importance du timing des naissances dans le cycle annuel, à la fois sur la valeur sélective de la mère, et des jeunes. Tout d'abord, (i) nos résultats suggèrent que le timing de la grossesse peut affecter le développement du jeune, avec une coloration (et donc un développement morphologique) plus rapide pour les petits des mères ayant eu une grossesse avec beaucoup de nourriture disponible dans l'environnement (Chapitre 2). De plus, les naissances qui ajustent le pic de lactation avec le pic saisonnier de nourriture tendent à maximiser le rythme reproductif de la mère (soit à minimiser les

intervalles entre naissances, c'est-à-dire à maximiser la future reproduction de la mère) pour nos deux populations (Chapitre 3 & 5). De plus, pour les babouins, nous trouvons que les timings de naissance ajustant la fin du sevrage avec ce pic saisonnier de nourriture maximisent la survie des jeunes. Les jeunes nés hors de ce timing optimal, avec donc un risque plus élevé de mourir, répondent à cela en augmentant leur crise de colère pendant le sevrage, un comportement typique chez les primates (Barrett & Henzi, 2000; Maestripieri, 2002).

2/ Déterminants évolutifs de la phénologie de la reproduction : pourquoi donner naissance à ce moment de l'année ?

Les babouins et espèces proches ont des caractéristiques spécifiques (flexibilité du régime alimentaire, nourriture de remplacement pendant la saison sèche, grande taille et capacité de stocker de grande quantité d'énergie : Swedell, 2011) leur permettant démarrer leur reproduction et de concevoir tout au long de l'année, et ainsi, les conceptions n'ont pas tendance à se produire exclusivement pendant la bonne saison de l'année (Chapitre 6). Ces espèces peuvent donc stratégiquement faire correspondre une autre étape de leur cycle de reproduction avec le pic alimentaire saisonnier.

Notre analyse comparative a révélé que, même si le pic de lactation a tendance à être préférentiellement synchronisé avec le pic de nourriture annuel, tout comme la plupart, si c'est tous, les mammifères vivant à plus hautes latitudes (F. H. Bronson, 2009; Franklin H. Bronson & Heideman, 1994), ce n'est en aucun cas la seule stratégie rencontrée chez les babouins et espèces apparentées (Chapitre 6). En effet, un bon exemple de l'importance du sevrage sur les pressions sélectives affectant la phénologie de la reproduction a été fourni par notre étude de population sur les babouins chacma (chapitre 3). L'existence de compromis reproductif sur les timings de naissance optimaux entre reproduction actuelle et future pourrait se retrouver chez de nombreuses espèces à rythme de vie lent, et peut ainsi contribuer à expliquer l'absence de patrons de phénologie de la reproduction communs à toutes les populations tropicales.

Plus largement, ce manuscrit souligne le fait que la phénologie de la reproduction optimale est plus complexe qu'on ne le pensait auparavant (F. H. Bronson, 2009), et que faire correspondre le pic de lactation avec la meilleur saison n'est en aucun cas la stratégie adaptative universelle chez les mammifères tropicaux. La phénologie de la reproduction des

espèces à longue durée de vie vivant sous les tropiques reste donc peu claire, et peut dépendre de nombreux facteurs jusque-là omis, tels que la qualité de l'habitat.

3/ Déterminants évolutifs de l'intensité de la saisonnalité reproductive

A travers ce travail, nous révélons de nombreux facteurs, à la fois climatique, d'histoire de vie, et sociaux, affectant l'intensité de la saisonnalité de la reproduction (voir Figure 1 de la discussion générale). Nous montrons (i) que même des individus omnivores vivant en régions tropicales voire équatoriales subissent des variations saisonnières de quantité de nourriture disponible. Puisque la plupart des, espèces perçoivent de la saisonnalité de leur ressource disponible, deux moyens principaux peuvent mener à l'évolution de l'absence de saisonnalité de la reproduction. Premièrement, la reproduction saisonnière ne représente qu'une adaptation parmi d'autres à la saisonnalité environnementale. Les espèces peuvent utiliser d'autres stratégies, telles que la capacité de stocker de l'énergie, d'utiliser des aliments de remplacement ou de changer de diète pendant la saison difficile, d'augmenter les soins allo-parentaux pendant la période difficile ou de réduire les coûts d'énergie associés à la reproduction (grâce à une reproduction plus lente par exemple) (Brockman & van Schaik, 2005a; Heldstab et al., 2017; Jönsson, 1997; Stephens et al., 2014; van Woerden et al., 2010). Deuxièmement, d'autres facteurs écologiques ou sociaux peuvent conduire à une diminution de la saisonnalité de la reproduction, et sont discutés à travers nos résultats principaux.

L'imprévisibilité de l'environnement, c'est-à-dire la quantité de variation interannuelle de pluie, diminue la saisonnalité de la reproduction des babouins et proches cousins, comme cela avait été montré uniquement chez les ongulés (English et al., 2012). En effet, dans des environnements peu prévisibles, il peut être plus avantageux pour les individus d'évoluer vers différentes adaptations que la saisonnalité reproductive, comme une capacité à stocker de l'énergie (Brockman & van Schaik, 2005a; van Schaik & van Noordwijk, 1985), à élargir son répertoire alimentaire (Grueter, 2017), à augmenter son temps de recherche de nourriture par jour (Alberts et al., 2005; Grueter, 2017), ou à moduler la durée de lactation (van Noordwijk, 2012) (voir le chapitre 6). L'imprévisibilité de l'environnement peut donc être un facteur climatique majeur expliquant l'évolution de la faible saisonnalité de la reproduction, chez les babouins, mais aussi chez l'homme et d'autres espèces à forte flexibilité écologique (et notamment avec une grande aire de distribution) (chapitre 6).

Au-delà de facteurs climatiques, ce travail a montré que l'histoire de vie des espèces peut également moduler l'intensité de la saisonnalité reproductive. En effet, le fait que les timings de naissance dans le cycle annuel peuvent causer un compromis reproductif peut impacter l'intensité de la saisonnalité reproductive. L'existence de deux timings de naissance distincts, maximisant la reproduction présente ou future, diminue l'intensité de la saisonnalité reproductive chez les babouins (Chapitre 3), alors qu'en l'absence de compromis reproductif a chez les mandrills, car il est plus avantageux pour les femelles de donner naissance dans le pic saisonnier de naissances, ce qui favorise donc l'évolution de la saisonnalité de la reproduction (Chapitre 5). De plus, notre travail suggère que de forts taux de mortalité extrinsèques (due à de la prédation, infanticide ou maladies non saisonnières) pourrait réduire la saisonnalité reproductive. En effet, la capacité de pouvoir entamer une nouvelle reproduction après la mortalité d'un jeune (non sevré) quel que soit la saison de l'année peut être avantageux pour les populations avec un fort taux de mortalité infantile. Toutefois, une étude comparative et/ou un modèle théorique serait nécessaire pour déterminer l'influence de la mortalité infantile extrinsèque sur l'intensité de la saisonnalité reproductive.

Chez les espèces sociales, des facteurs sociaux peuvent également affecter l'intensité de la reproduction saisonnière. (i) Nous avons mis en évidence avec les babouins chacma (Chapitre 4) que la compétition entre femelles autour de la reproduction, certainement pour l'accès à des soins paternels, entrainant de la suppression reproductive (plus intense pour les femelles subordonnées) entraine une diminution de la saisonnalité reproductive, contribuant à l'absence de saisonnalité reproductive chez cette population. La compétition entre femelles entrainant de la suppression reproductive est relativement commune et répandue chez de nombreuses espèces sociales de mammifères (T. Clutton-Brock & Huchard, 2013; Stockley & Bro-Jørgensen, 2011), et notamment de nombreux primates (Beehner & Lu, 2013), toutefois, ses effets sur la synchronie et/ou saisonnalité de la reproduction ont rarement été quantifié. (ii) De plus, nos travaux montrent l'importance du rang des femelles comme facteur individuel affectant fortement le succès reproducteur et la phénologie reproductive. En effet, par exemple, chez les mandrills (Chapitre 5), la distribution bimodale des intervalles entre naissance, où les femelles dominantes tentent de donner naissance tous les ans (même si l'intervalle de naissance moyen est légèrement supérieur à un an) alors que les subordonnées donnent naissance une fois tous les deux ans en moyenne, provoque une diminution de l'intensité de la saisonnalité reproductive à l'échelle de la population. De plus, et plus généralement, le rang des femelles affecte différentes composantes du succès reproducteur

(Pusey, 2012), comme les intervalles entre naissance, mais aussi la mortalité infantile ou le taux d'avortement, et ainsi, les pressions de sélection favorisant certaines dates de naissance dans le cycle annuel peuvent influencé différemment les femelles selon leur rang. (iii) Enfin, nous montrons que la relation entre infanticide et saisonnalité de la reproduction est plus complexe que précédemment pensé. En effet, même si l'infanticide est adaptatif dans les populations non-saisonnières (Lukas & Huchard, 2014), et la non-saisonnalité est souvent adaptatif en réponse à l'infanticide, nos résultats sur les mandrills (Chapitre 5), mettent en évidence qu'un risque d'infanticide saisonnier peut au contraire mener à une diminution de la largeur du pic de naissance.

Conclusion générale

Ce travail met l'accent sur le fait que ne s'intéresser qu'aux effets de la saisonnalité climatique sur la survie des descendants est loin d'être suffisant pour pleinement comprendre l'évolution de la saisonnalité de la reproduction. En effet, dans nos études populationnelles, examiner exclusivement la mortalité post-natale des jeunes avant le sevrage en relation avec leur timing de naissance nous aurait amené à conclure que les mandrills devraient être des reproducteurs non saisonniers, tandis que les babouins devraient être des reproducteurs saisonniers. Premièrement, l'imprévisibilité climatique, et non seulement sa saisonnalité, peut être un facteur majeur affectant l'intensité de la saisonnalité de la reproduction, en particulier sous les tropiques. Deuxièmement, la prise en compte de l'histoire de vie et de la socialité est essentielle pour comprendre les conséquences de la saisonnalité de la reproduction sur la valeur sélective de la mère et de sa progéniture, et donc de l'évolution de la saisonnalité de la reproduction. En effet, nos résultats montrent que des déterminants écologiques et sociaux interagissent avec le cycle biologique des espèces pour façonner la saisonnalité de la reproduction des mammifères (Boinski, 1987; Canu et al., 2015; Moe et al., 2007; Rutberg, 1987; Sinclair et al., 2000; Tinsley Johnson et al., 2018). La figure 13 résume les différents déterminants évolutifs, environnementaux, sociaux, mais aussi des facteurs additionnels au niveau de l'espèce (rythme de vie, taille, prédation) ou au niveau individuel (rang, âge, condition), à l'origine de la diversité des intensités de la saisonnalité de la reproduction – de la reproduction non saisonnière à la reproduction extrêmement saisonnière – observée dans le règne animale.

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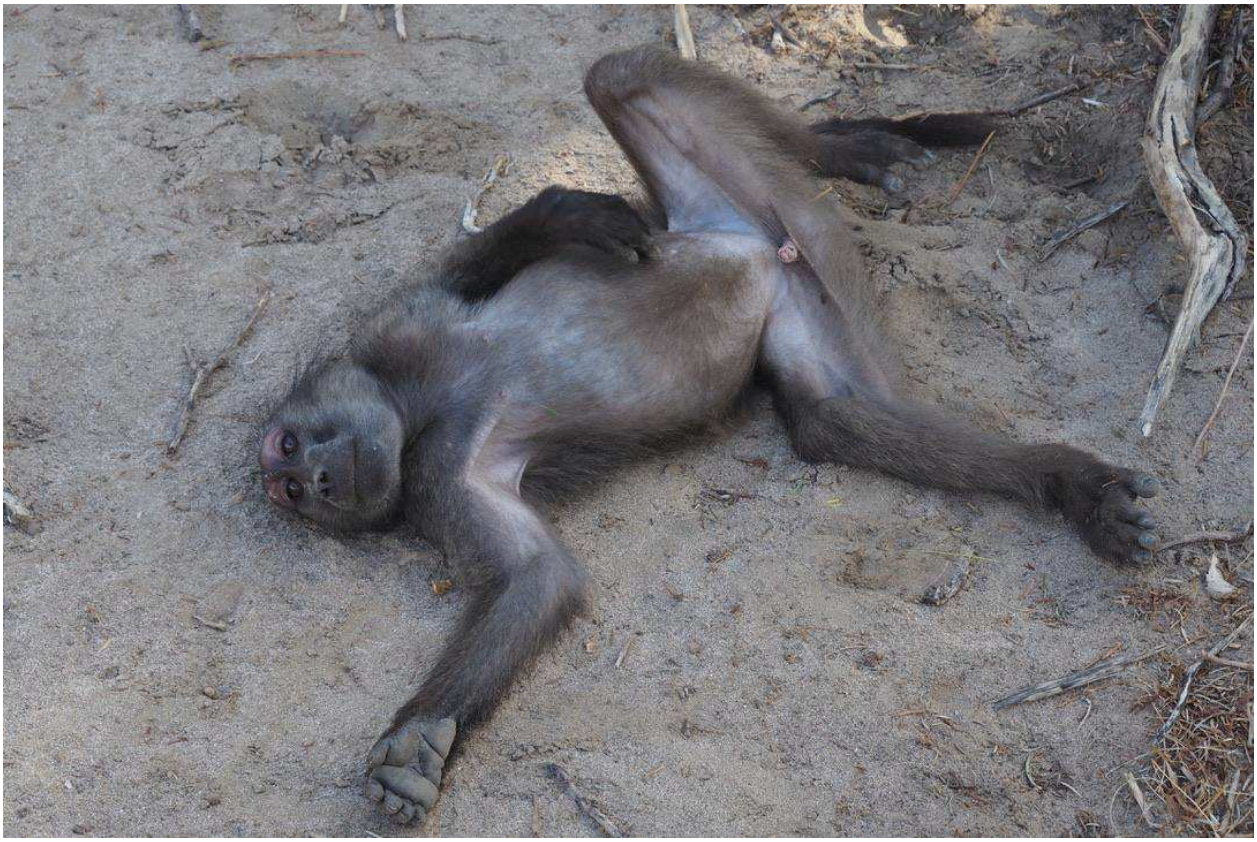

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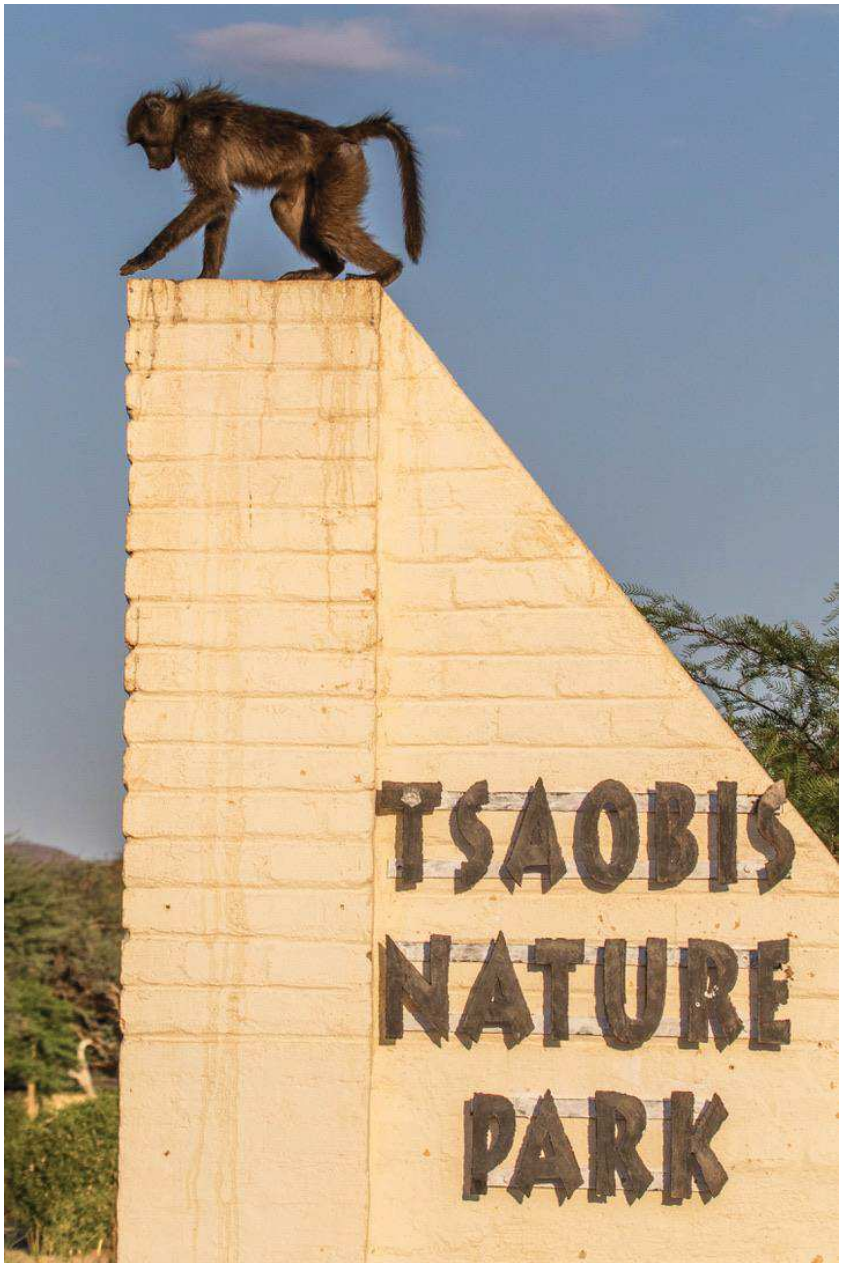
A couple of baboon stories



Here are some baboon stories written by volunteers at the end of each field season. They chose to express whatever they wanted that happened during the field season, and these wee stories are also used in the yearly Tsaobis Baboon Project report. It can give you a glimpse of how wonderful (or not) can be a field season at Tsaobis, and how addicted to baboons we can all quickly become there.

Giving us the Run-around

By Charlotte Bright

My time at Tsaobis was full of so many amazing ups and downs I would never have dreamed of that I wasn't sure which story to retell here. Tsaobis wasn't just the physical challenge of surviving 3.50am starts and 15-hour days in the searing desert sun. Or getting so sunburnt, because the baboons were hogging all the shade, that I wasn't sure if my skin would ever recover. Or the genuine fear of having a confrontation with one particularly troubled baboon called Byron. It was also our futile attempts to prevent curious young baboons from touching, licking and grooming us and our field gear. And getting to see the tiny pink little faces of newborn babies peeking out from their mother's embrace. It was the excitement and joy of rescuing a baby jackal and returning it safely to its den. And it was the unexpected comedy show when I first saw the baboons swimming around in rock pools like otters, splashing and dunking each other into the water, that made this experience so amazing.

The baboons provided endless entertainment and funny antics, as well as completely unexpected behaviours I had no idea they were capable of. But one of my most memorable experiences didn't actually involve our baboons at all. It was an afternoon in our first or second week, before we really knew the baboons or the landscape that well. We were following L troop back along the Swakop riverbed, on the home stretch before inevitably ending up at Baboon Hill, their favourite sleeping cliff. Trying to get away from the blinding dust kicked up by the afternoon winds, we followed a subgroup up towards the hills around the Potberg mountain. After leading us through one valley, the group reunited with the rest of the troop who had evidently come to meet us in the hills. After a bit of wahoo barking and uncertainty, the baboons picked up the pace, and started a fast-march up into the mountains. Great, we thought. Just our luck that the day L troop decide to stay at the infamous L024 sleeping cliff for the first time is also the day they're with the two research assistants who are terrified of heights! So we did our best to keep up, climbing all the way up a steep slope, layered with treacherous crumbly rocks, plants with hooked thorns, and sheer cliffs dropping off below us. Reaching the top out of breath and shaking from nerves, we looked down to see the troop waiting for us at the bottom of the next valley, ready to start the ascent of the next hill.

Frustrated, we climbed down as quickly as we could, and continued the chase, determined not to fall behind and lose the troop. After following the baboons over another two hills with no sign of slowing down, we gradually came to our senses and realised that the baboons were cleverly keeping their distance about 30m from us - close enough that we had naively thought nothing of it, but far enough that we couldn't actually see their ear notches even with our binoculars. We suddenly realised that this running over the hills just out of reach was such strange behaviour for L troop because it wasn't L troop at all! We had accidentally picked up another troop and begun pestering these poor animals into a chase we were never going to win, whilst they politely allowed us to follow at a safe distance.

Exhausted mentally and physically from our climb, and panicked because we had now lost L troop for several hours, we stopped our climb and looked around us, defeated. Despite everything, we had climbed to an amazing viewpoint somewhere in the mountains, able to see the whole of the Tsaobis landscape, from the flat plains in the East, to camp, and past over to the hills in the West. So we cheered ourselves up with a photoshoot in this stunning scenery. After a

long and terrifying climb back down to the riverbed, and on our walk back to camp just before dark, we of course bumped into L troop who were just settling down for the evening on Baboon Hill as if nothing had happened.

For me, this experience was a good analogy for a lot of my time at Tsaobis. It was stressful, exhausting, and just as everything seemed as if it was going wrong, there was a great silver lining that made it all worth it. Plus, everything turned out fine in the end!

Lightning Doesn't Strike Twice… Right?

By Chloe Hartland

Tsaobis has provided me with some of the most amazing memories I'll probably ever have, so it's quite hard to pick one to talk about. But mid-way through the field season we had a few days of humidity that led to some beautiful thunderstorms and rain, and one very close lighting experience.

You'll soon learn that if L troop rest at the old plantation for their midday nap that you should start to worry that the dreaded L024 sleeping cliff may be on the cards for the night. So I was watching the first movers of the troop like a hawk, mentally trying to steer them back to good old Baboon Hill. However, as I was trying to achieve mind control and change Varicella's mind (Varicella is the dominant female, and so exerts some influence over where the troop moves), I noticed in the distance a dog had dug itself a huge hole around the fencing of the plantation with just its head sticking out. I told Remi my field partner and we went to investigate. Now normally dogs and baboons don't get along and it causes a lot of barking from both sides, but this time the dog seemed unbothered and the baboons were just as unphased and curious. After slowly approaching the dog lying in its hole, it barely raised its head to look at us, let alone flinch when we touched it. I had never in my life before seen an animal that starved, and we soon noticed he was tangled in the wire from the fence and couldn't escape. So Remi decided to carry the dog back to camp and I'd continue with the troop and we'd join up again later. I then immediately realised that instead of heading west back to camp L troop were in fact heading very much south which could only mean one thing, I can't use mind control and L024 was a nice little trek ahead of us!

The further we walked into the mountains the stormier the atmosphere became. As we reached the waterhole by the sleeping cliff the baboons started to drink and play, and the thunderstorm broke. Despite how big and scary baboons can look they are in fact massive wimps. They ran for cover in holes in the rocks and under trees, leaving me with just a small rock to give me a little cover from the pelting rain. The thunder was echoing and rumbling off the mountains and making the ground shake, and the baboons were barking and wahooing back to it. Looking to my side under cover was Catscratch and Narco, two of the older juvenile males, skinny and lanky but still big. Looking at them huddled up and cuddling – with Catscratch lip-smacking (a friendly gesture) to every baboon in sight for comfort (I even got lip-smacked, but kindly refused) – you realise how soft these big animals can be. By now the lightning had started to get closer, and soon enough I could see it striking the floor 20m away. Being on an exposed mountainside carrying metal objects, I was a little more than scared. After 20 minutes with my eyes shut hoping not to get struck, some brave baboons decided to start walking again so I slowly crawled out and over the now very slippery rocks and started to follow. At that moment, my radio burst into life: it was

Remi telling me to come back asap as the weather was too dangerous to be out in the field. Safe to say, I immediately turned back round and ran the hour-long walk down the mountains. Back to safety and thanking my lucky stars I hadn't been hit by lightning, I found out our pup (named Lucky) had eaten a ton of food and drunk a lot of water. He stayed with us for a few days till he set off again, out into the wilderness with a full tum and hopefully safe. Which kind of made the whole near lightning strike all worth it… (*kind of*) and made me realise baboons can be some of the cutest animals out there.

Spare a Thought for the Cars at Tsaobis

By Nick Matthews

The hilly, sandy and scorching hot terrain at Tsaobis Nature Park in Namibia is definitely a tough environment to enter in to, especially coming from the cold countryside of the UK. However, it became apparent early in the field season that we humans have it easy compared to the vehicles that must take on the makeshift roads along the hills and dry riverbed of the Swakop. In my first week at Tsaobis, we took the two cars at our disposal for a spin along the riverbed which seemed easy enough. However, one of the cars that was sold to us as a '4-wheel drive' managed to get stuck in the sand almost instantly. We quickly came to the conclusion that the car was a 4-wheel drive in which the 4-wheel drive function didn't actually work. When we tried towing the car free with our other car (which had all 4 wheels working) that too almost got lodged. Luckily, there was a group of geology enthusiasts visiting Tsaobis for a workshop. They had their own fleet of working 4-wheel drive cars and were kind enough to drive over and help us out of our predicament. About five minutes after they set us free, the car got stuck again. And again, and again. This whole ordeal took place in the middle of the day, took about two hours, and ended with the geologists having to tow the car all the way back to camp. Needless to say, after that the car had to be returned to Windhoek and exchanged for a working 4-wheel drive.

A couple of days later, we went to set off down the riverbed again in the one working 4-wheel drive we had left. En route, the car's electrics kept cutting out which, understandably, we thought was quite strange. However, when the car's electrics cut out for the last time, we noticed smoke coming from under the bonnet which obviously isn't meant to happen. Upon opening the bonnet, the car burst into flames which, at the best of times, is definitely a cause for concern. However, in one of the driest environments in the world, this turns into a potentially very big problem. With the worry of causing an enormous desert fire in the middle of the riverbed and wiping out the entirety of vegetation at Tsaobis, we quickly fled the car and began to run back to camp for help. Because we didn't have another car to come to the rescue (see above) we had to call on our friends the geologists again. Luckily, they were still in camp relaxing – until we radioed them for assistance, asking them to bring as much water as they could. Fortunately they reached us before the car exploded and put out the fire. After this the car had suffered badly from the fire and, yet again, the geologists had to tow another casualty back to camp. That would be the last time we would see that car, as it had to be taken to Swakopmund for new parts and wouldn't be repaired until after my field season was over. We then had to complete the entire field season with just one car, which was hard, but we made it work. So, as tough as the field season can be for humans, it seems that cars definitely have it worse!

The Smarter Cousin

By Vittoria Roatti

Despite all the craziness of following wild baboons in Namibia during the summer season, like carrying six litres of water just to survive, to the almost unbearable heat and following baboons for 14 hours a day, I had lots of great and unbelievable experiences at Tsaobis. These included running away from a sand tornado, hiding in caves with baboons during a rainstorm, climbing through narrow gullies to follow the crazy guys of J troop hunting for natural pools after the rains, taking part in a rescue mission to save a zebra, and, most importantly, sharing the daily life of wild baboons. The greatest challenge I faced, though, was outsmarting naughty juveniles. And I didn't always succeed.

Working with baboons you can never get bored or distracted. In fact the first time a curious juvenile sees you taking a break, perhaps caught in your thoughts or lightly napping, it will surprise you by showing its face a few centimetres from yours or chewing one of your backpack's strings or literally shaking you out of your sleep. Actually, don't get too concerned, I am referring to a particularly naughty juvenile, the other naughty ones were not even close to his evilness! Coelho, a young male of whom I had been warned since the beginning, but who was too smart and bold to be avoided forever (see photo 5, back page). After I'd frustrated several of his attempts to touch me, he eventually sneaked behind me and touched me on my leg so gently that I took a few seconds to realize it. Looking down I met his gaze, stamped on the cutest face possible in search of approval. At that point, with my heart racing and praying he wouldn't scream or jump on me, I slightly moved and he surprisingly walked away, but his pace clearly showed his excitement for the new game he had discovered.

After pestering me for a couple of weeks, Coelho eventually got bored of the big hairless baboon who refused to play with him. But before that happened, he still managed to give me an awkward wake-up. There had been a period in which J troop used to sleep on hillsides, inside caves, during the hottest part of the day, which often left the unfortunate observers with no available shade for themselves. One day the baboons were resting in a big cave that still had a fair amount of space for me to fit in. During my break I lay down, exhausted by the heat and, a few minutes later, when I was already half asleep, I felt something pull at my shirt. I opened my eyes and the familiar face of Coelho appeared in front of me, apparently amazed by the consistency of my strange body hair. Before I could even think about how to get rid of him, the big male Dickens came over, displaced him, and sat down less than 1m away from me. I froze while he calmly looked at me, as if he were asking what was wrong. Though grateful to Dickens, the cave was definitely becoming much too crowded, and I crawled out to seek shelter under an uncomfortable small bush instead.

Despite being super cute and funny, I was glad that Coelho resumed (almost) the normal behaviour you would expect from a wild animal, relieving me of the worry of what his excessive confidence might lead to. Still, I didn't feel like I had won: baboon behaviour was more complicated than I'd expected and I struggled to put into practice what I needed to do about the juveniles' excessive confidence. It is not simply a question of moving away, because the juveniles could interpret that as a sign of submission. Rather you have to move while playing the part of one who'd already intended to move prior to being importuned, meanwhile avoiding abrupt movements of course. Although belonging to the most intelligent ape species on Earth, I was sure my baboon etiquette hadn't been good enough to outsmart my hairy cousin. But he apparently appreciated the effort and compassionately decided to leave me alone.

Mission (almost) Impossible: Observations of Shy Young Baboons

By 'juvenile' Jules Dezeure (1st season)

In just three-and-a-half months of fieldwork this year (so quite a short field season), we experienced a large number of adventures/problems. Our car burning in the riverbed? Done. Trying to save a dying zebra with its leg caught in a snare? Done. Volunteers being bitten by teenage baboons being a bit too weird and confident? Done. Fixing a gas fridge? Done. Being the witness of a farmer shooting and killing a baboon sitting a few metres away from us? Done. Having our campsite and our tents almost flooded by the Swakop river? Done. A meteorite falling on our office bungalow? Not done, we will keep this one for next year…

But I will not talk about these particular events right now. I focus here on our daily field days at Tsaobis, and the difficulties accompanying these more typical days. This year, as part of my PhD, our field observations were focusing on young baboons' development and conflicts with their mothers (see photos 1 and 2, back page). As my supervisors had warned me, it was very tough to follow and observe young baboons from 4 to 24 months old. Young ones are really hard to distinguish from one another. We were able to differentiate some of them after capture thanks to our markings (tissue biopsies are taken as ear notches), but conducting observations on un-notched individuals remained an impossible mission because they love to play with others also un-notched and you quickly lose track of who's who. Unlike adults the youngsters play a lot, and they don't walk from one food patch to another, they run. But you, the observer, cannot run, or all the baboons around you would freak out, which makes it very hard to follow the young ones. Lastly, they are tiny, and in a massive food patch like a *Prosopis* tree or *Salvadora* shrub, it is often impossible to keep them in sight.

I will now introduce you to Scabies. She is the shyest and the most fearful baboon of our habituated troops. She is Verruca's baby (a dominant female) and 18-months old. It is impossible to get closer to 15m from her without her panicking or running away. She never "travels" like other baboons, she "runs" or "sprints" all the time. She was the most difficult one for us to study and to obtain a full 'focal' observation, which involves 20 minutes of uninterrupted data collection. When you start a focal on this one, you know it will be a physical and mental challenge to finish it!

I remember very well a focal I did with her in the Swakop riverbed. I lost her, after a common "travelling running-sprinting" episode, just a few seconds before the end of my focal. Now when this happens a countdown launches: I have 10 minutes to find her again, or I will lose all the data I struggled to get during the first 19 minutes…. I walked around the troop, identifying all the young ones around. Time is running out. Just two minutes left to find her. Stress and frustration starts to rise. I try to remember where she was heading just before losing her, and I try to look for her mother, sisters, and good friends with whom she is often around. And suddenly, a bit far from me, alone, and running away (of course): Scabies! Just on time. What a relief. I have rarely been so happy during these last few months in the field, even though it's not a big deal and common to lose a baboon during focalling. I think it is a good example of how at Tsaobis baboons are your only obsession! From dawn until dusk, you walk among baboons, live and interact with them; and even during the night, after a while, you dream about them!!!

My Time at the Tsaobis Baboon Project

By Ndapandula Shihepo

I packed my bags to go do an internship at the Tsaobis Baboon Project, my very first internship on wild animals. I had little to no expectation, as I did not know much about chacma baboons, apart from being social animals, well adapted to arid or semi-arid environments, and usually known by people that live in close contact with them as problem animals. The beginning was tough as I was not used to mountain hiking and I knew nothing about how to behave around baboons, their ear notch combinations (used to identify individuals), or their names. Even then, I was determined to learn how to collect data on wild baboons, and to know more about their behaviour, their interactions, and the composition of their diet in a place with little vegetation.

Time passed by, and I slowly got to know the baboons and to understand a few of their interactions, including the dominance hierarchy and the different families in the troops. After that, things became easier. I had a phrase in the back of my mind "You have to finish what you started''. It definitely becomes more interesting when you know who is interacting with whom, and who is attacking your favourite baboons. You feel pity for the baboons during attacks or fights, watch the infants play, and laugh out loud in the middle of the troop like some crazy person. And you are amazed by the way they can recognize their relative's loud screams from a distance, during attacks or threats, and run to each other's aid (like the brothers Byron and Virunga). Baboons are amazing primates when you get to know them. Field team members also have to learn how to behave with the baboons, and how to make observations without causing disturbance. But good behaviour around them will lead to fun times with the Tsaobis chacma baboons. Best is when they all run behind you during an intertroop interaction, because they somehow know the baboons in the other troop (who have not been habituated to human observers) are scared of you. You are the baboons' best friend at this point. Baiting and capturing the baboons were the most interesting things ever. I would like to do them over and over again. Plant phenology was also interesting but I think is more enjoyable during the rainy season when all the plants are alive.

In the process of adapting and learning, I have made mistakes here and there which I believe is one step among many other steps involved in learning. Although I felt disappointed and useless, I feel grateful for being granted this opportunity. Even when the beginning was tough, I will happily shout loud THE EXPERIENCE WAS THE MOST REWARDING. Thank you for granting me the opportunity to have my first hand on wild baboons. I hope I won't be the first and last Namibian volunteer to join the project. It is at the Tsaobis Baboon Project where you learn more than just chacma baboons. You are introduced to all sorts of life activities (as a researcher in the field) from being a baboon lover, to a mechanic, chef and cleaner. All in one, achieved through working with the best team members, who are always willing to give a helping hand. Every day you come back to camp (home) you have learned a new thing about baboons, wildlife, and life in general. Thanks once more for the opportunity. THE BEST TEAM I HAVE EVER WORKED WITH. Keep up with the good team spirit.

Never Trust the GPS

By Harrison Anton

Our time spent with the baboons at Tsaobis was marked by many highs. These included getting to know over 160 baboons, not only by their ear notches but by their faces, their personalities and who they liked to hang out with, against the 'geologically stunning backdrop' of Tsaobis and the Swakop river. To spend every day waking up to the most spectacular sunrises and putting the baboons to bed under more stars than I had ever seen in my life, was truly amazing. There were also lows, as there are with everything. Working during the dry season, we witnessed some of the harsher conditions the baboons had to endure in terms of food and water availability. As a result, we lost six pink infants in our time there, as well as the progeniture of so many in J troop, Libreville, with a few more looking like they were feeling the effects of the food scarcity as we left.

My first full day with the baboons was particularly stressful. Having followed J troop for a few hours the previous afternoon, fellow research assistant Ndapandula and I were tasked with finding L troop far to the east of camp using the radio antenna. (One of the females in L troop wears a collar fitted with a radio transmitter, allowing us to locate the troop using the antenna.) We walked into the mountains from the car for about 40 minutes, following the monotonous binging sound which was slowly getting louder and louder, until we crested a hill and stopped to drink some water and admire the view. And there they were, all 80 or so of them, walking towards us. Remembering what I thought was the correct procedure I froze still, stared into the distance and made shaky, 'calm' and stilted conversation to Ndapandula, attempting not to convey the fear in my voice at suddenly being in the presence of so many large wild primates. The baboons didn't seem to care at all and went on their way, weaving in-between us, the odd one stopping to look, but mostly just passing by. Sweating profusely, not only from the slowly rising temperature of the day, I quickly packed away the antenna and adjusted my bag and Ndapandula and I set off after them, deeper into the mountains.

We trailed them for about 45 minutes or so, climbing up and down slopes, along dry stream beds and over ridges, attempting to get close so as to attempt to start identifying individuals but, at least in my case, freezing and staring intently at the horizon if one came within 20m of me, or happened to glance in my direction, terrified of invoking their wrath. We reached a spectacular site on the GPS known as L073, which had a long-dried waterfall nestled between two steep slopes. The baboons stopped in the shade here, and we were treated to a truly spectacular site as the infants wrestled and chased each other up and down this vertical face of smooth rock, moving across its surface like spiders Every once in a while one would fall off and tumble 5m or more only to scamper back up to re-join its kin. It was around this point, in awe of the spectacle before us that I realised, to my horror, that I was no longer carrying the Yagi antenna or radio receiver. This expensive piece of equipment was now lying somewhere in the vast expanse of boulders and rock that we had spent the last hour traversing through.

Telling this to Ndapandula, we quickly checked our two-way radios were working (so we could keep in contact) and then I set off to try and find the antenna. As I reached the summit of the first hill, I realised that the GPS we had been carrying had recorded our path with a seemingly helpful blue line. With a new hope that I might now find the antenna I set off back along the exact route, according to the GPS, from which we came. It seemed a bit odd that the route I seemed to be following, which fell right on top of the cyan coloured line on the GPS, was taking me along paths

I had no recollection of taking on the way there. I reached the point where we last had the antenna and…. nothing. I searched under rocks and from vantage points, yet saw no sign of the blue carrier bag. So, I retraced the path again, and again, each time somehow veering from the exact path I had taken the previous time, until after eight journeys back and forth I had painted the screen of my GPS a faint cyan colour, marking the route I had taken. I radioed Ndapandula, who by this point had moved into the riverbed by the entrance to the park. She was okay and was still with the baboons. I was beginning to panic at this point. Stressed at the loss of the equipment and running low on water, I thought I would never find the antenna. On the 9th trek back along this now well-trodden route I had given up all hope of finding it and stumbled beyond the cyan path marked out by the GPS, to a point on the hill where we first saw the baboons, four hours before. There, lying perched on a large slab of rock as I crested the hill, was a long, thin, canvass case. It was an overwhelming feeling, the stress and panic combined with the exhaustion of hiking non-stop for hours in the heat, and I sank to my knees, praising whatever gods were out there. Cursing the GPS for the wild route it had taken me on, with the 25m or so it was out of sync by costing me four hours of hiking. Standing back up I collected the antenna and made my way to the car to drive closer to where I last heard Ndapandula was. We reunited at a spot in the dry riverbed which the baboons had chosen for their midday nap, and sat to have our lunch. The rest of the day passed with far less drama. Still wary of the baboons I did not get too close to them, despite their continued indifference towards our presence, and willingness to walk near us. They took us back to L073 that evening and I have never been so happy to finish a day's work as I was that day.

Their intimidating first impressions soon disappeared and each and every one of them left an impression on me. Whether it be because they pushed the boundaries with personal space, by rubbing against my legs like a cat (Coehlo), or performed acts of heroism in the defence of screaming pink and grey babies from goats and dogs (Accra). More human in their characteristics than many would like to admit, they were amazing to study for the three and a half months we were there for and despite the trials of the first day, it was an incredibly enjoyable and unique project to be a part of and one I would highly recommend.

The Infant Baboon Emotional Rollercoaster

By Anna Cryer

Going into the field season at Tsaobis, I had no idea what to expect. I imagined watching the baboons at a distance, perhaps 50 meters, and studying them from afar. As soon as we had arrived at the sleeping cliff on my first day in the field, Houston (a juvenile male) came down and touched another team member Tess's leg. Expectations of keeping a distance were lost already. This first day set the tone of our field season: expect the unexpected from baboons.

There are a number of standout moments, including chasing after Cavity, one of the infants, as she tantrummed for 45 minutes on the way to the dreaded L024, a remote waterhole and sleeping cliff; tracking down the elusive M troop and seeing the difference in their infants as they became accustomed to us following them rather than running off at first sight; the old male Accra being a hero and saving the other baboons from dogs on two occasions; and Pseudomonas, the sweetest low-ranking female, who carried her infant and kept up with the troop 3-legged for three weeks as it couldn't cling on properly, a truly unstoppable baboon. During the entire season I don't think I was ever as scared as when a little pink infant decided to try and climb up my leg and dangle from my bag (if the infant became distressed and screamed at any point, the rest of the troop would assume I had attacked it and retaliate)… who knew a baby baboon could induce so much fear. I avoided the pink infants for the rest of the week.

However, my favourite moment of the season was on the day that Baby Doyle was born. It took Rachel, my field partner, and I a long time to figure out who was carrying around this new tiny pink infant as we hadn't realised Doyle was even pregnant! Later that day, whilst watching Doyle and her infant sitting alone under a tree, Doyle picked it up and held her in the air whilst lip-smacking. Totally besotted, a real 'Lion King' moment. This little moment of joy lasted all of 30 seconds but to see Doyle's happiness with her new baby was precious. It was the small moments like this that really made the field season such an amazing experience.

A Friend in Need

By Tess Nicholls

It's difficult to comprehend or explain the range of challenges and achievements you experience during a field season at Tsaobis. Along with integrating into the lives of baboon troops and meeting lifelong friends, you discover and learn many skills you never knew you had, wanted or needed! You become a master mechanic, changing an average of a tyre a week, while confidently misdiagnosing mysterious engine sounds and issues. Bread-making becomes a contest - who can create the perfect loaf? After exhausting the familiar tomato pasta dinners, each meal is welcomed as a challenge to create new cuisine with the relatively limited food stock available. Picking acacia thorns from your hiking boots becomes everyone's favourite pastime. You are acutely aware of the shifting lunar cycle and every night, treated to a spectacular display of stars.

While there were many beautiful moments that stick in my mind, the one I will recall here left my field partner and I marvelling at the ingenuity of one small baboon. We were following M troop and had found ourselves at a commonly frequented waterhole in the Swakop riverbed. This particular waterhole is a manmade well and is partially covered by a metal mesh, presumably originally installed to keep baboons out! To reach the water, they must climb down a hole in the wire before descending to the water below. One individual – The Gambia – had entered the well with her infant clinging to her back but when she came back up she had left her baby below the wire mesh. The infant was crying for help and unable to climb out. At first, various members of the troop came to investigate the noise, including Homer, the infant's father, but eventually the troop started to move away despite the infant's cries. The Gambia began trying to pull her infant through the wire but the holes were much too small for a baby baboon to fit through – the only way out was through the big hole further along. This continued for about 10 minutes while everyone involved became more and more distressed (us included - we had heard horror stories of baboon infants falling into wells). Suddenly, a slightly older infant we call AdelaideInf appeared. She climbed over the wire and swung down into the hole, clearly showing the stuck baby the way out! She repeated this process a number of times until the baby was able to copy AdelaideInf and climb free. Safe to say we all breathed a sigh of relief, including The Gambia who quickly put her baby safely back on her back and caught up with the rest of the troop.

Perhaps my favourite time of day is the final part of the walk to the sleeping cliff in the evening. The sun radiates colour and warmth and you feel truly part of the troop, all moving silently towards the cliff. One particular evening we had arrived early to Baboon Hill. The trials and frustrations of the day's data collection finished, we sat and watched as most of the infants and juveniles of L troop began playing together. I will forever be grateful for my time at Tsaobis, and hope very much to return one day.

Accra: the Humble Hero of L Troop

By 'sub-adult' Jules Dezeure (2nd season)

The 2019 field season was a lot easier than last year. The troop captures went smoothly, our data collection was efficient, the baboons were well behaved with us, and the volunteers worked hard and well without complaining, as well as the cars (almost all the time)! So I won't talk about the difficulty of completing focal follows on fast-moving infants as I did last year. Rather, I'll focus on a particular event that happened in the middle of the field season.

L troop, our largest troop with more than 80 baboons, was foraging in 'the plantation', a long-abandoned plot on the south bank of the Swakop River. After a while, they were joined by the Tsaobis goats, along with their three guard dogs. We were familiar with these dogs (Poupip, Bobby and Speedy) as they often came to our bungalow in camp for food and water. As usual when the baboons meet the goats, they gave alarm barks and fled from the area, afraid of the three dogs. But today, in the middle of this malarkey, Plague – a young, adolescent baboon – got trapped in a tree alone and was panicking. He repeatedly called to the other baboons running away for help, but no one seemed to take any notice…

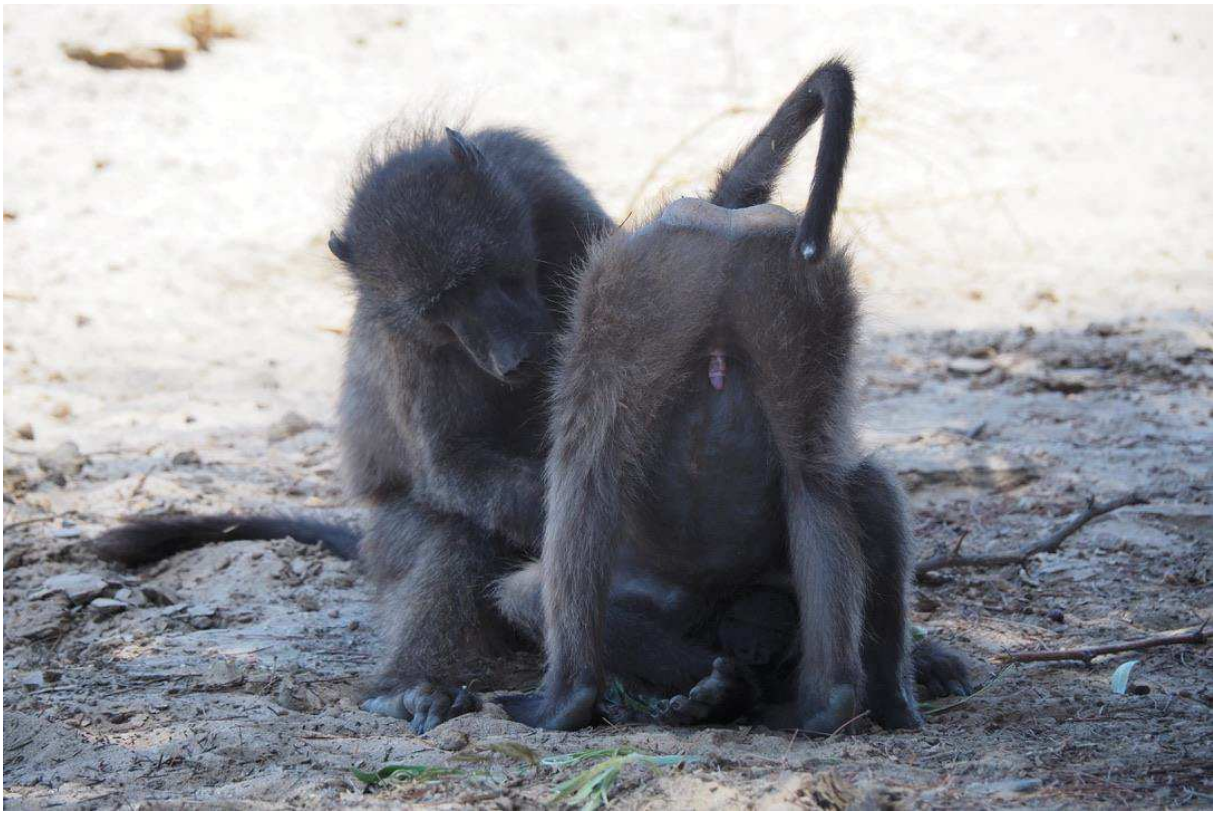
Then, after two or three minutes, coming from nowhere, Accra arrived. Accra is the grandpa of L troop (see cover photo, and photo 1, back page). He is around 14 years old (which is quite old for an adult male baboon), always accompanied by a bunch of juveniles, and a very good daddy. Accra sprinted towards the three dogs, chasing them away from the tree. It was a really bold move, and worked well. At least for Plague who, during this distraction, was able to escape the dogs and reach the other members of the troop.

Unfortunately it didn't work so well for Accra. Indeed, his attack really angered the three dogs, who then chased him very aggressively. Accra managed to find a shelter in a small tree, but he was now far away from the rest of the troop. Accra was calling to his groupmates, with wahoos and contact calls, but no one came to help him. The three dogs were now really worked up and barking at him continuously, trying from time to time to climb up the tree, but fortunately without success. Accra was answering by shaking branches, grinding his teeth, and foaming a lot. This situation lasted an hour and a half. It was a complete stand-off, and very stressful for Accra.

I was watching this scene with a volunteer and between us we tried to distract the dogs, and hold them away, but one of them (Bobby) was just out of control. Accra was clearly looking at us when we were trying to hold them, just waiting for the first opportunity to jump and run after the other baboons of the troop. Finally, after more than one hour of intense struggle, we managed to hold Bobby and Accra escaped.

We lost the troop during this sequence, as Accra ran away far too fast for us and completely vanished. We found L troop two hours later, quietly foraging, a couple of kilometres from the plantation. We were so happy to see Accra, in the middle of the troop. He was eating, without a scratch, as though nothing had happened. What a humble hero!! He became without any doubt my favourite baboon of this troop.

APPENDICES



Appendix 1: texte de vulgarisation scientifique publié à Conversation Junior.

Nous répondons à la question de Camille, 8 ans, « Pourquoi l'être humain est-il plus évolué que les autres animaux ? ». Co-écrit avec Axelle Delaunay, Lugdiwine Burtschell, Elise Huchard et Nikolaos Smit. Disponible sur : https://theconversation.com/camille-8-ans-pourquoi-letre-humain-est-il-plus-evolue-que-les-autres-animaux-151412

Tous les organismes présents sur Terre, dont les êtres humains, ne sont pas apparus tels qu'on les connaît aujourd'hui. Leurs formes actuelles sont le résultat de nombreux changements qui se sont accumulés au cours du temps : c'est ce qu'on appelle l'évolution des espèces.

Aujourd'hui, on pense que toutes les espèces descendent d'un unique organisme : on l'appelle LUCA, dont les initiales en anglais veulent dire « Dernier Ancêtre Commun Universel ». Ce lointain ancêtre aurait vécu il y a environ 3,5 milliards d'années puis ses descendants auraient progressivement donné naissance aux diverses lignées d'organismes que tu connais : les bactéries, les plantes, les animaux, etc. Tu es donc un cousin très éloigné du chêne !

Mais comment une espèce évolue-t-elle ? A la naissance, les individus d'une même espèce ne sont pas tous identiques. Par exemple, imaginons que dans une population de singes, un individu naisse avec une forme de main différente qui lui permette de mieux grimper aux arbres : il pourra mieux se nourrir et s'abriter des prédateurs.



Figure 1:Evolution des espèces actuelles depuis le "Dernier Ancêtre Commun Universel". MA: Millards d'années. Silhouettes adaptées d'après Phylopic.

Cette main bizarre lui permettra de vivre plus longtemps, donc d'avoir plus de petits que les autres. Si ses petits héritent de la même main, ils vont eux-mêmes faire plus de petits avec une main bizarre, et ainsi de suite jusqu'à ce que tous les singes de cette forêt possèdent cette « différence ».

Cela s'appelle la sélection naturelle, et c'est le moteur de l'évolution. Petit à petit, lorsque deux populations se retrouvent séparées par un obstacle ou une distance infranchissable, de telles différences s'accumulent jusqu'à obtenir deux espèces distinctes.

Peut-on alors dire qu'une espèce est plus évoluée qu'une autre selon les différences qu'elle possède ? Non ! Le plus souvent, ces différences ne sont des avantages que dans certains environnements. Par exemple, savoir grimper aux arbres est avantageux en forêt, mais pas dans le désert. A force de s'adapter à la grande diversité d'environnements présents sur Terre, les lignées du passé se sont diversifiées en d'innombrables espèces, à l'origine de notre biodiversité. On ne peut donc pas dire qu'une espèce est plus évoluée qu'une autre, seulement qu'elle est mieux adaptée à son environnement.

Les humains seraient-ils donc les meilleurs car capables de s'adapter à tout type d'environnement ? Pas forcément. Par exemple, les fourmis d'Argentine sont aussi présentes presque partout sur Terre, et bien plus nombreuses que nous. C'est sans doute parce que, comme les humains, elles forment des sociétés complexes et ont trouvé des solutions astucieuses : par exemple, elles ont commencé à élever des pucerons des millions d'années avant que les humains ne fassent de même avec les vaches. En effet, elles protègent les pucerons de prédateurs tels que les coccinelles, et récupèrent en échange leur miellat, une sorte d'eau sucrée dont elles sont très gourmandes. Exactement comme le font les humains avec le lait !

D'autres espèces survivent là où aucun humain ne le pourrait, comme les minuscules tardigrades qui supportent des températures qui vont de -272 à +150°C, et même le vide spatial !

Mais les humains sont quand même une espèce à part, capable de parler, d'écrire, d'accumuler et de transmettre beaucoup d'information ou encore de construire des fusées : ne sont-ils pas les plus intelligents ? Pas si sûr, car chaque jour, de nouvelles découvertes nous dévoilent d'extraordinaires capacités chez les autres espèces, qui partagent beaucoup des nôtres.

Par exemple, certains chimpanzés sont capables de mémoriser une suite de nombres si rapidement qu'ils battent tous les humains entraînés au même exercice (voir ici). Certains animaux possèdent des cultures, des systèmes de communication très efficaces, une capacité à se projeter dans le futur, ou encore de l'humour ; ils peuvent créer et manier des outils (comme les pieuvres), ressentir des émotions complexes comme la jalousie et le deuil, ou encore faire preuve d'une intelligence remarquable pour manipuler leurs congénères ou résoudre des problèmes complexes (comme les corbeaux).

Une chose est sûre, il est impossible de mesurer si une espèce est « plus évoluée » qu'une autre ! Chaque espèce possède des caractéristiques qui la rendent unique, et il nous reste encore beaucoup à apprendre sur les autres espèces. Qui sait, peut-être que toi aussi, un jour, tu feras des découvertes sur leurs étonnantes capacités ?

Appendix 2 : Subordinate females exhibit greater foraging specialisation in wild baboons



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(Article as a co-author, in preparation)

Summary

1. Intraspecific competition and ecological opportunity are generally considered to be the two main factors contributing to individual foraging specialisation. Nevertheless, the causes and consequences of individual foraging specialisation in social, group-living species are poorly understood.
2. In the present study we investigate the effects of social rank and seasonality on individual foraging specialisation in chacma baboons (*Papio ursinus*), conducting stable isotope analyses on hair samples taken from a wild population.
3. To determine individual foraging specialisation, we used a relative individual niche index (RINI) to examine individual niche area proportional to the population's niche area.
4. Social rank was a driver of individual specialisation in females only, with subordinates exhibiting smaller isotopic niches than their dominant counterparts. Season also drove individual foraging specialisation in females, with smaller isotopic niches in the drier season.
5. Our results suggest that, in accordance with niche-partitioning theory, low-ranking females restrict their foraging niches to reduce dietary overlap with high-ranking competitors as a possible competition avoidance strategy.

Key-words: Individual specialisation, niche size, *Papio ursinus*, social dominance, stable isotope analysis

Introduction

The ecological niche is a concept that plots the biotic and abiotic factors that allow a species to exist within an environment onto an abstract space – classically referred to as the 'n-dimensional hypervolume' (Hutchinson 1957; Holt 2009). Intraspecific variation in resource use within the ecological niche used to be viewed as rare, with little effect on ecological processes (Bolnick et al. 2003). However, it is now recognised that intraspecific variation in resource use is ubiquitous (Dall et al. 2012) and occurs from community- to individual-level (Devictor et al. 2010). Individual variation in resource use can occur due to differences in age (Newland et al. 2009), sex (Strauss et al. 2012) and morphology (Pegg et al. 2015). However, when an individual's niche is narrower than the population's for reasons other than age, sex or morphology, it is termed individual specialisation (Bolnick et al. 2003).

Three possible individual-level reasons for why individuals specialise within their species' niche have been proposed. First, phenotypic differences may affect an individuals' ability to acquire resources, and so they may rank resources differently to their conspecifics (Araújo et al. 2011). Secondly, certain individuals may prefer to use a resource that minimises predation risk while other, bolder individuals may choose foods that maximise energy uptake in spite of any predation risk (Schoener 1971; Balaban-Feld et al. 2019). Thirdly, social hierarchy may prevent subordinate individuals from exploiting a resource, with dominant individuals monopolising and possibly specialising on the highest quality foods (Sol et al. 2005; Araújo et al. 2011). The first two drivers of individual specialisation – differences in phenotype and risk-aversion – have been relatively well-explored (Tinker et al., 2009; Darimont et al., 2007; Eklöv & Svanbäck, 2006), but the third – social rank – has received less attention.

Social hierarchy is common feature of group-living species, and its importance in determining an individual's competitive ability as a forager is well-established (Waite and Field 2007). For example, in studies on surfperch (*Embiotoca lateralis*) (Holbrook & Schmitt 1992), zenaida doves (*Zenaida aurita*) (Sol et al. 2005) and chacma baboons (*Papio ursinus*; Marshall et al. 2012, Lee & Cowlishaw 2017)

dominant individuals had priority of access to the best quality food patches, while the subordinates had limited or no access. These differences in individuals' ability to access resources would be expected to lead to differences in individuals' diets and, potentially, their level of foraging specialisation (Sol et al. 2005; Araújo et al. 2011). Individual specialisation can influence survival and reproduction (Elliot-Smith et al., 2015; van Donk et al., 2017), and so studies on how specialisation is influenced by social rank are likely to have implications for our understanding of formation and dynamics of social groups (Araujo et al., 2011; Sheppard et al., 2018), and broaden insights into ecological and evolutionary implications of individual differences (Dall et al. 2012).

The expectation that social rank should influence individual diets is reinforced by the competing hypotheses about effects of intraspecific competition on foraging specialisation. Optimal foraging theory (OFT) suggests that individuals will expand their foraging niche and add new food items to their diets – the 'optimal foraging hypothesis' (Stephen and Krebs 1986). Studies on young-of-the-year perch (*perca fluviatilis*) and bluegill sunfish (*Lepomis macrochirus*) provide empirical evidence for the OFT, showing an increase in nutrient intake to maximise foraging efficiency and fitness in response to increased competition and predation risk (Huss et al., 2008; Mittelbach, 1981). Alternatively, competition theory predicts that, with increased competition, individuals will reduce their foraging niche to a small subset of food items and become individual specialists – the 'niche partitioning hypothesis' (Schoener 1974). Empirical evidence for the niche partitioning hypothesis is shown in recent studies on banded mongooses (*Mungos mungo*) (Sheppard et al. 2018) and female bottlenose dolphins (*Tursiops truncates*) (Rossman et al. 2015).

In addition to individual- or population-level factors (such as social rank and competition), individual foraging specialisation can also be influenced by seasonal variation in food availability (Bolnick et al., 2003). In highly seasonal environments, where there is little rainfall during the dry season, individuals are often forced to reduce their dietary niche due to reduced food availability. For example, seasonal changes in individual foraging niches have been observed in wild grey wolves *(Canis lupus*) (Darimont & Reimchen 2002) and American martens (*Martes Americana*) (Ben-David et al.

1997). Some wolves were found to shift to heavily marine-based diet during the autumn, whilst the majority of other individuals did not exhibit seasonal diet shifts (Darimont & Reimchen 2002). There is reason to expect that these effect of seasonality on foraging specialisation interact with potential effects of social rank, since the effect of rank on access to food resources is often dependent on environmental conditions (Stillman et al, 2002; Vahl et al. 2005; Marshall et al. 2012; Lee & Cowlishaw 2017). In particular, where resources are more defendable rank more strongly determines an individual's ability to access food resources (Marshall et al. 2012; Lee & Cowlishaw 2017).

In this study we aim to test the effects of social rank on individual foraging specialisation in a wild population of chacma baboons. Baboons (*Papio* sp.) are a suitable study system as they live in large, stable social groups with clear, linear dominance hierarchies (Altmann and Altmann 1970) which have important effects on individuals' access to food and the foraging competition they experience (King et al. 2009; Marshall et al. 2015).

First, we test competing hypotheses about the effect of rank on foraging specialisation. The 'optimal foraging hypothesis' posits that under increased levels of intraspecific competition individuals add more food items to their diets (Stephens and Krebs 1986), predicting lower levels of specialisation in subordinate individuals. In contrast, the 'niche partitioning hypothesis' posits that individuals respond increased levels of intraspecific competition by focussing on a smaller subset of food items (Schoener 1974), predicting higher levels of specialisation in subordinate individuals. Second, we also test the effect of seasonal food availability on foraging specialisation and its interaction with social rank. We predict that individuals will have smaller niches when food availability is lower, and that the effects of social rank will be more pronounced in these periods due to the increased intragroup competition for resources.

Materials and methods

Study site

Tsaobis Nature Park is situated on the edge of the Namib desert in Namibia (22°23'S, 15°45'E). The park landscape is made up of mountains and gullies, bordered by rocky hills and open plains. The total area of the reserve is 45,000 ha with a topographical range of 683-1445m in altitude. Tsaobis is an arid environment with a mean annual rainfall of 122mm, (*n* = 66 years). This wet season typically occurs from January – May while the dry season takes place from June – December.

The ephemeral Swakop River bisects the park and supports the woodland vegetation, mainly made up of five tree species: *Prosopis glandulosa*, *Faidherbia albida, Salvadora persica, Acacia erioloba,* and *A. tortilis.* The baboons' diet consists predominantly of the berries, pods, flowers, leaves, seeds and bark from the aforementioned tree species (Cowlishaw, 1997; see Cowlishaw & Davies 1997 for a full ecological description of the field site).

Population and sample collection

Two baboon troops were habituated to the presence of researchers at close proximity, with all habituated baboons being individually recognisable. The troops are hereafter referred to as 'J' troop (group size and compositions: *N* = 55, adult males = 11, adult females = 15, juveniles = 29), and 'L' troop (*N*= 32, adult males = 7, adult females = 9, juveniles = 16). Only samples from adults were used in this study. While there is a total of 42 adults between the troops, we only had samples for 40 of them.

Dominance ranks for adult males and females were determined for each troop by using pairwise agonistic interactions recorded during 1-hour focal follows and *ad libitum* between May 2006 and January 2007. These agonistic and approach-avoidance interactions were used to generate actor-receiver matrices which signified the number of agonistic interactions that occurred between each pair in each direction. There was a high degree of linearity in both sexes, using Landau's linearity index corrected for unknown relationships (Lee & Cowlishaw 2017; Huchard et al. 2009b).

J troop were lived-captured on the 12-Oct-2006 and L troop on the 26-Oct-2006. During trapping, baboons were immobilised and hair samples were collected using scissors from the thigh area of adults (*n* = 40). Tooth eruption and molar wear patterns were also collected, and used to

estimate ages where known birth dates were not available (Kahumbu and Eley 1991; Huchard et al. 2009a). Full description of trapping procedure can be found in Huchard et al. (2010).

Sample preparation and stable isotope analysis

Stable isotope analysis (SIA) is a useful tool to infer species' diet, dietary niche breadth and habitat composition as it can be used to reconstruct the diets of extinct and extant species by analysing the isotopic ratios in their body tissues (Crowley 2012). The stable isotope signatures in these tissues reflect an individual's diet during the time in which the tissue was produced (Bearhop et al. 2002). Whilst tissue isotope ratios are influenced by factors other than diet (Hette-Tronquart, 2019), they are useful measures of individual foraging patterns (Dalerum and Angerbjörn 2005; Marshall et al. 2019). The choice of tissue can vary greatly depending on the research question. Using hair keratin, which has usually been synthesised over months, for SIA means that one can estimate seasonal dietary and habitat changes as well as individual and population dietary specialisations (Bearhop et al., 2004; Crowley, 2012).

We used SIA to estimate individual foraging specialisation within baboon troops and between individuals. Previous studies have shown that the ratio of ^{12}C:^{13}C ($\delta^{13}C$) and ^{14}N:^{15}N ($\delta^{15}N$) stable isotopes are proficient in measuring population- and individual-level dietary specialisations (Newsome et al. 2009, 2015; Sheppard et al. 2018). Variation in mean carbon isotopic ratios are indicative of differences in habitat choice, while variation in mean nitrogen isotopic ratios suggest differences in trophic level (Post, 2002; Popa-Lisseanu et al., 2015). Each hair was washed thoroughly in deionised water and scraped with fine forceps to remove dirt and surface contaminants. The samples were dried in an oven 50-60°C for 10 minutes. We assumed baboon hair growth rates of approximately 1cm per month, based on hair growth rates observed across primates (Oelze 2016), and so beginning at the root, each hair was sectioned into 1cm segments using a ruler and scalpel, with each segment representing one month (mean ± SD: 7.15cm ± 1.9 *n* = 373) (Oelze 2016). The hair samples were collected in October, and so the first four centimetres of each hair, starting from the root, represented

the dry season growth (June-October, *n* = 162), and the remaining centimetres represented the wet season (January-May, *n* = 214). Each hair segment was then further cut into small pieces using scissors and approximately 0.7mg of these pieces were weighed out and sealed in small tin capsules (Elemental Microanalysis) for SIA (mean ± SD: 0.56mg ± 0.24 *n* = 373). This produced a mean± SD of 9± 2.2 segments per individual (*n* = 40).

Carbon and nitrogen isotope ratios were determined using continuous flow-isotope ratio monitoring mass spectronomy (CF-IRMS), using a SerCon Integra integrated elemental analyser and mass spectronometer (Exeter, UK). Isotope ratios were expressed as δ values, using parts per million (‰), according to the equation: $\delta X = ((R_{sample}/R_{standard}) - 1 \times 1000$

Where X represents ^{15}N or ^{13}C and R represents the ratio of heavy to light isotopes ($^{15}N/^{14}N$ or $^{13}C/^{12}C$). International reference materials (IAEA, Vienna) were also analysed within each run for calibration $\delta^{15}N$ and $\delta^{13}C$ samples values scaled to air and V-PDB, respectively.

Estimating individual niches

We estimated dietary variation among the baboons by using the 95% prediction ellipse area (ell95c), which displays the isotopic niche 'space' occupied by each individual (Jackson et al. 2011). These ell95c values, which had been corrected for sample size, were taken from baboons that had four or more isotopic samples per season (n = 75 based on 373 samples from 40 individuals; mean ± SD samples per individual = 9.3 ± 1.3, maximum = 12, fig. 1).

While the ell95c areas show the isotopic space occupied by each individual, it is important to calculate individual niche area relative to the populations total niche area when investigating between-individual variation in niche size (Roughgarden 1972). In species such as chacma baboons that move and forage as a discrete group it is more appropriate to consider an individual's niche relative to their social group's total niche (Sheppard et al. 2018). Subsequently, we calculated a relative individual niche index (RINI) which calculates the individual niche size as a proportion of the group niche size using SiberKapow in the SIBER package (Jackson et al. 2011; Sheppard et al. 2018).

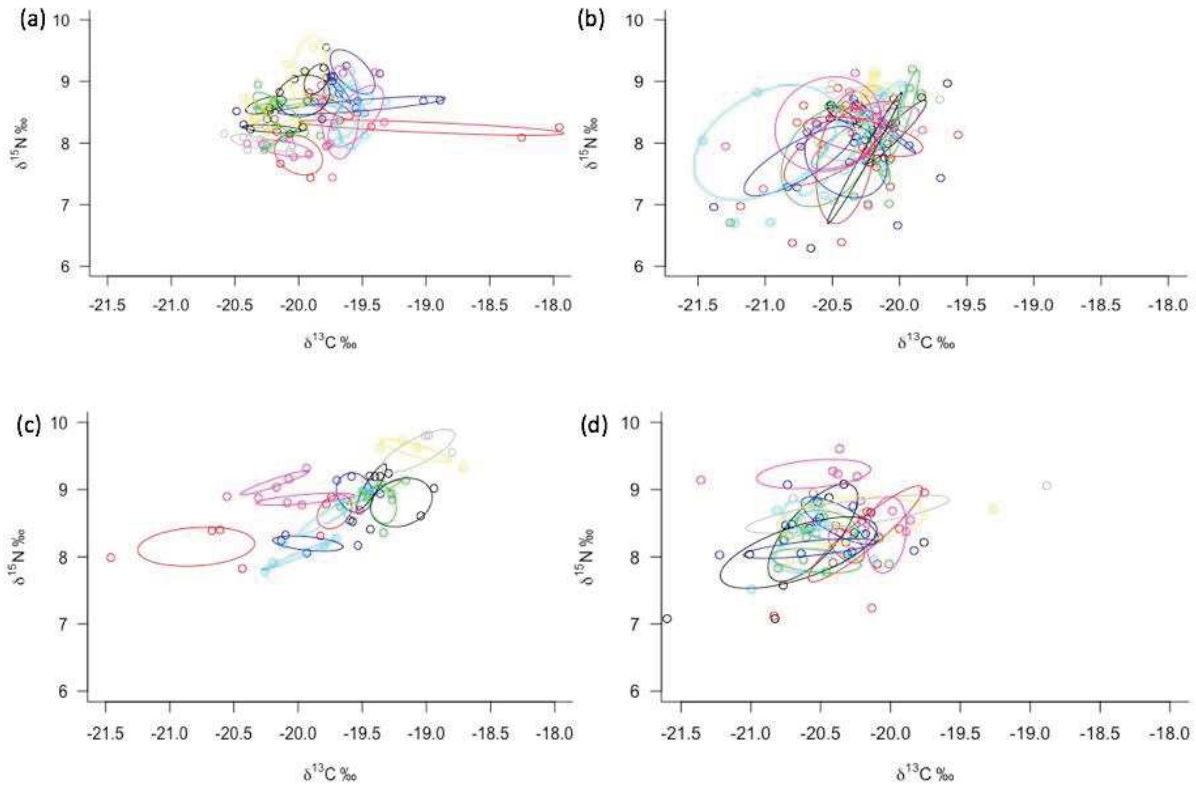

Figure 1. Chacma baboon (*Papio ursinus*) hair carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope ratios. J troop (1a & b) , L troop (1c & d). Each point represents the isotopic ratio of each sample from the stable isotope analysis. Ellipses are the 95% prediction ellipses, representing each individual's isotopic niche space and corrected for sample size (ell95c, Jackson et al. 2011) calculated from the data for each individual in the troops.

Statistical analysis

We used linear mixed effects models to test our predictions. Our analyses controlled for sex and age since individual specialisation is defined as variation not attributable to these factors (Bolnick et al. 2003). Our initial data exploration showed that rank and sex were correlated (Pearson's $r = 0.66$), whereby most of the high-ranking individuals were male and most of the low-ranking individuals were female. Therefore, we ran our analyses in two stages. First, we divided our data into males and females. We fitted models to each of these data sets including age, rank, season and the interaction between rank and season as fixed effects. The male model included 34 measures of RINI from 17 males during

the dry (n = 17) and wet (n = 17) seasons. The female model included 41 measures of RINI from 23 females during the dry (n = 23) and wet (n = 18) seasons. Individual ID and troop ID were included in all models as random effects to control for repeated measures.

Second, we fitted a model to the full data set; including sex, season and age as fixed effects, while rank was omitted. This model included 75 measures of RINI from 40 individuals, 40 from the dry season and 35 from the wet season. All model residuals were normally distributed with homogenous variance, and correlations between variables fitted in same models as fixed effects were lower than those shown to cause model fitting issues such as variance inflation in effect estimates (<0.6) (Freckleton, 2011). We used likelihood ratio tests, comparing the full model to a model without a particular variable, to test the significance of this variable's effect (Forstmeier & Schielzeth, 2011). In the male and female models, if the interaction between rank and sex did not have a significant effect, we dropped this from our final model to allow us to test the significance of the rank and sex main effects (Engqvist, 2005). We did not reduce our model further due to the issues with stepwise model reduction techniques (Forstmeier & Schielzeth, 2011; Mundry & Nunn, 2009; Whittingham et al. 2006).

We analysed our data in R version 3.6.1 (R Core Team 2019) and used the 'SIBER' package, version 2.1.4 to fit standard ellipses and calculate the ell95c values (Jackson et al. 2011). We fit linear mixed effects models (LMMs) using the 'lme4' package version 1.1-21 (Bates et al. 2015) to test each of our hypotheses. We calculated the r^2 values for the models using the 'MuMIn' package version 1.43.6 (Nakagawa and Schielzeth, 2013; Barton 2019).

Results

Low-ranking females had smaller isotopic niches than high ranking females (LMM: $\beta \pm SE = -0.006 \pm 0.002$, LRT = 4.902, P = 0.026; table 1; fig. 2) but no effect of rank was found in males. Females also had smaller isotopic niches during the dry season than the wet season (LMM: $\beta \pm SE = 0.103 \pm 0.036$, LRT = 7.606, P = 0.005; table 1; fig. 3) but again, there was no effect of seasonality in males. There was no interactive effect of social rank and season in males or females (table 1). Overall there

was no effect of sex, season or age on isotopic niche size across males and females combined (table 1).

Table 1. Linear mixed effect models predicting relative individual niche index (RINI) in male and female chacma baboons separately and in a combined model

	Effect	*Estimate*	*SE*	χ^2	*P*
Males	Intercept	0.168	0.047		
	Rank	0.0005	0.004	0.012	0.911
	Season	-0.001	0.048	0.0006	0.979
	Rank*Season	0.003	0.01	0.103	0.747
Females	Intercept	0.241	0.053		
	Rank	**-0.006**	**0.002**	**4.902**	**0.026**
	Season	**0.103**	**0.036**	**7.606**	**0.005**
	Rank*Season	-0.008	0.004	3.447	0.063
Combined model	Intercept	0.166	0.056		
	Sex	0.011	0.031	0.128	0.720
	Season	0.054	0.031	3.247	0.072
	Age	-0.001	0.003	0.035	0.851

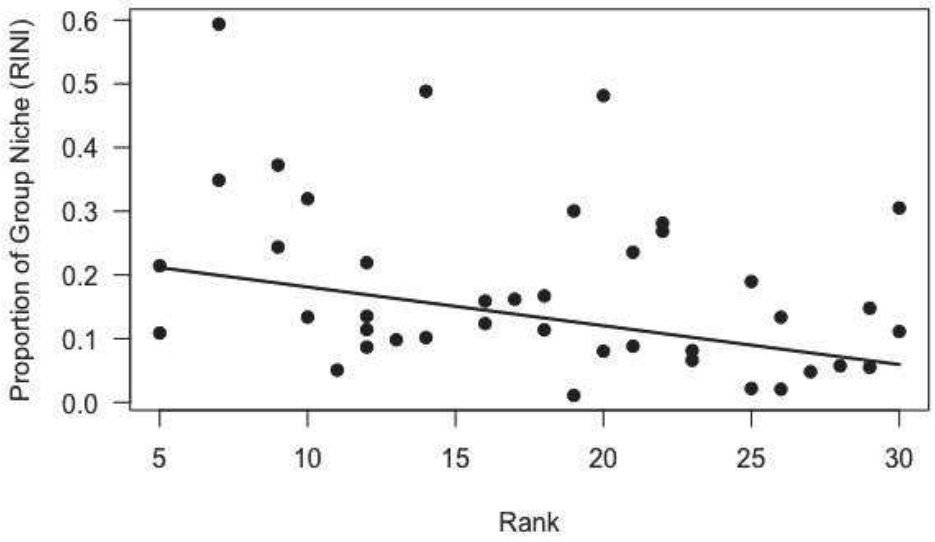

Figure 2. Low-ranked female chacma baboons have smaller isotopic niches as a proportion of their group's niche (RINI). The points represent the ellipse areas of the females during the dry and wet seasons. The line represents the relationship predicted by our model.

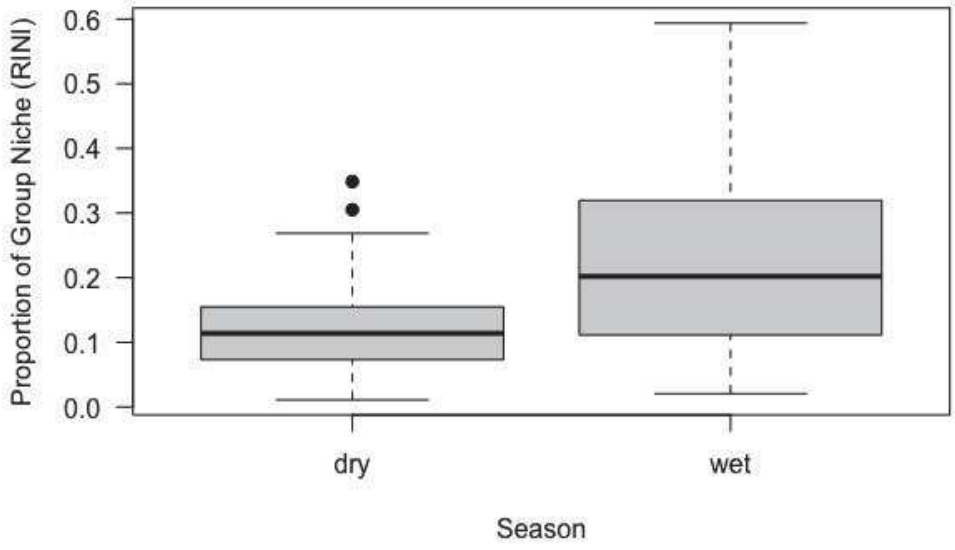

Figure 3. Female chacma baboons in the dry season have smaller isotopic niches as a proportion of the group's niche. Box and whisker plot showing the median and interquartile range (box), 1.5 times the interquartile range (whiskers) and any points that fall outside this.

Discussion

Our results suggest sex-dependent effects of rank and seasonality in foraging patterns. Low-ranking female baboons had smaller isotopic niches relative to their group's overall niche (RINI), suggesting greater individual foraging specialisation (Bearhop et al. 2002; Dalerum and Angerbjörn 2005; Marshall et al. 2019). This supports the niche partitioning hypothesis; which states that with increased competition, individuals will reduce their foraging niche to a small subset of food items, reducing the degree of dietary overlap between competitors (Schoener 1974). Females also had smaller relative isotopic niches in the dry season, supporting our prediction of greater individual foraging specialisation in period of low food availability. However we did not find any evidence for the effect of social rank being dependent on season, nor did we find any effects of rank or season on male baboon isotopic niches.

Social rank strongly reflects an individual's competitive ability for access to resources such as mates, territory and food (fish: Holbrook and Schmitt 1992, birds: Sol et al. 2005 and primates: Van Elsacker et al. 1999, Lee & Cowlishaw 2017). Therefore, our finding that low-ranked females exhibited greater levels of foraging specialisation supports previous studies suggesting that intraspecific competition is one of the main drivers for resource-use specialisation (Araújo et al. 2011). Increased intraspecific competition is common feature of group-living species due to increased competitor density (Krause & Ruxton, 2002), suggesting that levels of individual specialisation may be higher in these species (Sheppard et al. 2018). Most studies on the effects of intraspecific competition on individual foraging specialisation have been conducted on non-social species (Araújo et al. 2008; Tinker et al. 2008), despite the fact that social rank is a common feature of many animal groups. One of the few other studies on social rank and specialisation showed that, in group-living badgers, subordinate individuals reduced their use of scrubland habitat when their main food resource was in decline in this area, whereas dominant individuals increased their use of the habitat during the same time, signalling to an unequal use of resources based on social rank (Revilla and Palomares 2001).

Our findings support this pattern, and suggest dominance hierarchies may further increase the levels of individual specialisation in social groups, in addition to the effect of greater intraspecific

competition. In particular, our results support the idea that individual foraging specialisation (by subordinate females in our study) is a competition avoidance strategy that works by reducing dietary overlap with other individuals (Svanbäck and Bolnick 2007; Sheppard et al. 2018), commonly referred to as the niche partitioning hypothesis (Schoener 1974). As high-ranking individuals have better access to the higher-quality foods (Appleby, 1980; Dale et al. 2017), low-ranking individuals may be forced to specialise on the low-quality foods in low-quality habitats. This foraging specialisation by subordinates may be a passive response to avoid intraspecific competition, rather than be due to an active choice (Holbrook and Schmitt 1992). This and other studies that have found support for niche partitioning in response to competition within social groups suggest that ability for some individuals to specialise (e.g. by using different food items or areas) may be a pre-requisite for stable social groups to form (Revilla and Palomares 2001, Sheppard e al. 2018).

During competitive interactions, individuals are at greater risk of injury and mortality and so, avoiding intraspecific competition can be advantageous (Byers 1993), especially as low-ranking individuals generally have more to lose. For example, adult female fruitworms (*Acrobasis vaccinii*) avoid larval competition by avoiding host plants where conspecific eggs are already present (Nufio and Papaj 2001). Similarly, bark beetles (*Ips typographus*, *Pityogenes chalcographus*) have shown incidences of intraspecific competition avoidance whereby certain males avoid colonising denser areas where intraspecific competition is more intense, and favour sites with less competitors (Byers 1993).

Contrastingly, the optimal foraging hypothesis predicts that individuals will expand their foraging niche and add new food items to their diets in order to maximise their fitness (Stephen and Krebs 1986). In the context of seasonality, temporal variation in diet is widely accepted as a consequence of seasonal variation, (Dalerum and Angerbjörn 2005) due to fluctuations in food availability (Ben-David et al. 1997) and changes in environmental conditions (Kushlan et al. 1985). African lions (*Panthera leo*), living in semi-arid environments adapt their prey preferences during the dry season as reduced water source availability restricts prey distributions (Davidson et al. 2013), and

African bush elephants (*Loxodonta africana*) rely on trees and shrubs during the dry season when their preferred diet of wet-season grasses and forbs are unavailable (Viljoen 1989).

The results of our analyses somewhat support our predictions, as niches were smaller during times of low food availability, but in females only. This, to an extent, supports our prediction that the effects of social rank were more pronounced during the dry season as females tend to be lower in the dominance hierarchy. However, it is clear that while there was no interactive effect between rank and season in females, the fact that the p-value was so marginal, certainly hints at the possibility of a season-specific rank effect. Both competition and seasonality have been found to drive sex-specific foraging niches (González-Solis et al. 2000; Phillips et al. 2004). As females' niches were smaller during the dry season, our results also indicate some support for the optimal foraging hypothesis as niche size was relatively larger during the wet season. In order to infer the seasonal dietary shifts in the present study, further stable isotope analysis of the food items would be required.

Where our analyses found a sex-dependent rank effect on foraging niche size, many studies suggest that sex-differences in foraging niches are due to differences in foraging habit, caused by sexual size dimorphism (González-Solis et al. 2000) and nutritional requirements (Ismar et al. 2017). Sexual segregation in foraging strategies do occur due to size-mediated dominance (Phillips et al. 2004), which could also be true for the current study. For instance, baboon societies exhibit linear dominance hierarchies, with males being larger and dominant over females, while females rank closer to the bottom of the hierarchy (Altmann and Altmann 1970; Franz et al. 2015). Although baboons do exhibit sexual size dimorphism, we did not include size as a variable, nor did we find an effect of sex during our overall analyses model. It may be that the effects of rank on foraging specialisation are only evident as you move down the hierarchy, regardless of sex. To our knowledge, ours the first study to have discussed the effects of rank, and in turn, the sex-dependent effects of rank on individual foraging specialisation in a species of primate.

A previous study on habitat use by these baboons found that habitat use is determined by trade-offs between foraging and predation risk. The baboons showed a preference for foraging in low-

risk, food-poor habitats, rather than high-risk, food-rich habitats, regardless if the food-rich habitat was in the group's available home range (Cowlishaw 1997). Seasons also play a role in habitat selection, as food availability in different habitats peak at different times and influences species distribution and home ranges (Barton et al. 1992).

While the use of hair keratin allows for the testing of seasonal dietary and habitat changes and individual and population-level dietary specialisations (Bearhop et al. 2004; Crowley 2012), theoretical and empirical studies suggest that the δ^{13}C in keratin may be biased towards dietary protein rather than bulk diet (Jim et al. 2004; Crowley 2012). Furthermore, it is very important to ensure all hairs are being sectioned at the correct point along the hair. If one hair had been cut from the animal at a shorter length from the root than the other, then there could be disparity in the isotopic signatures and consequently, the seasons. In order to ensure the hairs are being taken from the same length, future studies should ensure the removal of the roots, so as to have a definitive growth point in the hair, or to use vibrissae, as these may be easier to ensure the removal of the root with the rest of the tissue sample, guaranteeing homogeny within the samples.

There is already substantial evidence that intrapopulation variation and specialisation occur as a response to spatial and temporal ecological change (Araújo et al. 2011; Bolnick et al. 2003). The impacts that this variation and specialisation have on population dynamics, interspecies co-existence and ecological activity directly relate to fundamental evolutionary processes, such as speciation and adaptation (Araújo et al. 2011; Bolnick et al. 2003). Our study suggests that social rank may feed into these processes through its effect on individual specialisation. Gaining further insight into social effects on individual specialisation will expand our knowledge of how rapidly changing environments may impact primate, and other group-living, species living in harsh and difficult habitats across the globe.

Conclusion

We provide evidence that social rank influences individual foraging specialisation in wild baboons, with low-ranking females exhibiting smaller isotopic niches – thereby supporting the niche

partitioning hypothesis (Schoener 1974). We also provide evidence that seasonality affects individual foraging specialisation in females, as they had relatively larger niche sizes during the wet season than they did during the dry season. Our results suggest that dominance hierarchies in group-living animals promote individual specialisation with subordinate individuals specialising as a competition avoidance strategy.

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Author contribution statement

RH, EH and HM conceived the research ideas; RH, GC, EH and HM designed the research methodologies; RH carried out stable isotope sample preparation; All authors contributed to field data collection and data interpretation; RH and HM analysed the data and led the writing of the manuscript; all authors contributed to the final draft.

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The evolution of reproductive seasonality in large tropical terrestrial monkeys

Reproductive seasonality refers to the periodic temporal clustering of reproductive events in the annual cycle. It is often adaptive, because synchronizing the costliest stage of the female reproductive cycle with the most productive season can enhance maternal and offspring conditions and survival. Most studies investigating the evolutionary determinants of reproductive seasonality were done on fast-lived species from temperate habitats, while little is known for long-lived tropical species. In this thesis, we investigated the evolutionary determinants and fitness consequences of reproductive seasonality in two wild primate populations: non-seasonal breeding chacma baboons (*Papio ursinus*) from the seasonal and arid Namibian savannah and seasonal breeding mandrills (*Mandrillus sphinx*) from the Gabonese equatorial forest. Using a combination of long-term life history, morphological, behavioural and climatic data, we first reveal that despite their omnivorous diet and tropical habitats, mandrills and baboons are both subject to important seasonal variation in food availability, mainly caused by rainfall fluctuations. Consequently, we find that matching the peak of lactation with the seasonal food peak enhances female future reproduction (i.e. maternal reproductive pace) in both populations. We further show that two distinct optimal birth timing in chacma baboons maximise either maternal reproductive pace or offspring survival, by matching early versus late weaning with the seasonal food peak, respectively. The occurrence of multiple optimal birth timings weakens the strength of reproductive seasonality. In contrast, mandrill females do not face a similar trade-off between current and future reproduction over birth timing, and maximise their fitness by giving birth seasonally. In these two social species, we further find social effects on reproductive synchrony and seasonality: rank-related reproductive suppression leading to birth asynchrony, contribute to explain the absence of seasonal reproduction in chacma baboons, and dominant females are less seasonal than subordinate ones in mandrills. Lastly, a comparative analysis on 16 populations from 7 species of wild baboons and relatives show unusually flexible patterns of reproductive phenology – with seasonal and non-seasonal breeding populations in a same species – and climatic unpredictability acts as a major driver of the loss of reproductive seasonality. Altogether, this work extends our understanding of the diverse patterns of reproductive seasonality observed in long-lived tropical species, by shedding light on previously overlooked determinants of reproductive phenology, such as climatic predictability, life history traits and trade-offs, and various social factors likely to affect other long-lived and social species.

Keywords: Reproductive phenology, seasonal breeding, life history, sociality, primate

L’évolution de la saisonnalité reproductive chez des grands singes terrestres tropicaux

La saisonnalité reproductive réfère au regroupement temporel périodique d’événements reproductifs dans le cycle annuel. Elle est souvent adaptative, car synchroniser l'étape la plus coûteuse du cycle reproducteur des femelles avec la meilleure saison peut améliorer la condition et survie des mères et de leurs progénitures. La plupart des études portant sur les déterminants évolutifs de la saisonnalité reproductive ont été menées sur des espèces à rythme de vie rapide des habitats tempérés, et l'on sait relativement peu de choses sur les espèces tropicales longévives. Dans cette thèse, nous avons étudié les déterminants évolutifs et les conséquences en termes de valeur sélective de la saisonnalité reproductive de deux populations de primates sauvages: les babouins chacma à reproduction non-saisonnière (*Papio ursinus*) de la savane aride et saisonnière namibienne et les mandrills à reproduction saisonnière (*Mandrillus sphinx*) de la forêt équatoriale gabonaise. En utilisant une combinaison de données de long-terme d’histoire de vie, morphologiques, comportementales et climatiques, nous révélons tout d'abord que malgré leurs régimes omnivores et leurs habitats tropicaux, mandrills et babouins sont tous deux soumis à d'importantes variations saisonnières de la disponibilité alimentaire, principalement causées par des fluctuations de précipitations. Par conséquent, nous constatons que faire correspondre le pic de lactation avec le pic alimentaire saisonnier améliore la reproduction future des femelles (accélère le rythme de reproduction maternel) chez les deux populations. En outre, nous montrons que deux périodes de naissance optimales distinctes chez les babouins chacma maximisent soit le rythme de reproduction maternel, soit la survie de la progéniture, en faisant correspondre le début ou la fin du sevrage avec le pic alimentaire saisonnier, respectivement. L'existence de multiples périodes optimales de naissance affaiblit l’intensité de leur saisonnalité reproductive. En revanche, les mandrills ne font pas face à ce même compromis entre reproduction actuelle et future sur le moment de la naissance, et maximisent leurs valeurs sélectives en donnant naissance dans le pic saisonnier de naissance. Chez ces deux espèces sociales, nous trouvons de plus des effets sociaux sur la saisonnalité reproductive: la suppression de la reproduction, liée au rang et conduisant à l'asynchronie des naissances dans un groupe, contribue à expliquer l'absence de reproduction saisonnière chez les babouins chacma, et les femelles dominantes sont moins saisonnières que les subordonnées chez les mandrills. Enfin, une analyse comparative sur 16 populations de 7 espèces de babouins sauvages et proches apparentés révèle une rare flexibilité de leur phénologie reproductive - avec des populations à reproduction saisonnière et non-saisonnière au sein d'une même espèce - et l'imprévisibilité climatique agit comme un facteur majeur de la perte de saisonnalité reproductive. Dans l'ensemble, ce travail élargit notre compréhension des divers patrons de saisonnalité reproductive observés chez les espèces tropicales à longue durée de vie, en mettant en lumière des déterminants précédemment négligés de la phénologie de la reproduction, tels que la prévisibilité climatique, les traits et compromis d’histoire de vie, et divers facteurs sociaux susceptibles d'affecter d'autres espèces sociales et à rythme de vie lent.

Mots-clés : phénologie reproductive, reproduction saisonnière, histoire de vie, socialité, primate